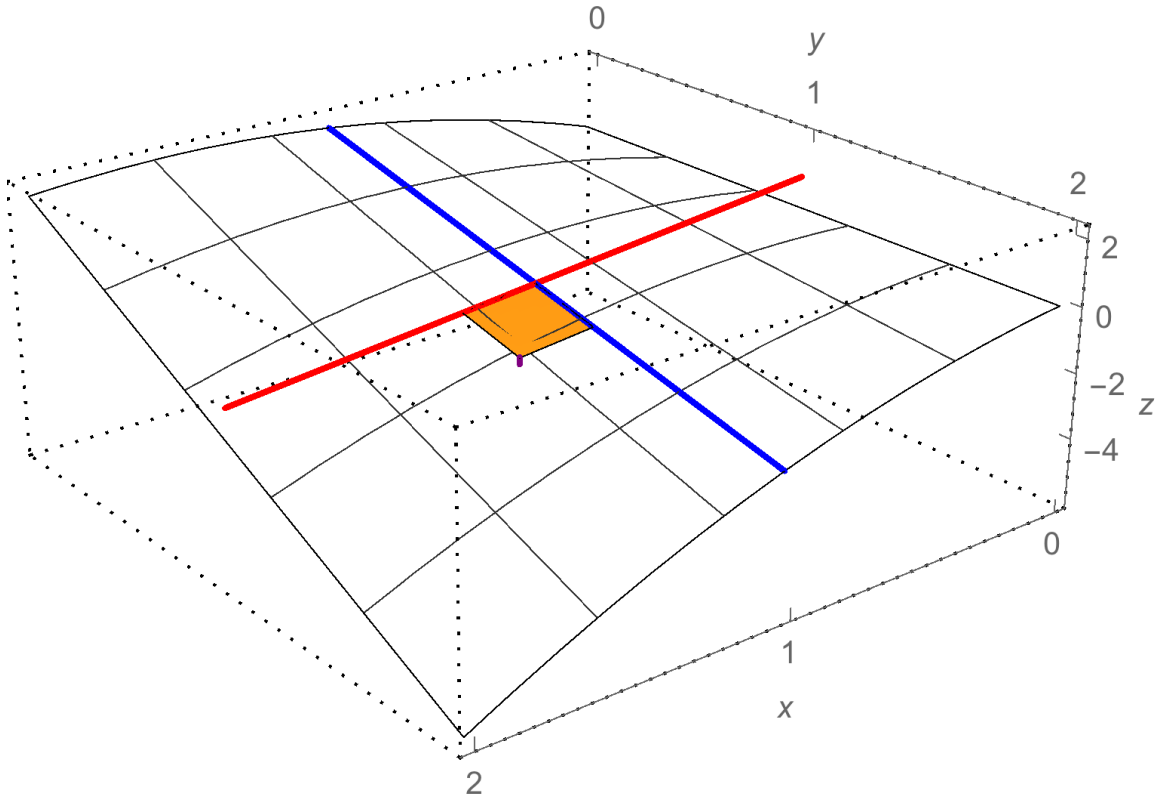
Matrices, Linearization, and the Jacobi matrix



$$\begin{cases} \mathrm{d}x/\mathrm{d}t = f(x,y) \\ \mathrm{d}y/\mathrm{d}t = g(x,y) \end{cases} \qquad J = \begin{pmatrix} \partial_x f & \partial_y f \\ \partial_x g & \partial_y g \end{pmatrix} \qquad \lambda_{1,2} = \frac{\mathrm{tr} \pm \sqrt{\mathrm{tr}^2 - 4\det}}{2}$$

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Ebook publically available at: 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 much more extensive reader called "Qualitative analysis of differential equations" that was written by Alexander Panfilov (2010), (`https://arxiv.org/abs/1803.05291`) 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 have shortened and simplified the text, made the notation consistent with the reader "Biological Modeling of Populations", added a few examples, and the full linearization of the stable spiral point of the Lotka Volterra model (Chapters 6 and 7). The Grind scripts referred to in the exercises can be found on tbb.bio.uu.nl/rdb/bm/models.

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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, one can use a vector to describe it (Fig. 2.1). Vectors are 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 either as a row, or a column, of numbers between brackets, and are then referred to as row or column vectors. For example, in a two-dimensional plane in which the force acting on an object has a x-component $V_x = 2$ and a y-component $V_y = 1$, this

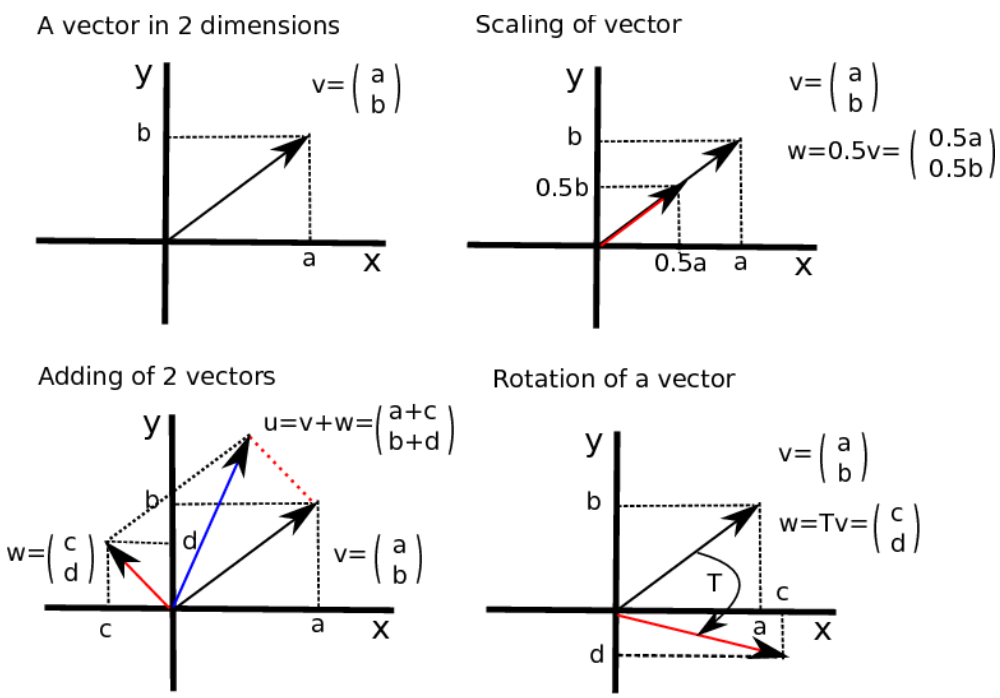


Figure 2.1: Vectors in a 2 dimensional plane: the scaling of a 2D vector, the addition of two 2D vectors, and finally the rotation of a 2D vector by multiplying it with a transformation matrix T.

force can be represented as:

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

The length of the force vector is given by $|V| = \sqrt{2^2 + 1^2}$, 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 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 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 (have 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, i.e., 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. 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:

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

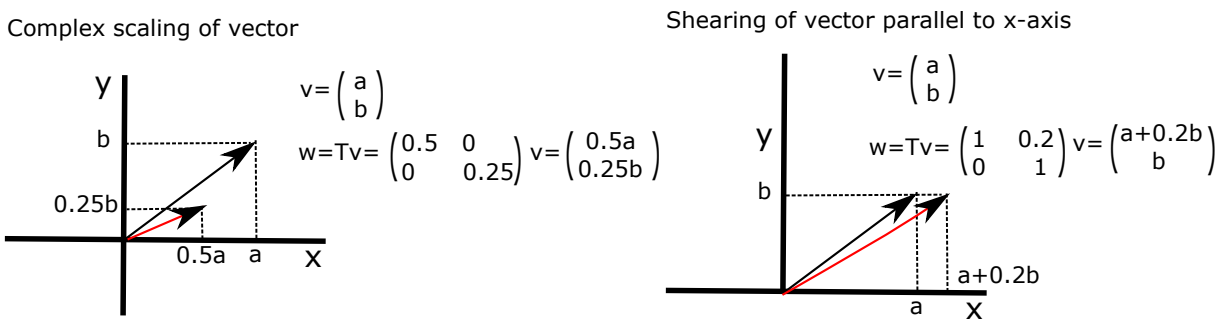


Figure 2.2: Scaling and shearing by matrix transformations of vectors.

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 $C_{ij} = A_{ij} + B_{ij}$, where C_{ij} is the value in matrix C at row i and column j.

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 one needs to multiply the ith row of the first matrix by the jth column of the second matrix[1]:

$$C_{ij} = \sum_{k=1}^{n} A_{ik} B_{kj} . \tag{2.1}$$

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

$$\begin{pmatrix} a & b \\ c & d \end{pmatrix} \begin{pmatrix} x & y \\ z & w \end{pmatrix} = \begin{pmatrix} ax+bz & ay+bw \\ cx+dz & cy+dw \end{pmatrix} , \tag{2.2}$$

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

$$\begin{pmatrix} a & b \\ c & d \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} ax+by \\ cx+dy \end{pmatrix} . \tag{2.3}$$

Note that in Eq. (2.2) the multiplication with the first matrix A produces a transformation of the second matrix. In other words, the first matrix is the transformation 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 transformations are applied in a different order, a different outcome will be produced.

A vector can be rotated and/or scaled by a matrix. Scaling a vector by a different amount in the x and y directions can also be performed by a transformation matrix (see Fig. 2.2):

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

[1]The 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, ..., up to $k = n$. In this case, n is the number of columns in the first matrix, and rows in the second matrix. To obtain the value in matrix C, row i, column j, one multiplies what is in matrix A, row i, column 1 with the value in matrix B, row 1, column j. One then adds 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 one has added the values for all columns and rows.

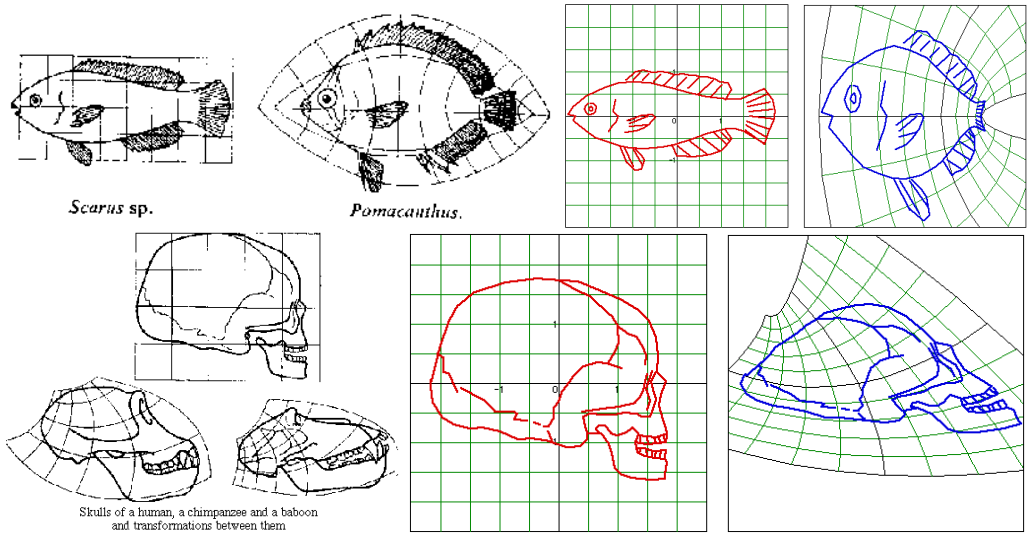


Figure 2.3: On the left the original pictures from "On Growth and Form" by D'Arcy Wentworth Thompson (1942) (which was first published in 1917). On the right pictures from a computer program of the School of Mathematics and Statistics of the University of St. Andrews in Scotland, performing similar shape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

Similarly, a matrix can be used to apply shearing to a vector. A shear force could stretch a vector 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, the multiplication of rotation, scaling and shearing matrices can result in a single matrix performing a complex transformation in one go. Also note that any point (x, y) on a flat object can be considered as a vector $\vec{v} = (x \ y)$. Thus, one can apply complex transformation matrices to objects (basically a collection of points), 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 one 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

$$\begin{cases} x - 2y = -5 \\ 2x + y = 10 \end{cases} , \tag{2.4}$$

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 one can write as a vector, i.e., $\vec{V} = (-5\ 10)$. Now if one writes x and y as a vector $\vec{X} = (x\ y)$, one can represent the system of Eq. (2.4), using the definition matrix multiplication in Eq. (2.3), as

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

To find the solution of this system one solves $x - 2y = -5$ to obtain $x = 2y - 5$. Substituting this into $2x + y = 10$ gives $2(2y - 5) + y = 10$, $4y - 10 + y = 10$, $5y = 20$, and finally $y = 4$. Substituting this into $x = 2y - 5$ gives $x = 2 \times 4 - 5 = 3$. Thus, the solution is $(x\ y) = (3\ 4)$.

