Mathematical Methods in Biology
Part 3: Vectors and matrices

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1 Introduction: A need for matrices

Learning matrix algebra is a major step towards biological modelling. Most biological models involve several variables: concentrations of various substances, frequencies of multiple alleles, numbers of individuals of different ages, states or species. There are countless many more examples where a number of variables change simultaneously. Multivariate models are much richer and more interesting than models of a single variable, and to analyse models with several variables beyond the elementary insights discussed in Part 1, matrix algebra is indispensable.

There is however a learning difficulty at this step. To start analysing multivariate models, one needs to master matrix algebra; and matrix algebra needs some time to learn. Matrix algebra is not particularly difficult, but at some intermediate stages it is not immediately obvious how particular bits of matrix algebra will be useful. In other words, the student sometimes needs to go on the good faith that soon we arrive at something of practical value. As before, we shall make every effort to learn the necessary mathematics via biological applications wherever it is possible.

As an introduction, we construct a few matrix models to illustrate why matrices are indispensable when studying models with several variables. The main direct applications of matrix algebra concern models in discrete time, and in the rest of this part of the course we shall analyse discrete-time models in more detail. However, in the present introductory chapter we also construct continuous-time models to show the same principles in both kinds of models. The continuous-time dynamics we shall investigate in Part 4.

1.1 Allele frequencies under mutation

We start with a discrete-time model which is simple enough to analyse without matrices, and then generalise the same problem to more variables which makes it necessary to use matrices. The next section will consider an analogous model in continuous time, again first without and then with matrices.

Consider a population with discrete generations where two alleles (A_1 and A_2) segregate in a locus. In every generation, each copy of allele A_1 mutates into A_2 with probability μ, whereas A_2 mutates into A_1 with probability ν:

$$A_1 \underset{\nu}{\overset{\mu}{\rightleftharpoons}} A_2$$

We assume that population size is constant, and therefore the total number of alleles, N, is the same in every generation. Denote the frequency of allele A_1 in generation t with p_t, such that the population harbours $p_t N$ copies of A_1 and $(1-p_t)N$ copies of A_2 at time t.

Assume that N is large enough so that stochastic variation in the number of alleles in the next generation (often referred to as genetic drift) can be neglected. How does p_t change from generation to generation under the force of mutation?

To calculate p_{t+1}, notice that an allele can be of type A_1 in the next generation for two reasons: either it was originally (in generation t) A_1 and did not mutate (i.e., remained A_1), or it was originally A_2 and mutated to become A_1. The former route produces $p_t N(1-\mu)$ copies of A_1, where $p_t N$ is the number of original A_1 alleles and a fraction $1-\mu$ of those will not mutate. The latter route gives $(1-p_t)N \cdot \nu$ copies of A_1 because of the original $(1-p_t)N$ alleles of type A_2, a fraction ν mutates and becomes A_1. Hence the number of A_1 alleles in generation $t+1$, $p_{t+1}N$, is given by $p_{t+1}N = (1-\mu)p_t N + \nu(1-p_t)N$; and after dividing with the constant N, we obtain

$$p_{t+1} = (1-\mu)p_t + \nu(1-p_t) \tag{1}$$

> In the probabilistic terms used in Part 2, μ and ν are conditional probabilities. μ is the probability that an allele will be A_2 in the next generation given that it is A_1 now; i.e., $\mu = P(A_2|A_1)$. The conditional probability that the allele will be A_1 if it is now A_1 is the probability that A_1 does not mutate, i.e., $1-\mu = P(A_1|A_1)$. Similarly, $\nu = P(A_1|A_2)$ and $1-\nu = P(A_2|A_2)$. Rewriting equation (1) with the notation of conditional probabilities gives $p_{t+1} = P(A_1|A_1)p_t + P(A_1|A_2)(1-p_t)$, which the reader will recognise as the law of total probability for having A_1 in the next generation.

To find the equilibrium of the mutational process, we set $p_{t+1} = p_t = p$ in equation (1),

$$p = (1-\mu)p + \nu(1-p)$$

and solve this equation for the equilibrium allele frequency

$$p = \frac{\nu}{\mu + \nu} \tag{2}$$

If A_1 denotes a functional allele and A_2 includes all its nonfunctional mutant varieties, then ν is typically much smaller than μ because it is easy to make a mistake when replicating the gene sequence but it is much less likely that a random mutation repairs a mistake and restores functionality. Therefore, under mutations only, the frequency of the functional allele would be small ($\nu \ll \mu$ implies $p = \nu/(\mu+\nu) \approx \nu/\mu \ll 1$). In reality, functional alleles are maintained at high frequencies by natural selection (which is not included in equation (1)).

How do we generalize the above model for more than two alleles? Many loci have a number of phenotypically distinguishable alleles (for example, in the AB0 blood group system there are three alleles, A, B and 0), and DNA sequencing uncovers a huge number of allele varieties. Crudely grouping the different sequences such as "functional" and "non-functional" is actually not accurate; for example there are many possible errors that destroy functionality and some are easier to restore than others, i.e., the back mutation

rate ν is not the same for each non-functional allele.