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

$$\det[A] = \begin{pmatrix} a & b \\ c & d \end{pmatrix} = ad - bc \quad \text{and} \quad \text{tr}[A] = a + d . \tag{2.5}$$

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

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

Start by solving x from the first equation, i.e., $x = p/a - by/a$. Use this solution to solve y from the second equation, i.e., substitution gives $cp/a - cby/a + dy = q$, or

$$cp - cby + ady = qa \quad \text{or} \quad y(ad - cb) = qa - cp \quad \text{or} \quad y = \frac{qa - cp}{ad - cb} ,$$

which only has a finite solution when the denominator $ad - cb$ is not equal to zero. This denominator indeed corresponds to the determinant $ad - bc$ of the matrix defining this linear system. Thus, there is no solution when the determinant equals zero. Note that one can also calculate the determinant of 3×3 matrices, or even large square matrices, (see Wikipedia or any book on linear algebra), but this lies outside the scope of this course. Finally, typing `determinant {{a,b},{c,d}}` (or even just `{{a,b},{c,d}}`) into WolframAlpha gives you the determinant of the matrix.

2.3 Forest succession

A simple example of a matrix model in ecology is the model developed by Henry Horn, who 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 at a rate 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 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. For instance, $\vec{V_0} = (1\ 0\ 0\ 0)$, 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:

$$\vec{V_{50}} = A\vec{V_0} = \begin{pmatrix} 0.05 & 0.36 & 0.5 & 0.09 \end{pmatrix}, \tag{2.6}$$

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

$$\vec{V_{100}} = A\vec{V_{50}} = \begin{pmatrix} 0.0061 & 0.2941 & 0.3927 & 0.3071 \end{pmatrix}, \tag{2.7}$$

and so on. Fig. 2.4a shows a time course that is obtained by applying this transformation 25 times, which reveals that 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 state? Actually, we can already see from the last two equations that $\vec{V_{100}} = A\vec{V_{50}} = A^2\vec{V_0}$, and hence 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

$$A^{100}\begin{pmatrix} x \\ y \\ z \\ w \end{pmatrix} = \begin{pmatrix} 0.005(x+y+z+w) \\ 0.048(x+y+z+w) \\ 0.085(x+y+z+w) \\ 0.866(x+y+z+w) \end{pmatrix} = \begin{pmatrix} 0.005 \\ 0.048 \\ 0.085 \\ 0.866 \end{pmatrix},$$

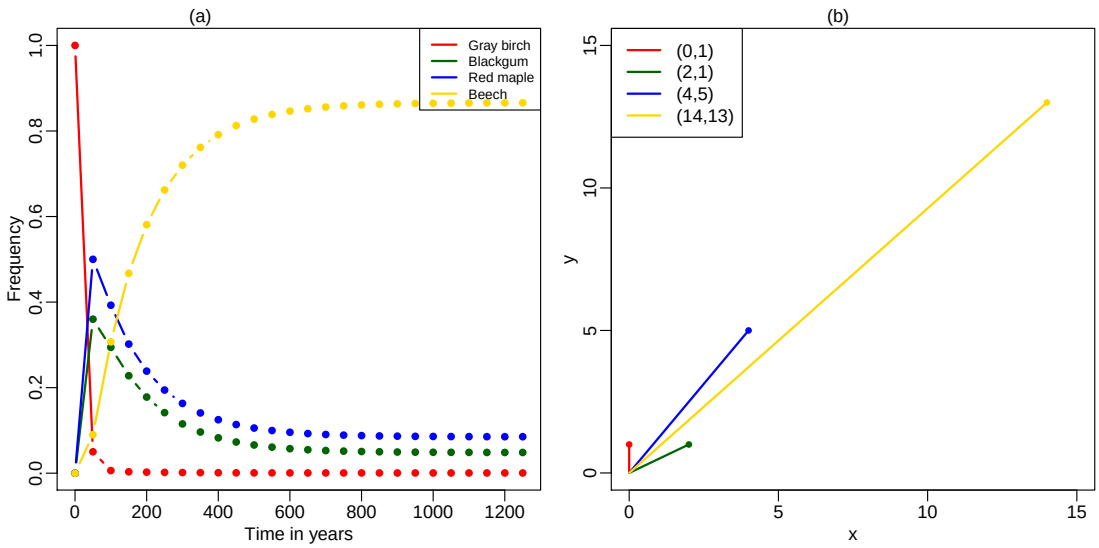


Figure 2.4: Repeated transformation of a vector by a matrix produces a vector with a direction closer and closer to the dominant eigenvector of that matrix, (in this case the eigenvector corresponding to the largest eigenvalue). Panel (a) depicts the vectors $\vec{V}$ representing the frequencies of four trees in a forest as a time plot. Starting with $\vec{V_0} = (1\ 0\ 0\ 0)$ the climax $\vec{V_\infty} = (0.005\ 0.048\ 0.085\ 0.866)$ is approached after about 800 years. This climax corresponds to the dominant eigenvector of the transition matrix observed by Horn (1975). Panel (b) depicts a few iterations with the transformation matrix $A = \left(\begin{smallmatrix} 1 & 2 \\ 2 & 1 \end{smallmatrix}\right)$ with eigenvalues $\lambda_1 = 3$ and $\lambda_2 = -1$, and corresponding eigenvectors $\vec{V_1} = \left(\begin{smallmatrix} 1 \\ 1 \end{smallmatrix}\right)$ and $\vec{V_2} = \left(\begin{smallmatrix} 1 \\ -1 \end{smallmatrix}\right)$. Starting with the red vector $\vec{v_0} = \left(\begin{smallmatrix} 0 \\ 1 \end{smallmatrix}\right)$ we obtain the green $\vec{v_1} = A\vec{v_0} = \left(\begin{smallmatrix} 2 \\ 1 \end{smallmatrix}\right)$. Applying the same transformation again, we obtain the blue $\vec{v_2} = A\vec{v_1} = \left(\begin{smallmatrix} 4 \\ 5 \end{smallmatrix}\right)$, and next the orange $\vec{v_3} = A\vec{v_r} = \left(\begin{smallmatrix} 14 \\ 13 \end{smallmatrix}\right)$. Note that the direction of these vectors approaches the eigenvector $\vec{V_1} = \left(\begin{smallmatrix} 1 \\ 1 \end{smallmatrix}\right)$. Panel (a) was made with the R script `horn.R` and Panel (b) with `eigen.R`. The latter script allows one to do more than just three iterations and to rescale the length of the vectors to one.

meaning that the succession converges into climax state. Since the columns of the matrix A^{100} are almost identical, we obtain that the state of the forest after 5000 years hardly depends on the initial vector. Next we will show that this climax vector is an eigenvector of the matrix A.

2.4 Eigenvalues and eigenvectors

We have learned above that using matrices one can transform vectors, and change both their length and their direction. It turns out that for each particular matrix there exists a set of special vectors called its "eigenvectors". Applying the matrix to an eigenvector will only change its length, and not its direction. Note that this is the same effect as multiplying the vector with a scalar, i.e., the transformation matrix in fact behaves as a scalar when applied to an eigenvector. The factor by which the eigenvector changes size when the matrix is applied to it, i.e., the scaling factor, is called the corresponding "eigenvalue". Each eigenvector will have its own eigenvalue, and an n-dimensional matrix can maximally have n eigenvectors and eigenvalues.

Formally, one can write this as follows

$$A\mathbf{v} = \lambda\mathbf{v}\ . \tag{2.8}$$

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

$$kA\mathbf{v} = k\lambda\mathbf{v} \quad \text{or} \quad A(k\mathbf{v}) = \lambda(k\mathbf{v}) \ . \tag{2.9}$$

therefore, one can say that $k\mathbf{v}$ is also an eigenvector of Eq. (2.8), corresponding to eigenvalue λ.

What is the use of knowing eigenvalues and eigenvectors of a matrix? We have seen in the forest-succession example that eigenvectors give the principal directions of change imposed by a matrix. Eigenvalues give the amount of change in each of these directions. Knowing the eigenvectors, one can to a large extent predict the effect of a matrix on a vector, and hence predict the behavior of the system, as it will be rotated into the direction of the dominant eigenvector (see Fig. 2.4). Technically, the dominant eigenvector is the eigenvector associated with the eigenvalue that is largest when they are ranked by their absolute values; below we will use the term largest eigenvalue to denote the eigenvalue that is largest by their real values. 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 only use it for the solution of systems of differential equations, which is considered in Chapter 3.

Let us now explain the general approach for solving the eigenvalues λ and eigenvectors v of an arbitrary 2×2 matrix. Thus, consider the problem

$$A\mathbf{v} = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} = \lambda \begin{pmatrix} x \\ y \end{pmatrix} . \tag{2.10}$$

First rewrite this into a system of two equations with three unknowns λ, x, y

$$\begin{cases} ax + by = \lambda x \\ cx + dy = \lambda y \end{cases} , \tag{2.11}$$

which can be further rewritten as:

$$\begin{cases} (a-\lambda)x + by = 0 \\ cx + (d-\lambda)y = 0 \end{cases} \quad \text{or in matrix form} \quad \begin{pmatrix} a-\lambda & b \\ c & d-\lambda \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix} . \tag{2.12}$$

This system always has a solution $x = y = 0$. However, eigenvectors are defined to be non-zero vectors, and hence the (0 0) solution does not correspond to an eigenvector. In order to find non-zero solutions, let us first cancel y from the system, by multiplying 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:

$$[(d-\lambda)(a-\lambda) - bc]x = 0 \ , \tag{2.13}$$

and given that $x \neq 0$ one obtains

$$(d-\lambda)(a-\lambda) - bc = \lambda^2 - (a+d)\lambda + (ad - cb) = \lambda^2 - \mathrm{tr}\lambda + \det = 0 \ , \tag{2.14}$$

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

$$\lambda_{1,2} = \frac{\mathrm{tr} \pm \sqrt{\mathrm{tr}^2 - 4\det}}{2} \ . \tag{2.15}$$

Eq. (2.14), or the equivalent Eq. (2.15), is called the "characteristic equation". In general, for an $n \times n$ matrix there are maximally n solutions for λ.

For example, use this approach to find the eigenvalues of the following matrix

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

with tr $= 2$ and det $= 1 - 4 = -3$. Using the characteristic equation one writes

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

giving $\lambda_1 = 3$ and $\lambda_2 = -1$. As a next step we have to find the eigenvectors belonging to these two eigenvalues. One can do this by substituting the eigenvalues into the original equation, Eq. (2.12), and solving the equations for x and y. For the eigenvector corresponding to the eigenvalue $\lambda_1 = 3$ one obtains:

$$\begin{cases} (1-3)x + 2y = 0 \\ 2x + (1-3)y = 0 \end{cases} \quad \text{or} \quad \begin{cases} -2x + 2y = 0 \\ 2x - 2y = 0 \end{cases} \quad \text{or} \quad \begin{cases} -2x = -2y \\ 2x = 2y \end{cases} . \tag{2.16}$$

The two equations give us the same solution: $x = y$. This means 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

$$\begin{pmatrix} x \\ y \end{pmatrix} = k \begin{pmatrix} 1 \\ 1 \end{pmatrix} , \tag{2.17}$$

where k is an arbitrary number. Eq. (2.17) thus gives us all possible solutions of Eq. (2.16). It also illustrates a general property of eigenvectors which we have already proven in Eq. (2.9), namely that if we multiply an eigenvector by an arbitrary number k, we will get another eigenvector of our matrix. Using this matrix to repeatedly transform an initial vector indeed turns these vectors into the direction of the dominant eigenvector (Fig. 2.4b).