Suppose thus that there are n alleles segregating in a locus $(A_1, ..., A_n)$, and each can mutate into each other (or if not, then we set some of the mutation probabilities to 0). Let p_i denote the frequency of allele A_i (where i can be any of the numbers $1, ..., n$). As before, the sum of all allele frequencies must add up to 1, i.e., we have $p_1 + p_2 + ... + p_n = 1$, or the same in more concise notation,

$$\sum_i p_i = 1$$

This means that we could express one of the frequencies with all the others; for example, we could substitute p_n with $p_n = 1 - (p_1 + ... + p_{n-1})$, and therefore we could work with only $p_1, ..., p_{n-1}$. This was useful in the case of only two alleles, where we obtained the frequency of A_2 as $1 - p$ and therefore could work with only one variable, p. With three or more alleles, however, the reduction by one variable is no real help in practice, and it is actually better to avoid singling out p_n from among the variables (in a more mathematical language, don't break the symmetry of the problem by treating some allele(s) differently from others).

We need new notation also for the mutation probabilities. As the number of alleles n increases, the number of possible mutations explodes [it equals $n^2 - n$], and it is not practical to assign a separate letter to each of them. Instead, let q_{ij} denote the probability that A_j mutates into A_i. Notice the order of indices: the *second* index j shows the original allele and the *first* index i is the new allele (the indices show the allele's identity "backwards" in time). q_{ii} (where the two indices are the same) is the probability that A_i produces A_i, i.e., that there was no mutation. More generally (i.e. also outside the context of genetics and mutations), the probabilities q_{ij} are called *transition probabilities*.

> In the two-allele example above, the probability that A_1 mutates into A_2 is μ and hence in the new notation $q_{21} = \mu$. q_{11} is the probability that A_1 remains A_1, i.e., $q_{11} = 1 - \mu$. Similarly, $q_{12} = \nu$ and $q_{22} = 1 - \nu$. The transition probabilities q_{ij} are precisely the same as the conditional probabilities $P(i|j)$, $q_{ij} = P(i|j)$. The sum $\sum_i q_{ij}$ is the sum of probabilities that A_j becomes A_1 or A_2 etc. up to A_n. Because A_j certainly becomes one of the possible alleles $A_1, ..., A_n$, we have $\sum_i q_{ij} = 1$.

We can now write down the frequencies of all n alleles in the next generation analogously to equation (1). Denoting the next generation with a prime (because the sub-index is now used to denote the identity of the allele), the equations for three alleles ($n = 3$) are

$$\begin{aligned} p_1' &= q_{11}p_1 + q_{12}p_2 + q_{13}p_3 \\ p_2' &= q_{21}p_1 + q_{22}p_2 + q_{23}p_3 \\ p_3' &= q_{31}p_1 + q_{32}p_2 + q_{33}p_3 \end{aligned} \tag{3}$$

Exercise: Expand these equations to the case of five alleles ($n = 5$).

With n more than only very few, the equations analogous to (3) become unwidely. When these equations are used e.g. to find the equilibrium allele frequencies, the results are not transparent simple formulas as equation (2) above, but complicated expressions that depend on the many transition probabilities. It is therefore imperative to simplify notation, find the structure of the problem, and study all problems with the same structure in one go independently of the particulars such as the exact value of n.

We therefore introduce a *vector* as a "list" of all variables. With three alleles we have the three variables p_1, p_2, p_3 and the corresponding vector is

$$\mathbf{p} = \begin{pmatrix} p_1 \\ p_2 \\ p_3 \end{pmatrix}$$

With n alleles, the vector has length n:

$$\mathbf{p} = \begin{pmatrix} p_1 \\ p_2 \\ \vdots \\ p_n \end{pmatrix}$$

The boldface notation[1] $\mathbf{p}$ reminds that the symbol means a vector, not just a number (although this is often omitted in more mathematical texts).

The transition probabilities we collect into a *matrix*, which is "table" of n rows and n columns; the ith row of the jth column contains the transition probability q_{ij}. For three alleles, the matrix of transition probabilities is

$$\mathbf{Q} = \begin{pmatrix} q_{11} & q_{12} & q_{13} \\ q_{21} & q_{22} & q_{23} \\ q_{31} & q_{32} & q_{33} \end{pmatrix}$$

whereas for n alleles, it is

$$\mathbf{Q} = \begin{pmatrix} q_{11} & \cdots & q_{1n} \\ \vdots & \ddots & \vdots \\ q_{n1} & \cdots & q_{nn} \end{pmatrix}$$

The boldface[2] capital is a reminder of a matrix. If the number of rows and columns is the same (as here), the matrix is a *square matrix*. Square matrices are the most common, and in this course we focus on them (even though one might note that an n-vector is actually a matrix with n rows and a single column, i.e., an $n \times 1$ matrix).

[1] in handwriting, one can underline the symbol of a vector

[2] in handwriting, the symbol of a matrix is twice underlined

As noted above, our matrix $\mathbf{Q}$ has the property that $\sum_i q_{ij} = 1$ for each choice of j, i.e., that each column of the matrix sums to 1. Such matrices are called *stochastic matrices*; they usually contain transition probabilities as in the present example.

Next, we need to know how to multiply a matrix and a vector. The result of such a multiplication is a new vector. To calculate the *first* element of the result vector, do the following using the *first* row of the matrix: multiply the 1st element in the row with the 1st element of the vector; to this, add the product of the 2nd element in the row and the 2nd element of the vector; to this, add the product of the 3rd element in the row and the 3rd element of the vector; and so on till the end of the row and of the vector. (If they do not have the same length, then the multiplication is not possible.) This sum of the products is the first element of the result vector. To obtain the second element of the result vector, do the same but using the second row of the matrix; and so on (see Figure 1). The result vector has as many elements as many rows the matrix has. An $n \times n$ square matrix can thus be multiplied with a vector of length n, and the result is again an n-vector.

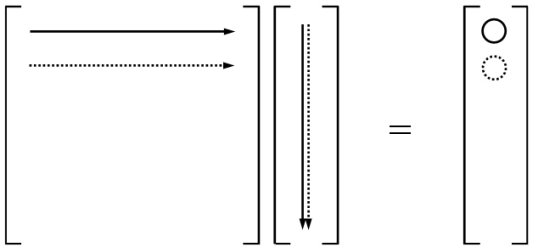

Figure 1: Multiplication of a matrix with a vector. The result is the vector on the right hand side. To obtain its first element, go through the first row of the matrix and through the vector; multiply the matching elements of the matrix and of the vector; add up these products. To obtain the second element of the result vector, do the same using the second row of the matrix; etc.

We write out the product $\mathbf{Qp}$ for the case $n = 3$:

$$\begin{bmatrix} q_{11} & q_{12} & q_{13} \\ q_{21} & q_{22} & q_{23} \\ q_{31} & q_{32} & q_{33} \end{bmatrix} \begin{pmatrix} p_1 \\ p_2 \\ p_3 \end{pmatrix} = \begin{pmatrix} q_{11}p_1 + q_{12}p_2 + q_{13}p_3 \\ q_{21}p_1 + q_{22}p_2 + q_{23}p_3 \\ q_{31}p_1 + q_{32}p_3 + q_{33}p_3 \end{pmatrix}$$

Notice that the vector on the right hand side contains p'_1, p'_2, p'_3 as given in equations (3)! Hence we can calculate the allele frequencies of the next generation as

$$\begin{pmatrix} p'_1 \\ p'_2 \\ p'_3 \end{pmatrix} = \begin{bmatrix} q_{11} & q_{12} & q_{13} \\ q_{21} & q_{22} & q_{23} \\ q_{31} & q_{32} & q_{33} \end{bmatrix} \begin{pmatrix} p_1 \\ p_2 \\ p_3 \end{pmatrix}$$

or more concisely,

$$\mathbf{p}' = \mathbf{Q}\mathbf{p} \quad \text{or} \quad \mathbf{p}_{t+1} = \mathbf{Q}\mathbf{p}_t \tag{4}$$

The rules of matrix multiplication may first seem somewhat arcane, but as this example illustrates, matrix multiplication is defined in the way as it proves useful.

In this model, the elements of matrix $\mathbf{Q}$ are constants. The transition probabilities (or conditional probabilities of having A_i in the next generation if we have A_j now) do not depend on the history of the alleles; A_j mutates into A_i with a fixed probability no matter from which other allele A_j might have arisen in the past. The vector $\mathbf{p}_t$ therefore gives a complete description of the system at time t, sufficient to predict its future $\mathbf{p}_{t+1}$ without reference to the past.

1.2 Conformational states of molecules

A piece of cell membrane has a given number N of transmembrane channels, which may be either open or closed. Open channels (denoted by A_1) close at rate α, whereas closed channels (A_2) open at rate β. This reaction scheme

$$A_1 \underset{\beta}{\overset{\alpha}{\rightleftharpoons}} A_2$$

is analogous to the forward-backward mutations between two alleles in section (1.1), except that this molecular dynamics plays out in continuous time (as opposed to the discrete generations we assumed in the mutation model). Accordingly, α and β are rates and not probabilities (cf. Part 1).