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

$$\begin{cases} (1-(-1))x + 2y = 0 \\ 2x + (1-(-1))y = 0 \end{cases} \quad \text{or} \quad \begin{cases} 2x + 2y = 0 \\ 2x + 2y = 0 \end{cases} \quad \text{or} \quad \begin{cases} 2x = -2y \\ 2x = -2y \end{cases} . \tag{2.18}$$

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 just the first equation to find the eigenvectors. In both cases the second equation did not provide any new information. Therefore we introduce a simpler method for finding the eigenvectors of a general system (see Eq. (2.11)). Consider that we found eigenvalues λ_1 and λ_2 from the characteristic equation, Eq. (2.14). To find the corresponding eigenvectors, one needs to substitute these eigenvalues into the matrix and solve the following system of linear equations (see Eq. (2.12)):

$$\begin{cases} (a - \lambda_1)x + by = 0 \\ cx + (d - \lambda_1)y = 0 \end{cases} \tag{2.19}$$

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

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

and substituting these expressions into the second equation provides

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

which is zero because $(d-\lambda_1)(a-\lambda_1)-cb = 0$, in accordance with the characteristic equation, Eq. (2.14). Therefore $x = -b$ and $y = a - \lambda_1$ give a solution of Eq. (2.19), which is an eigenvector corresponding to the eigenvalue λ_1. Similarly we find the eigenvector corresponding to the eigenvalue λ_2. Note that this approach will fail when both $b = 0$ and $a - \lambda = 0$ in Eq. (2.12). In such cases one 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:

$$\mathbf{v_1} = \begin{pmatrix} -b \\ a - \lambda_1 \end{pmatrix} \ \& \ \mathbf{v_2} = \begin{pmatrix} -b \\ a - \lambda_2 \end{pmatrix} \quad \text{or} \quad \mathbf{v_1} = \begin{pmatrix} d - \lambda_1 \\ -c \end{pmatrix} \ \& \ \mathbf{v_2} = \begin{pmatrix} d - \lambda_2 \\ -c \end{pmatrix} \ . \tag{2.20}$$

Applying this to 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. (2.20) 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 indeed equivalent to the eigenvectors, $\mathrm{v}_1 = \binom{1}{1}$ and $\mathrm{v}_2 = \binom{-1}{1}$, that were obtained above.

2.5 Exercises

1. We have seen that the determinant $ad - cb$ of a general 2-dimensional linear system,

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

tells us whether or not the system has a solution for any p or q. Note that the two rows define two lines, i.e., $y = (p - ax)/b$ and $y = (q - cx)/d$, and that the solution corresponds to the intersection point of these lines.
a. What is the slope of these two lines?
b. What would be a condition for them to not intersect?
c. Does this depend on p and q?

2. Find eigenvalues and eigenvectors of the following matrices:
a. $\begin{pmatrix} -2 & 1 \\ 1 & -2 \end{pmatrix}$
b. $\begin{pmatrix} 1 & 4 \\ 1 & 1 \end{pmatrix}$
c. $\begin{pmatrix} a & b \\ 0 & d \end{pmatrix}$

3. Study the model of Horn (1975) with the R script `horn.R`. Note the notation `%*%` for matrix muplication!
a. Will succession in this model approach the same climax state for any initial condition?

b. Is that biologically reasonable?

4. Write the following linear system in a matrix form $A\vec{X} = \vec{V}$, and compute the determinant of the matrix A to check whether or not the system has a solution.

   a. $\begin{cases} 2x - 4y = 3 \\ x + y = 1 \end{cases}$

Chapter 3

Systems of two differential equations

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

$$\begin{cases} \mathrm{d}x/\mathrm{d}t = f(x,y) \\ \mathrm{d}y/\mathrm{d}t = g(x,y) \end{cases} , \tag{3.1}$$

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

$$\begin{cases} \mathrm{d}x/\mathrm{d}t = ax + by \\ \mathrm{d}y/\mathrm{d}t = cx + dy \end{cases} . \tag{3.2}$$

This is called a linear system of differential equations because the equations only contain linear terms. Solving x and y from $ax + by = 0$ and $cx + dy = 0$ reveals that linear systems always has only one steady state: $(\bar{x}, \bar{y}) = (0, 0)$. Depending on the values and signs of the parameters a, b, c, d these equations can describe a range of different processes. For example, consider the specific case $a = -2, b = 1, c = 1, d = -2$:

$$\begin{cases} \mathrm{d}x/\mathrm{d}t = -2x + y \\ \mathrm{d}y/\mathrm{d}t = x - 2y \end{cases} \tag{3.3}$$

where x and y decay at a rate -1 per unit of time, and are converted into one another at a rate 1 (and, hence, each population has a total loss rate of -2 per unit of time).

3.1 Solutions of Linear 2D Systems

The analytical solution for the linear two-dimensional systems of Eq. (3.2) is known. Rather than deriving this solution, we will simply provide it to illustrate its analogy with the solution of linear one-dimensional systems. For one-dimensional linear systems of the form

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

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 equilbrium. 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

$$\begin{cases} \mathrm{d}x/\mathrm{d}t = ax + by \\ \mathrm{d}y/\mathrm{d}t = cx + dy \end{cases} ,$$

which in matrix notation can be written as

$$\begin{pmatrix} \mathrm{d}x/\mathrm{d}t \\ \mathrm{d}y/\mathrm{d}t \end{pmatrix} = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} = A \begin{pmatrix} x \\ y \end{pmatrix} ,$$

has as a general solution

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

which in vector notation can be written as:

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

where λ_1, λ_2 are the eigenvalues, and $\mathbf{v_1} = \binom{x_1}{y_1}$ and $\mathbf{v_2} = \binom{x_2}{y_2}$ the corresponding 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 apparently all solutions can be written as a linear combination of the change along the two eigenvectors. 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 that are defined by the initial values of x and y, i.e., $x(0) = C_1 x_1 + C_2 x_2$ and $y(0) = C_1 y_1 + C_2 y_2$ (because $\mathrm{e}^{\lambda 0} = 1$).

Similar to the single exponent a in the solution of one dimensional linear systems, the signs of the two eigenvalues determine the stability of the equilibrium point $(0, 0)$. Note that the equilibrium point will only be stable when both exponentials in the solution converge to zero, which implies that both eigenvalues need to be smaller than zero. In case of complex-valued eigenvalues (see Chapter 7), which occur for spiral (and center) points, 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 that the steady state $(0, 0)$ is
- 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., $\lambda_{1,2} = \alpha \pm \mathrm{i}\beta$, we obtain that $(0, 0)$ is
- 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, derive the general solution of the system in Eq. (3.3) for the matrix

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

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

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

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

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

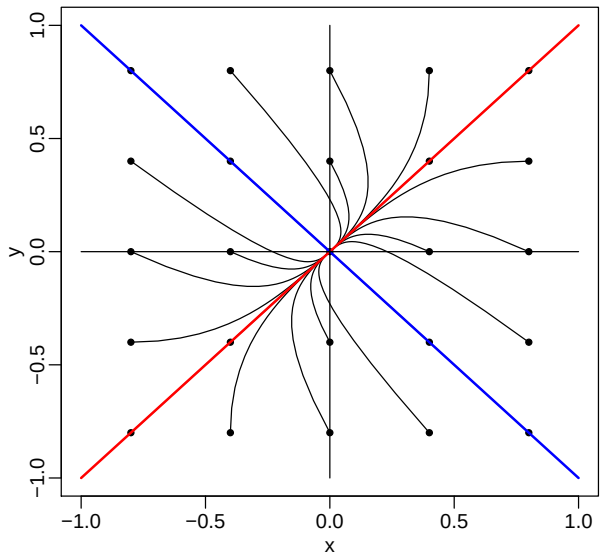


Figure 3.1: The eigenvectors and a phase portrait of the model defined by Eq. (3.3). The red line is defined by the eigenvector $v_1 = \binom{1}{1}$ and the blue line by $v_2 = \binom{-1}{1}$. The bullets are starting points of trajectories (that are depicted as black lines). Note that all trajectories approach an eigenvector and then the origin. Initial conditions starting on an eigenvector form trajectories on that eigenvector. This figure was made with the script `linear.R`).

and for v_2 we can write

$$\mathbf{v_2} = \begin{pmatrix} -b \\ a - \lambda_2 \end{pmatrix} = \begin{pmatrix} -1 \\ 1 \end{pmatrix} ,$$

(see Fig. 3.1). We write the general solution as

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

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 $y(0) = C_1 + C_2$. One can check this solution by substituting it into Eq. (3.3), and compare that to the derivative of the solution (see the slides and the video).

3.2 Exercises

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

$$\begin{pmatrix} \mathrm{d}x/\mathrm{d}t \\ \mathrm{d}y/\mathrm{d}t \end{pmatrix} = \begin{pmatrix} 1 & -2 \\ 5 & 8 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} \qquad \text{with} \quad \begin{pmatrix} x(0) \\ y(0) \end{pmatrix} = \begin{pmatrix} 3 \\ -3 \end{pmatrix}$$

   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

$$\begin{cases} \mathrm{d}A/\mathrm{d}t = -\frac{k}{V_1}(A - B) \\ \mathrm{d}B/\mathrm{d}t = \frac{k}{V_2}(A - B) \end{cases} ,$$

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 at which the chemical exchanges between the two compartments. Let $V_1 = 20$ liters, $V_2 = 5$ liters, and $k = 0.2$ liters/min. Start with $A(0) = 3$ moles/liter and $B(0) = 0$, and find $A(t)$ and $B(t)$ as functions of time. Hint: this exercise is similar to the previous one!

a. Find the solution of this system.

b. What is the steady state, and does this match the initial condition?

c. Is this a stable steady state?

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. One can then establish the stability of that steady state by solving the linearized system. The analytical solution of the approximate linear system approaches the behavior of the original system closely as long as we remain close to an equilibrium point.

We will linearize functions, $f(x)$, by approximating them by their local derivative for a particular x-value, $\bar{x}$ (see Fig. 4.1a). Since the derivative of a function $f(x)$ at point $\bar{x}$ can be written as

$$f'(\bar{x}) = \lim_{x \to \bar{x}} \frac{f(x) - f(\bar{x})}{x - \bar{x}} \quad \text{or} \quad f'(\bar{x}) = \lim_{h \to 0} \frac{f(\bar{x} + h) - f(\bar{x})}{h} \ ,$$

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

$$f(x) \simeq f(\bar{x}) + f'(\bar{x})\,(x - \bar{x}) \quad \text{or} \quad f(x) \simeq f(\bar{x}) + f'(\bar{x})\,h \ ,$$

where $h \to 0$. 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 $x - \bar{x}$ 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. For example, with $a = 2$ and $b = 1$ and $x = 3$ we obtain that $f(3) = 2 \times 9 + 1 = 19$, and that $\partial_x f(3) = 2 \times 2 \times 3 = 12$. One would estimate the value of $f(3.1)$ by writing $f(3.1) \simeq f(3) + \partial_x f(3) \times 0.1 = 19 + 12 \times 0.1 = 20.2$, while the true value $f(3.1) = 20.22$. When $h \to 0$ this linear approximation becomes extremely good.

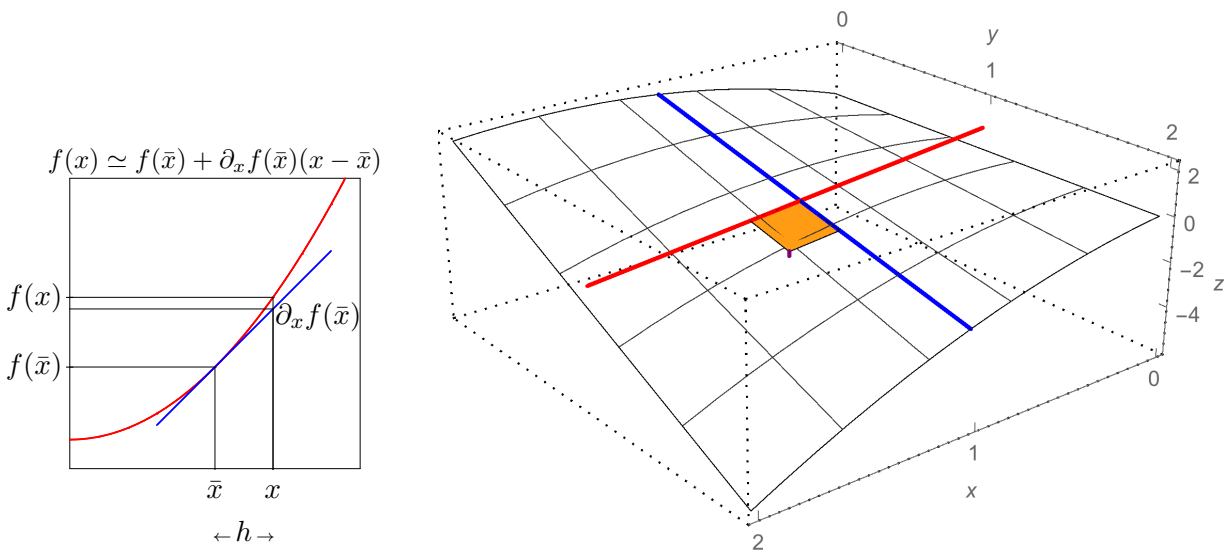


Figure 4.1: On the left we have the function $f(x) = ax^2 + b$ (curved red line) with its local derivative in the point $\bar{x}$ depicted as $\partial_x f(\bar{x}) = 2a\bar{x}$ (straight blue line). On the right we depict the function $f(x, y) = 3x - x^2 - 2xy$, with in the point $(\bar{x}, \bar{y}) = (1, 1)$ 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.