Denote the number of open channels by n_1 and the number of closed channels by n_2. The dynamics of open and closed channels is given by

$$\begin{aligned} \frac{dn_1}{dt} &= -\alpha n_1 + \beta n_2 \\ \frac{dn_2}{dt} &= \alpha n_1 - \beta n_2 \end{aligned}$$

The sum of these two equations is obviously zero:

$$\frac{dn_1}{dt} + \frac{dn_2}{dt} = -\alpha n_1 + \beta n_2 + \alpha n_1 - \beta n_2 = 0$$

and this is because the total number of membrane channels, $n_1 + n_2 = N$, does not change with time. One of the two differential equations is superfluous; the two equations

don't give independent information and if we know n_1 at some time, we immediately have $n_2 = N - n_1$ at the same time. We can thus continue with using only the first equation and substituting $n_2 = N - n_1$ into it:

$$\frac{dn_1}{dt} = -\alpha n_1 + \beta(N - n_1)$$

If we like, we can also divide this equation with N. If we define $p = n_1/N$ to be the fraction of open channels, then we obtain

$$\frac{dp}{dt} = -\alpha p + \beta(1 - p) \tag{5}$$

To compare with the mutation model, note that the above equation gives the change of p whereas equation (1) gives its value next year. In continuous time, there is no "next" time step. Expressing the change of p also from equation (1), we obtain $p_{t+1} - p_t = -\mu p_t + \nu(1 - p_t)$, which is directly analogous to equation (5). To find the equilibrium of the opening-closing process, we set the change in equation (5) to zero and solve for the equilibrium fraction of open channels:

$$\begin{aligned} -\alpha p + \beta(1 - p) &= 0 \\ p &= \frac{\beta}{\alpha + \beta} \end{aligned}$$

This is again analogous to the equilibrium allele frequency of the mutation model in equation (2).

How do we generalize this continuous-time model to n conformational states of a biomolecule? Let us take $n = 3$ for illustration, and, as before, let the vector

$$\mathbf{p} = \begin{pmatrix} p_1 \\ p_2 \\ p_3 \end{pmatrix}$$

contain the fractions of molecules in the first, second, and third conformational state. Furthermore, let k_{ij} denote the transition rate at which a molecule in state j switches to state i (notice again the "backward" notation, the second index marks the initial state). The equations describing the dynamics are

$$\begin{aligned} \frac{dp_1}{dt} &= -(k_{21} + k_{31})p_1 + k_{12}p_2 + k_{13}p_3 \\ \frac{dp_2}{dt} &= k_{21}p_1 - (k_{12} + k_{32})p_2 + k_{23}p_3 \\ \frac{dp_3}{dt} &= k_{31}p_1 + k_{32}p_2 - (k_{13} + k_{23})p_3 \end{aligned}$$

where the sum $(k_{21} + k_{31})$ in the first equation is the rate at which molecules quit state 1 by going either to state 2 or to state 3; the other equations have analogous terms. These

equations can be written as

$$\frac{d\mathbf{p}}{dt} = \mathbf{K}\mathbf{p} \tag{6}$$

where the derivative on the left hand side is the vector of the derivatives,

$$\frac{d\mathbf{p}}{dt} = \begin{pmatrix} dp_1/dt \\ dp_2/dt \\ dp_3/dt \end{pmatrix}$$

and the matrix of the transition rates is

$$\mathbf{K} = \begin{pmatrix} -(k_{21}+k_{31}) & k_{12} & k_{13} \\ k_{21} & -(k_{12}+k_{32}) & k_{23} \\ k_{31} & k_{32} & -(k_{13}+k_{23}) \end{pmatrix}$$

Exercise: Check that $\mathbf{K}\mathbf{p}$ indeed gives the derivative $d\mathbf{p}/dt$ correctly.

Exercise: Each column of matrix $\mathbf{K}$ sums to 0; explain why.

Exercise: Compare the matrix of transition probabilities $\mathbf{Q}$ in the discrete-time model with the matrix of transition rates $\mathbf{K}$ in the continuous-time model.

1.3 Growth of a structured population

Both of our previous examples described transitions between a number of states assuming that the total number of "individuals" (alleles or molecules) is constant. Here we investigate an example where it is not so. In part 1, we have studied the simplest model of population growth,

$$\frac{dN}{dt} = (b-d)N \tag{7}$$

where N is the number of individuals and b and d are respectively the birth and death rates. This equation predicts exponential population growth when the growth rate $(b-d)$ is positive, and exponential decline towards extinction if the growth rate is negative.

As discussed in Part 1, sustained exponential growth is ecologically unrealistic. A small initial population may however exhibit (approximately) exponential growth for a while (i.e., until population size becomes large enough such that the impact of conspecifics is felt). If the birth and death rates are evaluated for a small initial population in the "virgin" environment (where resources are at their maximum), then equation (7) tells whether a small population goes extinct or can initially grow and thereby establish itself, i.e., whether the population is *viable*.

Equation (7) assumes that all individuals are equivalent, i.e., they all have the same birth and death rates; such an unstructured population can be described by a single variable N, the number of equivalent individuals. Suppose now that the population contains juveniles and adults, and let respectively N_1 and N_2 denote their numbers. Adults

produce juveniles at rate b and die at rate d. Juveniles mature into adults at rate m and die at rate δ. The dynamics of this structured population is thus given by

$$\begin{aligned} \frac{dN_1}{dt} &= bN_2 - mN_1 - \delta N_1 \\ \frac{dN_2}{dt} &= mN_1 - dN_2 \end{aligned} \tag{8}$$

Notice that the only positive term in dN_1/dt is bN_2, because the only way to get new juveniles added to N_1 is the reproduction of adults. The term mN_1 appears as a negative term in the first equation but a positive term in the second equation: by maturation, juveniles cease to be juveniles and are removed from N_1; they however do not disappear from the population but become adults and are added to N_2. Death affects each stage separately.

Exercise: By rewriting equations (8) into matrix-vector form, show that the model is equivalent to

$$\begin{bmatrix} dN_1/dt \\ dN_2/dt \end{bmatrix} = \begin{bmatrix} -(m+\delta) & b \\ m & -d \end{bmatrix} \begin{bmatrix} N_1 \\ N_2 \end{bmatrix}$$

For which parameter values will this structured population grow? The answer is much less straightforward than for equation (7)! Some intuition helps us to appreciate the significance of the juvenile stage. If m is very large, then juveniles mature almost instantaneously after birth; in this case, the model is very close to equation (7) and the approximate condition for population growth is again $b - d > 0$. If however m is very small, then the offspring spend an enormously long time as juveniles and (assuming $\delta > 0$) almost all of them die before they would maturre; hence the population goes extinct (unless b is enormously large to compensate for juvenile mortality).

In this particular example, we can find a shortcut to evaluating the condition of population growth, using what we have learnt about exponential decay in Part 1. Maturation and death are two exponential decay processes that remove juveniles; hence the probability that a juvenile matures rather than dies is $m/(m+\delta)$. Adults die as an exponential decay process at rate d, so that the average adult lifetime is $1/d$. During this lifetime, an adult produces $b \cdot (1/d)$ juveniles. Putting these together, an adult produces on average $R_0 = \frac{m}{m+\delta}\frac{b}{d}$ adults before it dies. R_0 is called the *basic reproduction number* or *lifetime reproductive success*. If R_0 exceeds 1, then an adult replaces herself with more than one adult; hence the population grows. If R_0 is less than 1, then adults on average die before they would have produced one replacement; hence the population declines. If m is very large, then $R_0 \approx b/d$ as in the unstructured population model, whereas if m is very small, then so is R_0.

We must admit that in reality, maturation is often very much different from an exponential decay process. Maturation often takes an approximately fixed length of time. A tadpole just hatched from its egg has no chance to mature in the next short time interval dt; but a large tadpole with legs has a rather high probability of maturing soon. m is therefore not

constant. Yet in much theoretical work, it is assumed to be constant (in the hope that it does not make a qualitative difference in the end) because the mathematical analysis of an exponential process is much simpler.

Note that the above shortcut was facilitated by the fact that the juvenile and adult stages are consecutive, and therefore we could separately calculate the probability of surviving the juvenile stage and then the number of offspring produced during the adult stage. As our next example will illustrate, the states of many structured population models are not consecutive.

1.4 A metapopulation model

A metapopulation is a collection of local populations connected by dispersal (migration). For a simple example, consider a metapopulation of only two local populations with discrete-time population dynamics. At the beginning of a year, each member of population i (where i is 1 or 2) produces F_i offspring on average. Adults survive till the next year with probability P_i. Only the offspring disperse (juvenile dispersal) such that an offspring born in population i moves to population j with probability m_{ji} (recall the order of indices); m_{ii} (with identical indices) is the probability that an offspring born in population i "moves" to population i, i.e., that it does not disperse.

If all dispersing individuals reach their destination, then an offspring born in population i ends up either in population 1 or in population 2, and therefore $m_{1i} + m_{2i} = 1$ for $i = 1, 2$. Dispersal is however a risky process, and offspring that move out of their natal population may incur a mortality cost. If so, then $m_{1i} + m_{2i} < 1$ because a fraction of offspring who left population i has never arrived at population j.

With N_1 and N_2 denoting respectively the number of individuals in populations 1 and 2, the model assumptions lead to the equations

$$\begin{aligned} N_1' &= m_{11}F_1N_1 + m_{12}F_2N_2 + P_1N_1 \\ N_2' &= m_{21}F_1N_1 + m_{22}F_2N_2 + P_2N_2 \end{aligned} \tag{9}$$

where prime denotes the next generation. The $m_{11}F_1N_1$ term of the first equation gives the number of offspring produced in population 1 that also stayed in population 1. In contrast, the term $m_{12}F_2N_2$ is the number of offspring produced in population 2 that moved over to population 1. P_1N_1 is the number of adults of population 1 that are still alive in the next year. Because adults do not move, only local adults contribute to population size. The second equation is constructed analogously.

Exercise: Rewrite this model into a matrix-vector form to obtain

$$\mathbf{N}' = \mathbf{A}\mathbf{N}$$

with

$$\mathbf{A} = \begin{bmatrix} m_{11}F_1 + P_1 & m_{12}F_2 \\ m_{21}F_1 & m_{22}F_2 + P_2 \end{bmatrix}$$

Matrix $\mathbf{A}$ is called the *projection matrix* of the model because it "projects" the current population vector $\mathbf{N}$ into the next population vector $\mathbf{N}'$. The transition probability matrix $\mathbf{Q}$ in section (1.1) is also a projection matrix, albeit a special one, because it is also a stochastic matrix (its columns sum to 1). The matrices of rates in the continuous-time models are however not projection matrices because they describe change ($d\mathbf{N}/dt$) rather than project to the next value $\mathbf{N}'$.