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 $z = f(x, y)$ on the upward axis. The function 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.,

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

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

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

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 fairly large 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 systems of ODEs: Jacobian

Consider a general system of two differential equations:

$$\begin{cases} \mathrm{d}x/\mathrm{d}t = f(x, y) \\ \mathrm{d}y/\mathrm{d}t = g(x, y) \end{cases} , \tag{4.3}$$

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. (4.1) we find a linear approximation of $f(x, y)$ close to the equilibrium

$$f(x, y) \simeq 0 + \partial_x f(\bar{x}, \bar{y})\,(x - \bar{x}) + \partial_y f(\bar{x}, \bar{y})\,(y - \bar{y}) = \partial_x f\,(x - \bar{x}) + \partial_y f\,(y - \bar{y}) \ , \tag{4.4}$$

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

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

where $\partial_x g = \partial_x g(\bar{x}, \bar{y})$ is an abbreviation for the partial derivative of $g(x, y)$ at the steady state $(\bar{x}, \bar{y})$. If we now replace the right hand sides of Eq. (4.3) by their local approximations around $(\bar{x}, \bar{y})$, i.e., Eq. (4.4) and Eq. (4.5), we obtain

$$\begin{cases} \mathrm{d}x/\mathrm{d}t \simeq \partial_x f\,(x - \bar{x}) + \partial_y f\,(y - \bar{y}) \\ \mathrm{d}y/\mathrm{d}t \simeq \partial_x g\,(x - \bar{x}) + \partial_y g\,(y - \bar{y}) \end{cases} \tag{4.6}$$

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 *constants* simply representing a slope at the equilibrium point $(\bar{x}, \bar{y})$. We therefore rewrite Eq. (4.6) into

$$\begin{cases} \mathrm{d}x/\mathrm{d}t = a(x - \bar{x}) + b(y - \bar{y}) \\ \mathrm{d}y/\mathrm{d}t = c(x - \bar{x}) + d(y - \bar{y}) \end{cases} , \tag{4.7}$$

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 time derivatives $\mathrm{d}\bar{x}/\mathrm{d}t$ and $\mathrm{d}\bar{y}/\mathrm{d}t$ are zero, we can apply a trick and write

$$\frac{\mathrm{d}x}{\mathrm{d}t} = \frac{\mathrm{d}x}{\mathrm{d}t} - \frac{\mathrm{d}\bar{x}}{\mathrm{d}t} = \frac{\mathrm{d}(x - \bar{x})}{\mathrm{d}t} \quad \text{and} \quad \frac{\mathrm{d}y}{\mathrm{d}t} = \frac{\mathrm{d}y}{\mathrm{d}t} - \frac{\mathrm{d}\bar{y}}{\mathrm{d}t} = \frac{\mathrm{d}(y - \bar{y})}{\mathrm{d}t}$$

giving

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

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.,

$$\begin{cases} \mathrm{d}h_x/\mathrm{d}t = ah_x + bh_y \\ \mathrm{d}h_y/\mathrm{d}t = ch_x + dh_y \end{cases} . \tag{4.9}$$

Since this has the form of a general linear system (see Chapter 3), we know the solution

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

where λ_1 and λ_2 are the eigenvalues of the matrix defined by the four constants in Eq. (4.9), and $\mathbf{v_1} = \binom{x_1}{y_1}$ and $\mathbf{v_2} = \binom{x_2}{y_2}$ 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.

Having this solution one can see that the rate at which perturbations die out is determined by the largest eigenvalue. Hence, the return time is defined by

$$T_R = \frac{-1}{\max(\lambda_1, \lambda_2)}$$

when $\lambda_{1,2} < 0$ (otherwise the return time is negative and not defined).

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:

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

This matrix is called the Jacobian of system Eq. (4.3) in the point $(\bar{x}, \bar{y})$. This Jacobi matrix allows us to determine the eigenvalues and hence establish the type of the equilibrium of the original non-linear 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 eigenvalues of that matrix to establish the stability, and/or type, of the equilibrium point.

4.3 Example

Let us finish with a 2-dimensional example to illustrate how this is actually performed. Consider two (biological) populations, $x \geq 0$ and $y \geq 0$, with a source for x, death for both, and a mass-action interaction term,

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x, y) = a - bx - cxy \quad \text{and} \quad \frac{\mathrm{d}y}{\mathrm{d}t} = g(x, y) = dxy - ey \ ,$$

with a steady state $\bar{x} = \frac{a}{b}$ when $y = 0$, and a non-trivial steady state $\bar{x} = \frac{e}{d}$ and $\bar{y} = \frac{ad}{ce} - \frac{b}{c}$. To find the Jacobi matrix in these steady states, we need to take the partial derivatives of $f(x, y)$ and $g(x, y)$ with respect to x and y respectively, i.e.,

$$J = \begin{pmatrix} \partial_x f & \partial_y f \\ \partial_x g & \partial_y g \end{pmatrix} = \begin{pmatrix} -b - c\bar{y} & -c\bar{x} \\ d\bar{y} & d\bar{x} - e \end{pmatrix} .$$

First consider the trivial steady steady state and fill in $\bar{x} = \frac{a}{b}$ and $\bar{y} = 0$,

$$J_1 = \begin{pmatrix} -b & -\frac{ca}{b} \\ 0 & \frac{da}{b} - e \end{pmatrix} .$$

Since this matrix is in a diagonal form we know that the diagonal elements provide the eigenvalues, i.e., $\lambda_1 = -b$ and $\lambda_2 = \frac{da}{b} - e$ (see Eq. (2.13)). Since $\lambda_1 < 0$, the trivial steady state will

be stable whenever $\lambda_2 < 0$, i.e., whenever $\frac{a}{b} < \frac{e}{d}$. Note this parameter condition also determines whether or not $\bar{y} = \frac{ad}{ce} - \frac{b}{c}$ in the non-trivial steady state is positive, i.e., the trivial steady state is stable only when $\bar{y} < 0$, which is not realistic. Next we consider the Jacobian of the (positive) non-trivial steady state, and let us first fill in $\bar{x} = \frac{e}{d}$, i.e.,

$$J_2 = \begin{pmatrix} -b - c\bar{y} & -\frac{ce}{d} \\ d\bar{y} & 0 \end{pmatrix} .$$

Since $\bar{y} > 0$, the signs of this matrix are given by

$$J_3 = \begin{pmatrix} -\alpha & -\beta \\ \gamma & 0 \end{pmatrix} \quad \text{with} \quad \mathrm{tr} J_3 = -\alpha < 0 \quad \text{and} \quad \det J_3 = \beta\gamma > 0 \ ,$$

such that

$$\lambda_{1,2} = \frac{\mathrm{tr} \pm \sqrt{\mathrm{tr}^2 - 4\det}}{2} = \frac{-\alpha \pm \sqrt{\alpha^2 - 4\beta\gamma}}{2} \ ,$$

implying that both eigenvalues are negative (because $\sqrt{\alpha^2 - 4\beta\gamma} < \alpha$), and hence for $\bar{y} > 0$ the non-trivial steady state is stable. Summarizing we find that for $\frac{a}{b} < \frac{e}{d}$ the steady state $(\bar{x}, \bar{y}) = (a/b, 0)$ is stable and the non-trivial steady state is non-existent (i.e., located at negative $\bar{y}$), and that for $\frac{a}{b} > \frac{e}{d}$ the $(a/b, 0)$ state is unstable and the $(\bar{x}, \bar{y}) = \left(\frac{e}{d}, \frac{ad}{ce} - \frac{b}{c}\right)$ steady state is stable.

4.4 Exercises

1. Find partial derivatives of these functions. After finding derivatives evaluate their value at the given point.
   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, $\mathrm{d}x/\mathrm{d}t = f(x, y)$ and $\mathrm{d}y/\mathrm{d}t = g(x, y)$, and find the partial derivatives, $\partial_x f, \partial_y f, \partial_x g$ and $\partial_y g$, at each equilibrium point
   a. $\begin{cases} \mathrm{d}x/\mathrm{d}t = -4y \\ \mathrm{d}y/\mathrm{d}t = 4x - x^2 - 0.5y \end{cases}$
   b. $\begin{cases} \mathrm{d}x/\mathrm{d}t = 9x + y^2 \\ \mathrm{d}y/\mathrm{d}t = x - y \end{cases}$
   c. $\begin{cases} \mathrm{d}x/\mathrm{d}t = 2x - xy \\ \mathrm{d}y/\mathrm{d}t = -y + y^2 x \end{cases}$

4. Find the Jacobian matrix of the non-trivial steady state of the Lotka-Volterra model, $\mathrm{d}R/\mathrm{d}t = aR - bR^2 - cRN$ and $\mathrm{d}N/\mathrm{d}t = dRN - eN$.

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 interaction 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 the stability and the type of equilibrium. However, at the end of Chapter 4 we used a simple method for determining the type of equilibrium from just from the coefficients of the matrix, without actually computing the eigenvalues. We generalize that simple method here.

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.,

$$\begin{cases} \mathrm{d}x/\mathrm{d}t = f(x,y) \\ \mathrm{d}y/\mathrm{d}t = g(x,y) \end{cases} ,$$

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

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

where $\mathrm{tr} = a + d$, $\det = ad - bc$, and D is the discriminant.

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, $\mathrm{tr}[J]$ 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 one can prove that they obey the following expressions

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

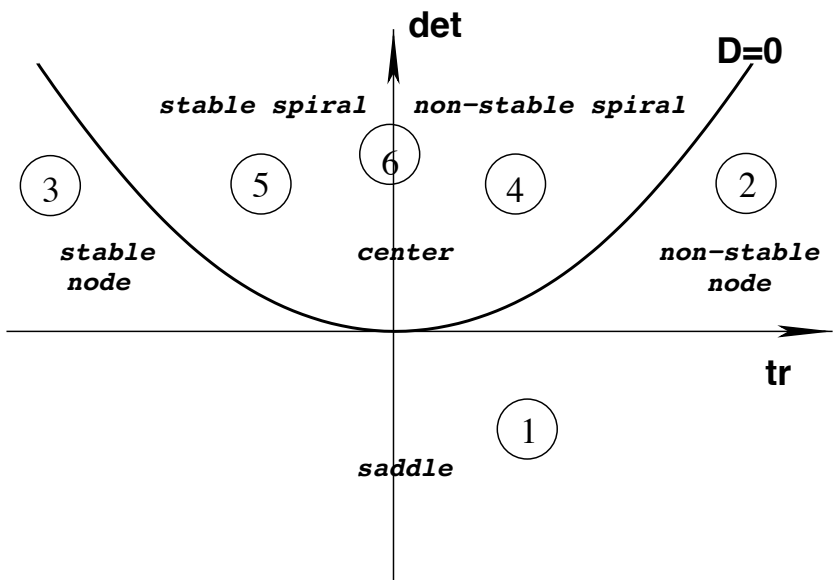


Figure 5.1: The trace and the determinant determine the type of steady state. Plotting the trace, tr, along the horizontal axis and the determinant, det, along the vertical axis, we can plot the parabola where the discriminant $D = 0$. Saddle points (case 1 in the text) corresponds to the lower half 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 $\mathrm{tr}[J] = 0$. 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 $\lambda_1 + \lambda_2 = (\mathrm{tr} + \sqrt{D} + \mathrm{tr} - \sqrt{D})/2 = \mathrm{tr}$, and the latter can be checked by writing

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

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

Although it is typically sufficient to know whether or not a steady state is stable, 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 $\det < 0$ then $D > 0$, both eigenvalues are real, with $\lambda_{1,2}$ having unequal signs: saddle point.
2. if $\det > 0$, $\mathrm{tr} > 0$ and $D > 0$ the eigenvalues are real, with $\lambda_{1,2} > 0$: unstable node.
3. if $\det > 0$, $\mathrm{tr} < 0$ and $D > 0$ the eigenvalues are real, with $\lambda_{1,2} < 0$: stable node. The return time is defined as $T_R = -1/\lambda_{\max}$
4. if $\det > 0$, $\mathrm{tr} > 0$ and $D < 0$ the eigenvalues form a complex pair (see Chapter 7),

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

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

5. if det > 0, tr < 0 and $D < 0$ the eigenvalues form a similar complex pair, but since the real part of the eigenvalues, $-\mathrm{tr}/2$, now is negative, the steady state is a stable spiral point (see Chapter 7). The return time is now defined as $T_R = -1/\lambda_{\mathrm{Re}} = 2/\mathrm{tr}$

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 known the signs of the partial derivatives that make up the Jacobian. Fortuitously, the sign of the partial derivatives (+, −, 0) in the equilibrium can be obtained from the vector field 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 $\mathrm{d}x/\mathrm{d}t = f(x, y) = 0$ nullcline, and the dashed $\mathrm{d}y/\mathrm{d}t = g(x, y) = 0$ nullcline. Using the definition of a derivative, the partial derivative $\partial_x f(x, y)$, in the equilibrium point $(\bar{x}, \bar{y})$, can be approximated by

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

because $f(\bar{x}, \bar{y}) = 0$, and where $h = x - \bar{x}$ is a small increase in x. This is the difference in the $f(x, y)$ value between the original point $(\bar{x}, \bar{y})$, where $f(\bar{x}, \bar{y}) = 0$, 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. The sign of $f(\bar{x} + h, \bar{y})$ can be read from the vector field close to the original point $(\bar{x}, \bar{y})$. Similarly, since $\partial_y f(\bar{x}, \bar{y}) \simeq f(\bar{x}, \bar{y} + h)/h$, 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

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

with $\mathrm{tr}[J] = \alpha + \delta$ 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.