Note that even if the model distinguishes offspring from their parents (because only the offspring disperse), there is no population structure within a local population (N_1, the total number of individuals in population 1, is sufficient to describe the first population, and the same holds for N_2). This is because the model assumes that offspring produced this year will become adults by the next year. At the time of census (when we count N_1 and N_2), just before reproduction, all individuals are adults.

The modeller is of course free to choose the census point. We might for example decide that we count the populations when the offspring are already born but have not yet dispersed. With this choice, however, we should distinguish offspring who may disperse and adults who may not; hence each local population would have a stage structure in addition to the spatial structure of the metapopulation. The resulting model would have a 4x4 matrix, which is unnecessarily more complicated than the model above. It is worthwhile to choose the census point such that the resulting model is as simple as possible. Naturally, a more complicated model alternative would eventually predict the same behaviour (after all, populations do not "know" when we count them, so their behaviour cannot depend on the choice of census), but the analysis can be much harder.

Exercise: The metapopulation model presented here could be criticized by saying that its offspring are born and disperse, but they do not die before they become adults. Discuss whether offspring survival could be factored into fecundity, i.e., if F_i could represent not just the number of offspring produced per parent but the product of the number of offspring and the probability of their survival during the first year of life. This product might be called *effective fecundity*, which does not count the offspring who die before reaching the first census after their birth.

In this model, it is not at all obvious whether the projection matrix describes a population that grows or declines. In fact, it might happen that the population declines for a while but then starts to grow (despite that we assume constant parameters!). To see this, suppose that population 1 lives in a good environment so that it has high fecundity and survival, whereas in population 2 these parameters are so small that without immigration from population 1, population 2 would quickly go extinct. If most of the initial individuals happen to be in population 2, then the dynamics of the first few generations will be dominated by their death. Population 1 will however grow and eventually total population size will be dominated by its growth; via dispersal, it will also maintain population 2 that otherwise would be extinct.

1.5 Age-structured populations

The best known ecological example of matrix models addresses the discrete-time dynamics of age-structured populations. This model applies to organisms with seasonal reproduction (for simplicity we assume that reproduction occurs once a year, e.g. in spring) whose survival and fecundity depend on age. The population is divided into age classes. The most convenient is to count (or "census") the individuals immediately before reproduction; then the youngest ones are 1 year old (they were born in the previous reproductive season) and the population consists of $N_1, N_2, ..., N_\omega$ individuals of age $1, 2, ..., \omega$. To have only a finite number of age classes, we assume that there is a maximum age ω. The maximum age can however be set so high that neglecting individuals older than ω does not make an appreciable difference.The population is thus given by the vector

$$\mathbf{N} = \begin{bmatrix} N_1 \\ N_2 \\ \vdots \\ N_\omega \end{bmatrix}$$

Let P_i denote the probability that an i-year old individual survives the coming year such that next year we shall census it as an $i+1$-year old individual, and let F_i be the number of offspring produced by an i-year old parent. By the next year, the offspring will be 1-year old. Notice, however, that we census only those individuals who are present at the beginning of a year (immediately before reproduction); hence if an offspring does not survive its first year of life, we shall never count it. Hence F_i is not simply the number of newborns produced, but the number of offspring who are alive at the next census ("effective fecundity"); it is often much fewer than the newborns. It is also customary to count only females (and hence female offspring), assuming that there are enough males for each female to be mated.

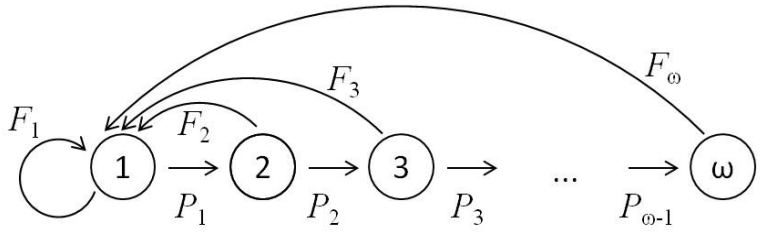

Figure 2: Life cycle graph of an age-structured population.

To construct the projection matrix, let us first draw the so-called *life cycle graph* that depicts the life history of this population (Figure 2). Because we want to obtain a matrix that projects over 1 year, it is very important that each arrow in this graph represents a change over one year. In an age-structured population, all surviving individuals enter the next age class and each age class produces offspring that are 1-year old in one year's

time. The members of the last age class are removed.