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 signs of 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 of $\partial_x g(\bar{x}, \bar{y})$, and the vertical arrow in point $(\bar{x}, \bar{y} + h)$ determines the sign of of $\partial_y g(\bar{x}, \bar{y})$.

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

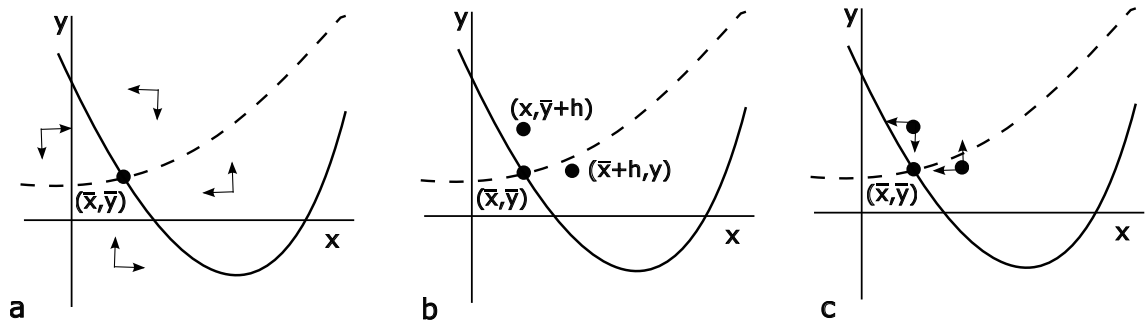


Figure 5.2: The graphical Jacobian method. Panel (a) shows the nullclines, vectorfield, and the location of the equilibrium $(\bar{x}, \bar{y})$. The solid line corresponds to $\mathrm{d}x/\mathrm{d}t = 0$ and the dashed line to the $\mathrm{d}y/\mathrm{d}t = 0$ nullcline. Panel (b) shows two reference 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.

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 $\partial_g(\bar{x}, \bar{y}) = \delta < 0$.

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

5.3 Plan of qualitative analysis

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

$$\begin{cases} \mathrm{d}x/\mathrm{d}t = f(x, y) \\ \mathrm{d}y/\mathrm{d}t = g(x, y) \end{cases} . \tag{5.4}$$

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 (see the online tutorial at tbb.bio.uu.nl/rdb/bm/clips/nullclines):

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 $f(x, y)$ and $g(x, y) = 0$ nullclines in this phase space.
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 $f(x, y) < 0$.
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 $\mathrm{d}y/\mathrm{d}t = 0$ nullcline.
5. Study the vector field in the four different regions surrounding each equilibrium point, and see if this provides enough information on stability of the equilibrium. This can be done when

the steady state is a stable node, an unstable node, or a saddle point.

Should the vector field be insufficient to determine the stability of an equilibrium, which probably means it is a spiral point, 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 $\mathrm{tr} < 0$ and $\det > 0$, and see if this identifies the type of equilibrium (see 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 $(\bar{x}, \bar{y})$

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

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

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

and $\mathrm{tr} = a + d$ 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, the local vector field and nullclines, of each equilibrium, to draw a local phase portrait with trajectories around that 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. $\begin{cases} \mathrm{d}x/\mathrm{d}t = 3x + y \\ \mathrm{d}y/\mathrm{d}t = -20x + 6y \end{cases}$ **b.** $\begin{cases} \mathrm{d}x/\mathrm{d}t = 2x + y \\ \mathrm{d}y/\mathrm{d}t = 2x - 10y \end{cases}$ **c.** $\begin{cases} \mathrm{d}x/\mathrm{d}t = 2x + y \\ \mathrm{d}y/\mathrm{d}t = 5x - 2y \end{cases}$

2. Consider the following model

   $$\frac{\mathrm{d}x}{\mathrm{d}t} = 2x(1 - y) \quad \text{and} \quad \frac{\mathrm{d}y}{\mathrm{d}t} = 2 - y - x^2 ,$$

   assuming $x \geq 0$ and $y \geq 0$.
   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.
   d. Sketch the qualitative local phase portraits around each equilibrium point by computing eigenvalues and eigenvectors, and try to connect these into a global phase space.

3. Study the model of the previous question again using the graphical Jacobian approach:
   a. Sketch the vector field for the system using nullclines.
   b. Find type and stability of equilibria using the graphical Jacobian.
   c. Compare your results to the previous question.

4. On the webpage we provide the Grind script `linear.R` which encodes Eq. (3.2).
   a. Find values of a, b, c and d such that the origin is a stable node, an unstable node, a saddle point, and a spiral point. Help yourself by reducing this problem to find the proper trace, determinant, and discriminant of this matrix.
   b. Draw the nullclines with a phase portrait for each situation (`plane(portrait=TRUE)`).

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:

$$\frac{\mathrm{d}R}{\mathrm{d}t} = aR - bR^2 - cRN \quad \text{and} \quad \frac{\mathrm{d}N}{\mathrm{d}t} = dRN - eN \ , \tag{6.1}$$

where a, b, c, d, and e are positive constant parameters, and R and N are the prey and predator densities. In the online tutorial tbb.bio.uu.nl/rdb/bm/clips/nullclines/script.pdf we show that the nullclines can intersect in three (Fig. 6.1a) or two (Fig. 6.1b) steady states, and that these steady states are given by

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

which confirms that the non-trivial steady state only exists when $da > eb$. The same tutorial explains how to obtain the vector field, and explains that this is sufficient to see that the origin is a saddle point, and that the steady state $(R, N) = (a/b, 0)$ is saddle in Fig. 6.1a and a stable node in Fig. 6.1b.

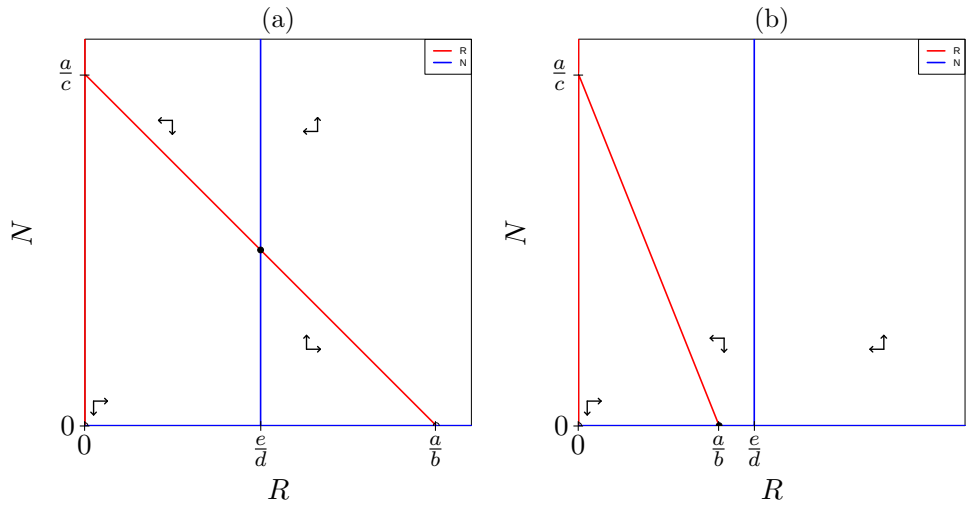


Figure 6.1: The two qualitatively different phase spaces of the Lotka-Volterra model, with the vector field indicated by arrows.

To establish the stability of the non-trivial steady state in Fig. 6.1a we next apply our method of linearization. Thus, we define two functions

$$\frac{\mathrm{d}R}{\mathrm{d}t} = aR - bR^2 - cRN = f(R,N) \quad \text{and} \quad \frac{\mathrm{d}N}{\mathrm{d}t} = dRN - eN = g(R,N) \ , \tag{6.2}$$

and rewrite the model into two new variables h_R and h_N that define the distance to the steady state $(\bar{R},\bar{N})$ by adopting Eq. (4.1),

$$\frac{\mathrm{d}(\bar{R}+h_R)}{\mathrm{d}t} = \frac{\mathrm{d}h_R}{\mathrm{d}t} = f(\bar{R}+h_R,\bar{N}+h_N) \simeq f(\bar{R},\bar{N}) + \partial_R f(\bar{R},\bar{N})\ h_R + \partial_N f(\bar{R},\bar{N})\ h_N \ , \tag{6.3}$$

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

$$\frac{\mathrm{d}(\bar{N}+h_N)}{\mathrm{d}t} = \frac{\mathrm{d}h_N}{\mathrm{d}t} = g(\bar{R}+h_R,\bar{N}+h_N) \simeq g(\bar{R},\bar{N}) + \partial_R g(\bar{R},\bar{N})\ h_R + \partial_N g(\bar{R},\bar{N})\ h_N \ , \tag{6.4}$$

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

$$\frac{\mathrm{d}h_R}{\mathrm{d}t} = \partial_R f(\bar{R},\bar{N})\ h_R + \partial_N f(\bar{R},\bar{N})\ h_N \ , \tag{6.5}$$

and

$$\frac{\mathrm{d}h_N}{\mathrm{d}t} = \partial_R g(\bar{R},\bar{N})\ h_R + \partial_N g(\bar{R},\bar{N})\ h_N \ . \tag{6.6}$$

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,

$$J = \begin{pmatrix} a - 2b\bar{R} - c\bar{N} & -c\bar{R} \\ d\bar{N} & d\bar{R} - e \end{pmatrix} \ , \tag{6.7}$$

and the general solution of the linear system has the form

$$\begin{pmatrix} h_R(t) \\ h_N(t) \end{pmatrix} = c_1 \begin{pmatrix} R_1 \\ N_1 \end{pmatrix} \mathrm{e}^{\lambda_1 t} + c_2 \begin{pmatrix} R_2 \\ N_2 \end{pmatrix} \mathrm{e}^{\lambda_2 t} \ , \tag{6.8}$$

where $\lambda_{1,2}$ are the eigenvalues, and $\mathbf{v_1} = \binom{R_1}{N_1}$ and $\mathbf{v_2} = \binom{R_2}{N_2}$ 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 in Fig. 6.1a, 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

$$J = \begin{pmatrix} a & 0 \\ 0 & -e \end{pmatrix} \ . \tag{6.9}$$

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

$$J = \begin{pmatrix} -a & -\frac{ac}{b} \\ 0 & \frac{da-eb}{b} \end{pmatrix} \ . \tag{6.10}$$

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 $(\bar{R}, \bar{N}) = \left(\frac{e}{d}, \frac{da-eb}{dc}\right)$ one obtains

$$J = \begin{pmatrix} -\frac{be}{d} & -\frac{ce}{d} \\ \frac{da-eb}{c} & 0 \end{pmatrix} = \begin{pmatrix} -b\bar{R} & -c\bar{R} \\ d\bar{N} & 0 \end{pmatrix} . \tag{6.11}$$

One finds

$$\mathrm{tr} J = -b\bar{R} < 0 \quad \text{and} \quad \det J = cd\bar{R}\bar{N} > 0 , \tag{6.12}$$

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 $\mathrm{d}x/\mathrm{d}t = f(x, y)$ and $\mathrm{d}y/\mathrm{d}t = g(x, y)$. Around the steady state $(\bar{x}, \bar{y})$ in the phase space (x, y) the sign of $\mathrm{d}x/\mathrm{d}t$ 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 $\mathrm{d}x/\mathrm{d}t$ from the vector field. Similarly, a small step upwards gives the effect of y on $\mathrm{d}x/\mathrm{d}t$, 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. 6.1a:

$$J = \begin{pmatrix} \partial_x f & \partial_y f \\ \partial_x g & \partial_y g \end{pmatrix} = \begin{pmatrix} \alpha & 0 \\ 0 & -\beta \end{pmatrix} , \tag{6.13}$$

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 in Fig. 6.1a

$$J = \begin{pmatrix} -\alpha & -\beta \\ 0 & \gamma \end{pmatrix} , \tag{6.14}$$

Because $\det(J) = -\alpha\gamma < 0$ the equilibrium is a saddle point. For the non-trivial steady state in Fig. 6.1a one finds

$$J = \begin{pmatrix} -\alpha & -\beta \\ \gamma & 0 \end{pmatrix} , \tag{6.15}$$

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

6.1 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

Consider a general quadratic equation

$$a\lambda^2 + b\lambda + c = 0 \ , \tag{7.1}$$

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 $D < 0$? Can it still have roots in this case?