One can set up the projection matrix directly from the life cycle graph, keeping in mind that the ij element of the matrix gives the contribution of the jth class to next year's ith class. The fecundity F_j of the jth class contributes to the 1st class of the next year; hence the F_j's occupy the first row of the matrix. P_i gives the transition probability from class i to class $i+1$, and hence it is placed into the it row and $i+1$st column. All other elements of the matrix are zero, because no other transitions are possible between the age classes. As a result, we obtain the projection matrix

$$\mathbf{L} = \begin{bmatrix} F_1 & F_2 & \dots & F_{\omega-1} & F_\omega \\ P_1 & 0 & \dots & 0 & 0 \\ 0 & P_2 & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & P_{\omega-1} & 0 \end{bmatrix} \tag{10}$$

which is often referred to as the *Leslie matrix* and therefore denoted by **L**.

Exercise: Write down the individual equations to calculate the size of various age classes next year (N_i') analogously to equations (3), and verify that the projection matrix given in (10) is correct.

Exercise: Draw the life cycle graph of the metapopulation model in section 1.4.

We can investigate whether the population described by the Leslie matrix in equation (10) is able to grow by calculating its basic reproduction number (also called the lifetime reproductive success, R_0) analogously to section 1.3. In an age-structured population, R_0 is the number of offspring a 1-year old individual can expect to produce throughout its life. Let l_i denote the probability that a 1-year old individual will survive till age i; if it does, then it produces F_i offspring at that age. Summing all offspring over every possible age, we obtain the expected lifetime number of offspring as $R_0 = \sum_i l_i F_i$. To calculate l_i, notice that, obviously, l_1=1 (a 1-year old is alive now). The probability of surviving from age 1 to age 2 is given by P_1 (cf. Figure 2), so that $l_2 = P_1$. To survive from age 1 to age 3, the individual must survive from age 1 to age 2 (with probability P_1) and then from age 2 to age 3 (with probability P_2), and hence $l_3 = P_1 P_2$. By the same logic, we have $l_i = P_1 P_2 ... P_{i-1}$; this completes the calculation of R_0 directly from the parameters given in the Leslie matrix.

If $R_0 > 1$, then the population has the capacity to grow, because every 1-year old will eventually replace itself by more than one offspring. This does not however imply that the population will grow in every year. Suppose that maturation occurs at age 2 such that 1-year old individuals do not reproduce yet ($F_1 = 0$). If the initial population consists of only 1-year old individuals, then in the first year there is no reproduction and all what happens is that some of the individuals die.

$R_0 > 1$ does not guarantee population growth even in the long term if there are post-reproductive age classes. Suppose, for example, that $F_{\omega-1} = 0$ and $F_\omega = 0$, i.e., the last

two age classes do not reproduce. If the initial population contains only these two age classes, then there will be no reproduction ever, and the population will go extinct when the initial individuals die[3]. $R_0 > 1$ implies long-term population growth if 1-year old individuals are either present in the initial population or will be produced before the initial individuals die; afterwards, the 1-year old individuals will replace themselves by more than one offspring each.

The reason why R_0 is straightforward to calculate in the structured population model of section 1.3 and in the present age-structured model is that both models have a single state through which all individuals must pass. In the model of section 1.3, everybody is born as a juvenile; in an age-structured model, everybody is first 1-year old. These models are said to have a *single renewal state*. In models with a single renewal state, R_0 is the number of future descendants in the renewal state per one individual in the renewal state now; for example in the age-structured model, R_0 is the number of 1-year old descendants of an individual who is 1-year old now. In the simple model of section 1.3, one can actaully use either the juvenile or the adult state as the renewal state, it does not make a difference. The metapopulation model in section 1.4, however, does not have a single renewal state because offspring are born in both populations; and therefore calculating R_0 is not straightforward.

2 Matrix operations

In section 1.1, we already introduced matrix-vector mutiplication. In this chapter, we review all basic operations and their important properties.

2.1 Multiplication

When a matrix and a vector are multiplied, the result is a new vector. The ith element of this vector is calculated by multiplying the elements of the ith row of the matrix with the corresponding elements of the vector, and adding up the products (see Figure 1). For a 2x2 matrix, the multiplication is

$$\mathbf{Ax} = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix} = \begin{bmatrix} a_{11}x_1 + a_{12}x_2 \\ a_{21}x_1 + a_{22}x_2 \end{bmatrix}$$

whereas in general, the ith element of the result is given by

$$[\mathbf{Ax}]_i = \sum_j a_{ij}x_j$$

If the matrix has a different number of elements in its rows than the number of elements in the vector, then the procedure of multiplication cannot be carried out (one series of

[3]Sometimes it is convenient to set ω to be the last reproductive age, and simply not count the post-reproductive individuals in the model. If however survival or fecundity depends on population size (or explicitly on some limiting resource, etc.; this we do not assume in the current model), then also the post-reproductive individuals influence the growth of the population by contributing to population size (or by exhausting the resources).

numbers runs out before the other); in these cases, the product does not exist. Hence an n-vector can be multiplied only with matrices that have n columns. If the matrix is a square matrix (i.e., it has also n rows), then the result will be an n-vector.