You have probably learned that a quadratic equation cannot be solved when $D < 0$. 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, one 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:

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

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

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

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 $\lambda_{1,2} = \pm a\mathrm{i}$. As calculations with complex numbers may in the end deliver an outcome composes of real numbers only, the definition $\mathrm{i}^2 = -1$ can be very useful in real life applications. A general complex number z can be written as $z = \alpha + \mathrm{i}\beta$, where α is called the real part and $\mathrm{i}\beta$ is called the imaginary part of the complex number z.

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 $\sqrt{D} = \sqrt{-1} \times \sqrt{-D} = \mathrm{i}\sqrt{-D}$, and

$$\lambda_{1,2} = \frac{-b \pm \mathrm{i}\sqrt{-D}}{2a} \ . \tag{7.4}$$

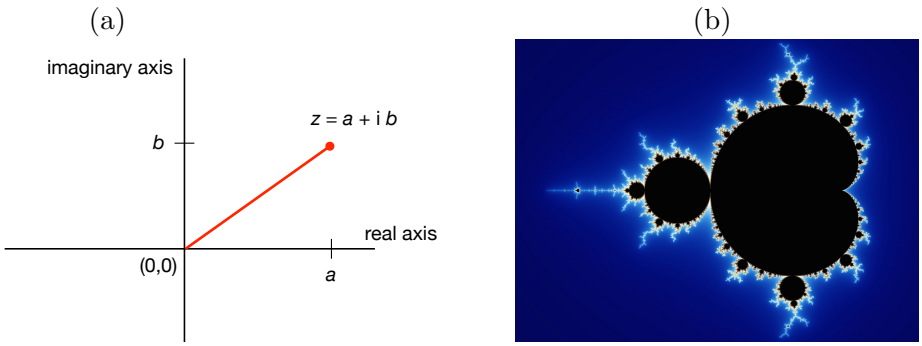


Figure 7.1: Panel (a): complex numbers represented as points or vectors on a complex plane. This is called an Argand diagram. Panel (b): the Mandelbrot set created by the series $z_i = z_{i-1}^2 + c$, where $z_0 = 0$ and c is a point in the Argand diagram (defined by the horizontal and vertical axes of Panel (b)). The color indicates the size of z_n after a fixed number of iterations $i = 1, 2, \ldots, n$. This image was taken from Wikipedia (which also provides further explanation).

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

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

In other words, $\lambda_1 = -1 + 3\mathrm{i}$ and $\lambda_2 = -1 - 3\mathrm{i}$. 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 $z_2 = a - \mathrm{i}b$ is called the complex conjugate to the number $z_1 = a + \mathrm{i}b$. Roots of a quadratic equation with a negative discriminant ($D < 0$) are always complex conjugates to each other (see Eq. (7.4)).

Complex numbers can be plotted as vectors in 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 $z = \alpha + \mathrm{i}\beta$ 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 those 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 $z_1 = 3 + 10\mathrm{i}$ and $z_2 = -5 + 4\mathrm{i}$,

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

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 $\mathrm{i}^2 = -1$. 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 $z_1 = 3 + 10\mathrm{i}$ then $10z_1 = 10(3 + 10\mathrm{i}) = 30 + 100\mathrm{i}$.

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, $z_1 = 3 + 10\mathrm{i}$ and $z_2 = -5 + 4\mathrm{i}$

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

Similarly, one can check that $(z_1)^2 = (3+10\mathrm{i})^2 = -91 + 60\mathrm{i}$. Now that we can do addition and multiplication with complex numbers, we can check that $\lambda_1 = -1 + 3\mathrm{i}$ 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 $z_0 = x + y\mathrm{i}$ 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 $i = 1, 2, \ldots, n$).

Dividing two complex numbers is somewhat more difficult. We need a little trick to remove the imaginary value in the denominator. Remember that one 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 $\frac{\bar{z_2}}{\bar{z_2}} = 1$,

$$\frac{z_1}{z_2} = \frac{z_1\bar{z_2}}{z_2\bar{z_2}}\ , \tag{7.6}$$

which allows us to eliminate the i from the denominator. An example would be

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

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

$$\frac{z_1}{z_2} = \frac{z_1\bar{z_2}}{z_2\bar{z_2}} = \frac{z_1\bar{z_2}}{|z_2|^2} = \frac{(a_1+b_1i)(a_2-b_2i)}{{a_2}^2+{b_2}^2}.$$

7.1 Complex valued eigenvalues of ODEs

Consider the general linear system of ODEs:

$$\begin{cases} \mathrm{d}x/\mathrm{d}t = ax + by \\ \mathrm{d}y/\mathrm{d}t = cx + dy \end{cases} \quad \text{with eigenvalues} \quad \lambda_{1,2} = \frac{\mathrm{tr} \pm \sqrt{D}}{2}\ ,$$

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

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

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

$$\mathbf{v_1} = k\begin{pmatrix} -b \\ a-\lambda_1 \end{pmatrix} = k\begin{pmatrix} -b \\ a-(\alpha+\mathrm{i}\beta) \end{pmatrix} = k\begin{pmatrix} -b \\ a-\alpha \end{pmatrix} - \mathrm{i}k\begin{pmatrix} 0 \\ \beta \end{pmatrix} = k\mathbf{w_1} - \mathrm{i}k\mathbf{w_2} \ , \tag{7.8}$$

where k is an arbitrary real constant, and $\mathbf{w_1} = \binom{-b}{a-\alpha}$ and $\mathbf{w_2} = \binom{0}{\beta}$ correspond to the real and imaginary parts of the eigenvector $\mathbf{v_1}$. Similarly

$$\mathbf{v_2} = k\begin{pmatrix} -b \\ a-\lambda_2 \end{pmatrix} = k\begin{pmatrix} -b \\ a-(\alpha-\mathrm{i}\beta) \end{pmatrix} = k\mathbf{w_1} + \mathrm{i}k\mathbf{w_2} \ . \tag{7.9}$$

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

$$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = C_1(\mathbf{w_1} - \mathrm{i}\mathbf{w_2})\mathrm{e}^{(\alpha+\mathrm{i}\beta)t} + C_2(\mathbf{w_1} + \mathrm{i}\mathbf{w_2})\mathrm{e}^{(\alpha-\mathrm{i}\beta)t} \ , \tag{7.10}$$

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. $e^{a+b} = \mathrm{e}^a \times \mathrm{e}^b$), there also is a special function relating trigonometric and exponential functions via complex numbers:

$$\mathrm{e}^{\mathrm{i}x} = \cos x + \mathrm{i}\sin x \quad \text{or} \quad \mathrm{e}^{-\mathrm{i}x} = \cos x - \mathrm{i}\sin x \ . \tag{7.11}$$

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

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

and hence

$$\begin{aligned} \begin{pmatrix} x(t) \\ y(t) \end{pmatrix} &= C_1(\mathbf{w_1} - \mathrm{i}\mathbf{w_2})\mathrm{e}^{\alpha t}(\cos\beta t + \mathrm{i}\sin\beta t) + C_2(\mathbf{w_1} + \mathrm{i}\mathbf{w_2})\mathrm{e}^{\alpha t}(\cos\beta t - \mathrm{i}\sin\beta t) \\ &= \mathrm{e}^{\alpha t}\left[C_1(\mathbf{w_1} - \mathrm{i}\mathbf{w_2})(\cos\beta t + \mathrm{i}\sin\beta t) + C_2(\mathbf{w_1} + \mathrm{i}\mathbf{w_2})(\cos\beta t - \mathrm{i}\sin\beta t)\right] \ . \end{aligned}$$

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 $\alpha = \mathrm{tr}/2 < 0$, demonstrating 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 $t = 0$, $\mathrm{e}^{\alpha t} = 1$, $\cos\beta t = 1$ and $\mathrm{i}\sin\beta t = 0$, and where have the initial condition $(x(0)\ y(0))$, corresponding to two real numbers, i.e.,

$$\begin{pmatrix} x(0) \\ y(0) \end{pmatrix} = C_1(\mathbf{w_1} - \mathrm{i}\mathbf{w_2}) + C_2(\mathbf{w_1} + \mathrm{i}\mathbf{w_2}) = \mathbf{w_1}(C_1 + C_2) + \mathrm{i}\mathbf{w_2}(C_2 - C_1) \ ,$$

or

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

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 $\mathbf{w_1}\mathrm{i}\sin\beta t$ and the $\mathrm{i}\mathbf{w_2}\cos\beta t$ terms, such that the full solution $(x(t)\ y(t))$ remains real. The remaining $\mathbf{w_1}\cos\beta t$ and $\mathbf{w_2}\sin\beta t$ terms define oscillatory behavior of real $x(t)$ and $y(t)$

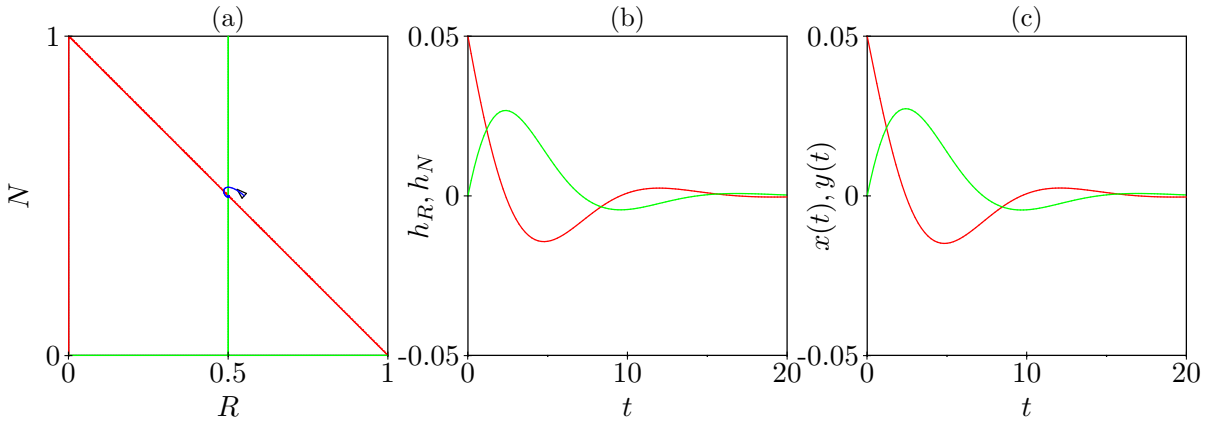


Figure 7.2: The stable spiral point of the Lotka Volterra model. Panel (a) depicts the nullclines with a nontrivial steady state at $\bar{R} = 0.5$ and $\bar{N} = 0.5$. The trajectory starting at $\bar{R} = 0.55$ and $\bar{N} = 0.5$ spirals into the steady state. Panel (b) depicts for this trajectory the distances $h_R = 0.5 - R$ (red) and $h_N = 0.5 - R$ (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 $e = 0.5$.

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 $\alpha = \mathrm{tr}/2 < 0$. For complex eigenvalues stability is therefore guaranteed when the trace is negative (see Fig. 5.1).

7.2 Example: the Lotka Volterra model

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

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

as the nontrivial steady state, with 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

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

implying that

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

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 of $1/\beta$ time units. 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 intro 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 $N(0) = 0.5$. The corresponding eigenvectors are

$$\mathbf{v_1} = \begin{pmatrix} 0.5 \\ -0.5 - \lambda_1 \end{pmatrix} = \begin{pmatrix} 0.5 \\ -0.25 - \mathrm{i}0.43 \end{pmatrix} \quad \text{and} \quad \mathbf{v_2} = \begin{pmatrix} 0.5 \\ -0.5 - \lambda_2 \end{pmatrix} = \begin{pmatrix} 0.5 \\ -0.25 + \mathrm{i}0.43 \end{pmatrix} .$$

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

$$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = \mathrm{e}^{-0.25t} \left[C_1 \mathbf{v_1} (\cos 0.43t + \mathrm{i} \sin 0.43t) + C_2 \mathbf{v_2} (\cos 0.43t - \mathrm{i} \sin 0.43t) \right] ,$$

or

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

Similarly, using $\mathrm{i}^2 = -1$, we obtain

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

For the initial condition, where $t = 0$, $\mathrm{e}^{-0.25t} = 1$, $\cos 0.43t = 1$, 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 $y(0) = 0 = \mathrm{i}0.43(C_2 - C_1) - 0.25(C_1 + C_2)$. Together, this delivers $C_1 = 0.05 + \mathrm{i}0.029$ and $C_2 = 0.05 - \mathrm{i}0.029$. Substituting these two constants into Eq. (7.14) and Eq. (7.15) gives

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

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

7.3 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**. $-a/b$ and $-c/d$ respectively.
   b. When the lines are parallel to each other they will never intersect, i.e., when $a/b = c/d$ or $ad = bc$, there is no solution.
   c. p and q are absent from the slopes.

2. **a**. The matrix $A = \left(\begin{smallmatrix} -2 & 1 \\ 1 & -2 \end{smallmatrix}\right)$ has $\mathrm{tr}(A) = -4$ and $\det(A) = 3$ such that $\lambda^2 - \mathrm{tr}\lambda + \det = \lambda^2 + 4\lambda + 3 = (\lambda+3)(\lambda+1) = 0$ giving $\lambda_1 = -1$ with $\mathbf{v_1} = k\left(\begin{smallmatrix} -1 \\ -2-(-1) \end{smallmatrix}\right) = k\left(\begin{smallmatrix} -1 \\ -1 \end{smallmatrix}\right)$, and $\lambda_2 = -3$ with $\mathbf{v_2} = k\left(\begin{smallmatrix} -1 \\ -2-(-3) \end{smallmatrix}\right) = k\left(\begin{smallmatrix} -1 \\ 1 \end{smallmatrix}\right)$, where k is an arbitrary constant.
   b. The matrix $A = \left(\begin{smallmatrix} 1 & 4 \\ 1 & 1 \end{smallmatrix}\right)$ has $\mathrm{tr}(A) = 2$ and $\det(A) = -3$ such that

$$\lambda_{1,2} = \frac{2 \pm \sqrt{2^2 + 4 \times 3}}{2} = \frac{2 \pm \sqrt{16}}{2} = \frac{2 \pm 4}{2} = 1 \pm 2 \ ,$$

   For $\lambda_1 = -1$ one obtains $\mathbf{v_1} = k\left(\begin{smallmatrix} -4 \\ 1-(-1) \end{smallmatrix}\right) = k\left(\begin{smallmatrix} -4 \\ 2 \end{smallmatrix}\right)$ or $\mathbf{v_1} = k\left(\begin{smallmatrix} -2 \\ 1 \end{smallmatrix}\right)$, and for $\lambda_2 = 3$ one obtains $\mathbf{v_2} = k\left(\begin{smallmatrix} -4 \\ 1-3 \end{smallmatrix}\right) = k\left(\begin{smallmatrix} -4 \\ -2 \end{smallmatrix}\right)$ or $\mathbf{v_2} = k\left(\begin{smallmatrix} -2 \\ -1 \end{smallmatrix}\right)$, where k is an arbitrary constant.
   c. The matrix $A = \left(\begin{smallmatrix} a & b \\ 0 & d \end{smallmatrix}\right)$ is in a diagonal form and hence the eigenvalues correspond to its diagonal elements (see also Chapter 5). This can be checked by seeing that the characteristic equation simplifies into $(d-\lambda)(a-\lambda) - 0 = 0$, immediate giving the two solutions, $\lambda_1 = a$ and $\lambda_2 = d$, which are indeed the diagonal elements of the matrix. For the eigenvectors we fill in $\mathbf{v_1} = k\left(\begin{smallmatrix} -b \\ a-\lambda_1 \end{smallmatrix}\right) = k\left(\begin{smallmatrix} -b \\ 0 \end{smallmatrix}\right)$ and $\mathbf{v_2} = k\left(\begin{smallmatrix} -b \\ a-\lambda_2 \end{smallmatrix}\right) = k\left(\begin{smallmatrix} -b \\ a-d \end{smallmatrix}\right)$

3. **a**. Yes the forest will approach the eigenvector corresponding to the dominant eigenvalue for every initial condition except $\vec{V_0} = (0\ 0\ 0\ 0)$.
   b. The latter illustrates that a forest not a containing a particular species should also not have that species in its climax state. Thus, the model assumes that all species are present, which here is a natural assumption because all species were counted as saplings in the original data matrix.

4. **a**. $\begin{pmatrix} 2 & -4 \\ 1 & 1 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} 3 \\ 1 \end{pmatrix}$, $\det = 2 \times 1 - (-4) \times 1 = 2 + 4 = 6$. So this has a solution.

Exercises Chapter 3

1. The eigenvalues of matrix of this system of ODEs are solved from $\lambda^2 - \mathrm{tr}\lambda + \det = \lambda^2 - 9\lambda + 18 = (\lambda - 6)(\lambda - 3) = 0$ 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

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

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

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

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:

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

from which we see that the system moves along the first eigenvector (which is due to the fact that we started on the first eigenvector with the initial condition $x(0) = 3$ and $y(0) = -3$). The origin is unstable and from this initial condition the system moves to infinitely large values of x and infinitely negative values of y.

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

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

Finding the eigenvalues $\lambda^2 - \mathrm{tr}\lambda + \det = \lambda^2 + 0.05\lambda = \lambda(\lambda + 0.05) = 0$ so $\lambda_1 = 0$ and $\lambda_2 = -0.05$. The fact that the largest eigenvalue is zero, immediately reveals that the steady state has neutral stability. The eigenvectors are

$$\mathbf{v_1} = k \begin{pmatrix} -0.01 \\ -0.01 - 0 \end{pmatrix} = k \begin{pmatrix} -0.01 \\ -0.01 \end{pmatrix} \quad \text{or} \quad \mathbf{v_1} = k \begin{pmatrix} 1 \\ 1 \end{pmatrix} ,$$

and

$$\mathbf{v_2} = k \begin{pmatrix} -0.01 \\ -0.01 - (-0.05) \end{pmatrix} = k \begin{pmatrix} -0.01 \\ 0.04 \end{pmatrix} \quad \text{or} \quad \mathbf{v_2} = k \begin{pmatrix} -1 \\ 4 \end{pmatrix} ,$$

where k is an arbitrary constant. The general solution is

$$\begin{pmatrix} A(t) \\ B(t) \end{pmatrix} = C_1 \begin{pmatrix} 1 \\ 1 \end{pmatrix} \mathrm{e}^{0t} + C_2 \begin{pmatrix} -1 \\ 4 \end{pmatrix} e^{-0.05t} = C_1 \begin{pmatrix} 1 \\ 1 \end{pmatrix} + C_2 \begin{pmatrix} -1 \\ 4 \end{pmatrix} \mathrm{e}^{-0.05t} .$$

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

$$\begin{pmatrix} 3 \\ 0 \end{pmatrix} = C_1 \begin{pmatrix} 1 \\ 1 \end{pmatrix} + C_2 \begin{pmatrix} -1 \\ 4 \end{pmatrix} \mathrm{e}^{-0.05\times 0} = C_1 \begin{pmatrix} 1 \\ 1 \end{pmatrix} + C_2 \begin{pmatrix} -1 \\ 4 \end{pmatrix} ,$$

and writes $3 = C_1 - C_2$ or $C_1 = 3 + C_2$, and $0 = C_1 + 4C_2$. Substituting the first into the second equation gives $0 = 3 + 5C_2$ meaning that $C_2 = -3/5 = -0.6$ and hence that $C_1 = 2.4$. Thus, the solution of the initial value problem is

$$\begin{pmatrix} A(t) \\ B(t) \end{pmatrix} = 2.4 \begin{pmatrix} 1 \\ 1 \end{pmatrix} - 0.6 \begin{pmatrix} -1 \\ 4 \end{pmatrix} \mathrm{e}^{-0.05t}$$

b. Because ultimately $\mathrm{e}^{-0.05t} \to 0$, the final state is given by $A = B = 2.4$ moles/liter, which makes sense because the diffusion should lead to equal concentrations. The total amount in the final state, $(20 + 5) \times 2.4 = 60$ moles is equal to that of the initial condition, $20 \times 3 = 60$ moles.

c. No, since the largest eigenvalue is zero, the system is not stable to perturbations. Instead, every other initial condition leads to another steady state.

Exercises Chapter 4

1. **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.

2. Note that $f(1, 1) = 2$, that $\partial_x f = 2x$, which in $(1, 1)$ also equals 2, and that $\partial_y f = 2y$ which in $(1, 1)$ also equals 2. Hence $f(x, y) \simeq 2+2(x-1)+2(y-1) = 2+2x-2+2y-2 = -2 + 2x + 2y$.

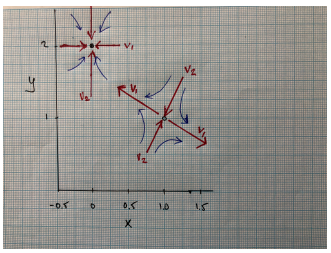
3. **a**. Solving $\mathrm{d}x/\mathrm{d}t = -4y = 0$ gives $y = 0$, and substituting this into $\mathrm{d}y/\mathrm{d}t$ gives $4x - x^2 = x(4 - x) = 0$, having two solutions, $x = 0$ and $x = 4$. Thus, there are two equilibria $(\bar{x}, \bar{y}) = (0, 0)$ and $(4, 0)$. For the Jacobian we first define the partial derivatives $J = \begin{pmatrix} \partial_x f = 0 & \partial_y f = -4 \\ \partial_x g = 4 - 2\bar{x} & \partial_y g = -0.5 \end{pmatrix}$. For $(\bar{x}, \bar{y}) = (0, 0)$ one obtains $J_1 = \begin{pmatrix} 0 & -4 \\ 4 & -0.5 \end{pmatrix}$, and for $(\bar{x}, \bar{y}) = (4, 0)$ one finds $J_2 = \begin{pmatrix} 0 & -4 \\ -4 & -0.5 \end{pmatrix}$. You may like to draw the nullclines and compute the eigenvalues with the first model in the Grind script `exercise4.3.R`.
   b. Solving $\mathrm{d}y/\mathrm{d}t = x - y = 0$ gives $x = y$, and substituting this into $\mathrm{d}x/\mathrm{d}t = 0$ gives $9x + x^2 = x(9 + x) = 0$, having two solutions, $x = 0$ and $x = -9$. Thus, there are two equilibria $(0, 0)$ and $(-9, -9)$. For the Jacobian we first define the partial derivatives $J = \begin{pmatrix} \partial_x f = 9 & \partial_y f = 2\bar{y} \\ \partial_x g = 1 & \partial_y g = -1 \end{pmatrix}$. Hence, for the steady state $(\bar{x}, \bar{y}) = (0, 0)$ one obtains $J = \begin{pmatrix} 9 & 0 \\ 1 & -1 \end{pmatrix}$, and for $(\bar{x}, \bar{y}) = (-9, -9)$ one finds $J = \begin{pmatrix} 9 & -18 \\ 1 & -1 \end{pmatrix}$. You may like to draw the nullclines and compute the eigenvalues with the second model in the Grind script `exercise4.3.R`.
   c. Solving $\mathrm{d}x/\mathrm{d}t = 2x - xy = x(2 - y) = 0$ gives $x = 0$ or $y = 2$. Substituting $x = 0$ into $\mathrm{d}y/\mathrm{d}t = 0$ gives $-y = 0$ or $y = 0$. Substituting $y = 2$ into $\mathrm{d}y/\mathrm{d}t = 0$ gives $-2 + 4x = 0$ so $x = 0.5$. Thus, the equilibria are $(0, 0)$ and $(0.5, 2)$. For the Jacobian we first define the partial derivatives $J = \begin{pmatrix} \partial_x f = 2 - \bar{y} & \partial_y f = -\bar{x} \\ \partial_x g = \bar{y}^2 & \partial_y g = -1 + 2\bar{x}\bar{y} \end{pmatrix}$. meaning that in $(\bar{x}, \bar{y}) = (0, 0)$ the Jacobian $J = \begin{pmatrix} 2 & 0 \\ 0 & -1 \end{pmatrix}$, whereas in the other steady state, $(\bar{x}, \bar{y}) = (0.5, 2)$, one finds $J = \begin{pmatrix} 0 & -0.5 \\ 4 & 1 \end{pmatrix}$. You may like to draw the nullclines and compute the eigenvalues with the third model in the Grind script `exercise4.3.R`.

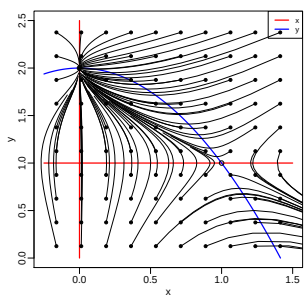
4. See Eq. (6.11) in Chapter 6.

Exercises Chapter 5

1. Because these are linear systems $(\bar{x}, \bar{y}) = (0, 0)$ is the steady state.
   a. Here (0,0) is not a saddle point because $\det = 3 \times 6 - 1 \times -20 = 38 > 0$, it is unstable because $\mathrm{tr} = 3 + 6 = 9 > 0$, and because $D = \mathrm{tr}^2 - 4\det = 9^2 - 4 \times 38 = 81 - 152 = -71 < 0$, the eigenvalues are complex numbers, and this has to be an unstable spiral.
   b. Here (0,0) is a saddle point because $\det = 2 \times -10 - 1 \times 2 = -20 - 2 = -22 < 0$.
   c. Here (0,0) is also a saddle point because $\det = 2 \times -2 - 1 \times 5 = -4 - 5 = -9 < 0$.

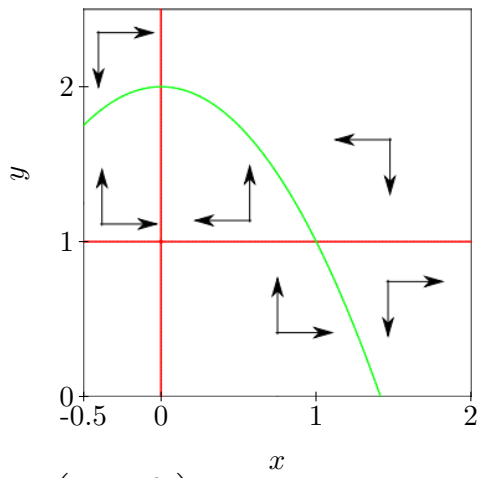
2. **a**. Solving $\mathrm{d}x/\mathrm{d}t = 2x(1 - y) = 0$ gives $x = 0$ or $y = 1$. First substitute $x = 0$ into $\mathrm{d}y/\mathrm{d}t$ to find that $\mathrm{d}y/\mathrm{d}t = 2 - y = 0$, which gives $y = 2$. Next substitute $y = 1$ in $\mathrm{d}y/\mathrm{d}t$ to find that $\mathrm{d}y/\mathrm{d}t = 2 - 1 - x^2 = 1 - x^2 = 0$, 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 $x \geq 0$.
   b. Defining $f(x, y) = 2x(1 - y)$ 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 $J = \begin{pmatrix} 2(1-\bar{y}) & -2\bar{x} \\ -2\bar{x} & -1 \end{pmatrix}$.
   c. For the steady state $(\bar{x}, \bar{y}) = (0, 2)$ one obtains $J = \begin{pmatrix} -2 & 0 \\ 0 & -1 \end{pmatrix}$ with $\det = (-2 \times -1) - 0 = 2 > 0$ and $\mathrm{tr} = -2 - 1 = -3 < 0$. This point is stable, and because $D = \mathrm{tr}^2 - 4\det = 9 - 4 \times 2 = 9 - 8 = 1 > 0$ it is a stable node. For the equilibrium $(1, 1)$ we obtain $J = \begin{pmatrix} 0 & -2 \\ -2 & -1 \end{pmatrix}$ with $\mathrm{tr} = -1$ and $\det = (0 \times -1) - (-2 \times -2) = -4 < 0$, implying that it is a saddle point (which is always unstable).
   d. To sketch the phase portrait we compute for the steady state $(0, 2)$ that $\lambda_1 = -2$ and $\lambda_2 = -1$, with corresponding eigenvectors $(1, 0)$ and $(0, 1)$, respectively. Thus, the two stable directions are horizontal and vertical, respectively. For the second steady state $(1, 1)$ one obtains the unstable largest $\lambda_1 = (-1+\sqrt{17})/2 \simeq 1.56$ and the stable smallest $\lambda_2 = (-1 - \sqrt{17})/2 \simeq -2.56$. The corresponding eigenvectors, $v_1 = ((-1 - \sqrt{17})/2, 2)$ or $v_1 = ((-1 - \sqrt{17})/4, 1) \simeq (-1.28, 1)$ and $v_2 = ((-1 + \sqrt{17})/2, 2)$ or $v_2 = ((-1 + \sqrt{17})/4, 1) \simeq (0.78, 1)$ reveal that the unstable direction is a line with a negative slope (of about -0.78), and that the stable direction is a line with a slope of 1.28. Sketching these eigenvectors as red signed arrows around the two steady state reveals the following phase portrait:





where the blue arrows are trajectories, and the second picture was made with the Grind model `exercise5.2.R`.

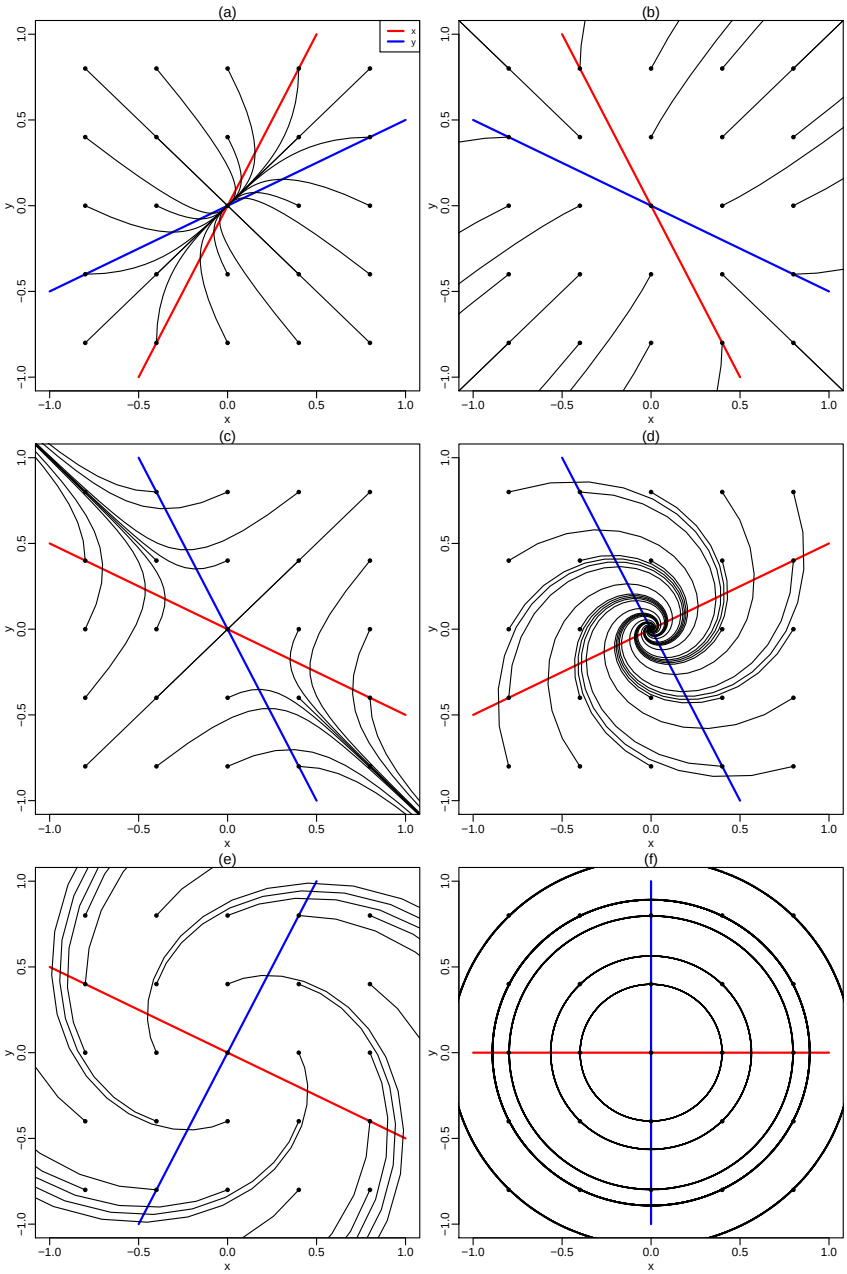
3. **a**. $\mathrm{d}x/\mathrm{d}t = 2x(1 - y) = 0$ gives $x = 0$ or $y = 1$ as the $x' = 0$ nullclines, and $\mathrm{d}y/\mathrm{d}t = 2 - y - x^2 = 0$ gives $y = 2 - x^2$ as the $y' = 0$ nullcline. Having no free parameters we can simply fill in numbers here. Let us fill in $x = 2$ and $y = 2$. This gives $\mathrm{d}x/\mathrm{d}t = 2 \times 2(1 - 2) = 4 \times -1 = -4$ so the vector field points leftward ($\leftarrow$) and $\mathrm{d}y/\mathrm{d}t = 2 - 2 - 2^2 = -4$ 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 $\det = -\alpha \times -\gamma - 0 \times 0 = \alpha \times \beta > 0$, 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.

4. The model `linear.R` illustrates all cases by making the following figure:



a. To make a stable node we need to have a tr < 0, det > 0, and discriminant, $D > 0$. The first is guaranteed if both diagonal elements, a and d, are negative. Since we require $ad - bc > 0$ we make the absolute values of a and d relatively large, which also helps the $D = \text{tr}^2 - 4\det > 0$ condition. This is all satisfied when $a = -2, b = 1, c = 1$ and $d = -2$ (see Panel (a)). The script provides a function `algebra` that calculates the eigenvalues and eigenvectors.

b. To make an unstable node we need to have a tr > 0, det > 0, and discriminant, $D > 0$, and just reverse the sign of the diagonal elements, i.e., $a = 2, b = 1, c = 1$ and $d = 2$ (see Panel (b)).

c. To make a saddle point we need det < 0, so we need sufficiently small diagonal elements, e.g., $a = -1, b = -2, c = -2$, and $d = -1$ (see Panel (c)).

d. To make a stable spiral point we need a tr < 0, det > 0, and discriminant, $D < 0$. This can be achieved by having a small trace due to small diagonal elements and a large determinant by setting $c = -2$, i.e., $a = -1, b = 2, c = -2$ and $d = -1$ (see Panel (d)).

e. To make a stable spiral point we need a tr > 0, det > 0, and discriminant, $D < 0$, which can be achieved by reversing the sign of diagonal elements, i.e., $a = 1, b = 2, c = -2$ and $d = 1$ (see Panel (e)).

f. A neutrally stable center point is obtained when tr $= 0$, det > 0, and discriminant, $D < 0$, which is achieved by setting the diagonal elements to zero, i.e., $a = 0, b = 2, c = -2$ and $d = 0$ (see Panel (f)).

Exercises Chapter 6

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

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

with 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

$$\lambda_{\pm} \quad = \quad \pm \frac{\sqrt{-4ae}}{2} \quad = \quad \pm \, \mathrm{i} \, \sqrt{ae} \, .$$

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 tr $= 2$ and det $= 2$ we obtain

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

For $\lambda_1 = -1 + \mathrm{i}$ we obtain

$$\mathbf{v_1} = k \begin{pmatrix} -b \\ a - \lambda_1 \end{pmatrix} = k \begin{pmatrix} -5 \\ -1 - (1 + \mathrm{i}) \end{pmatrix} = k \begin{pmatrix} -5 \\ -2 - \mathrm{i} \end{pmatrix} = k \begin{pmatrix} -5 \\ -2 \end{pmatrix} - \mathrm{i}k \begin{pmatrix} 0 \\ 1 \end{pmatrix} ,$$

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

$$\mathbf{v_2} = k \begin{pmatrix} -5 \\ -1 - (1 - \mathrm{i}) \end{pmatrix} = k \begin{pmatrix} -5 \\ -2 \end{pmatrix} + \mathrm{i}k \begin{pmatrix} 0 \\ 1 \end{pmatrix} ,$$

where k is an arbitrary real number.

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