> When seen for the first time, matrix-vector multiplication may appear haphazard ("why is this the way it's done and why not some other?"). The examples of the previous chapter should convince the reader that matrix multiplication is defined in the way as it is useful.

To multiply two matrices, think of the columns of the second matrix as if they were separate vectors. For example, in the matrix product

$$\mathbf{AB} = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} \begin{bmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{bmatrix}$$

think of $\mathbf{B}$ as a "collection" of two vectors, $\begin{bmatrix} b_{11} \\ b_{21} \end{bmatrix}$ and $\begin{bmatrix} b_{12} \\ b_{22} \end{bmatrix}$. The first column of the result matrix is $\mathbf{A}$ times $\begin{bmatrix} b_{11} \\ b_{21} \end{bmatrix}$; the second column of the result is $\mathbf{A}$ times $\begin{bmatrix} b_{12} \\ b_{22} \end{bmatrix}$. Hence we have

$$\mathbf{AB} = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} \begin{bmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{bmatrix} = \begin{bmatrix} a_{11}b_{11} + a_{12}b_{21} & a_{11}b_{12} + a_{12}b_{22} \\ a_{21}b_{11} + a_{22}b_{21} & a_{21}b_{12} + a_{22}b_{22} \end{bmatrix}$$

In general, the element in the ith row, jth column of the result matrix is

$$[\mathbf{AB}]_{ij} = \sum_k a_{ik}b_{kj}$$

Once again, the product does not exist if the number of columns of the first matrix does not match the number of rows of the second matrix. For example, the matrix-vector product

$$\begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix}$$

exists because the matrix has 2 columns and the vector (think of it as a 2x1 matrix) has 2 rows. The product

$$\begin{bmatrix} x_1 \\ x_2 \end{bmatrix} \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}$$

however does not exist, because the vector has only 1 column but the matrix has 2 rows.

The most important fact about matrix multiplication is that *the order of matrices matters* (multiplication is not commutative). This means that

$$\mathbf{AB} \neq \mathbf{BA}$$

Exercise: Let $\mathbf{A} = \begin{bmatrix} 1 & 2 \\ 0 & 3 \end{bmatrix}$ and $\mathbf{B} = \begin{bmatrix} 5 & 0 \\ 6 & 1 \end{bmatrix}$. Calculate both $\mathbf{AB}$ and $\mathbf{BA}$ to show that they are different.

Matrix products however do satisfy the following two properties:

$$\begin{aligned} (\mathbf{AB})\mathbf{C} &= \mathbf{A}(\mathbf{BC}) \quad \text{(associative)} \\ \mathbf{A}(\mathbf{B}+\mathbf{C}) &= \mathbf{AB}+\mathbf{AC} \quad \text{(distributive)} \end{aligned}$$

All what matters is that the order must be kept; hence $\mathbf{AB}+\mathbf{AC} = \mathbf{A}(\mathbf{B}+\mathbf{C})$ is correct (matrix $\mathbf{A}$ is factored out to the front) but $\mathbf{AB}+\mathbf{AC}$ is not the same as $(\mathbf{B}+\mathbf{C})\mathbf{A}$ (because the order has changed). Nothing can be factored out of $\mathbf{AB}+\mathbf{CA}$ (because $\mathbf{A}$ is once in the front and once in the back). To emphasise the order, we say that in $\mathbf{AB}$, $\mathbf{A}$ *pre-multiplies* $\mathbf{B}$ whereas $\mathbf{B}$ *post-multiplies* $\mathbf{A}$.

2.2 Transposed vectors and vector products

One can change the orientation of a vector by taking its *transpose*:

$$\mathbf{x}^T = \begin{bmatrix} x_1 \\ x_2 \end{bmatrix}^T = \begin{bmatrix} x_1 & x_2 \end{bmatrix}$$

which transforms a column vector into a row vector and *vice versa*. (When it is not specified, a "vector" is always taken to be a column vector.) A row vector can be post-multiplied with a matrix as in

$$\begin{bmatrix} x_1 & x_2 \end{bmatrix} \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} = \begin{bmatrix} a_{11}x_1 + a_{21}x_2 & a_{12}x_1 + a_{22}x_2 \end{bmatrix}$$

but the opposite order is not possible. The result of $\mathbf{x}^T\mathbf{A}$ is a row vector, and its elements are different from the elements of the column vector $\mathbf{Ax}$.

A row vector and a column vector can be multiplied in both orders, but the results are *qualitatively* different. The product

$$\begin{bmatrix} x_1 & x_2 \end{bmatrix} \begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = x_1y_1 + x_2y_2$$

yields a scalar number $(x_1y_1 + x_2y_2)$ and therefore it is called the *scalar* (or *inner*) *product* of the two vectors. The opposite order

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} \begin{bmatrix} x_1 & x_2 \end{bmatrix} = \begin{bmatrix} x_1y_1 & x_2y_1 \\ x_1y_2 & x_2y_2 \end{bmatrix}$$

is the *outer product* and it gives a matrix.

2.3 The identity matrix and the inverse matrix

In multiplication of numbers, number "1" plays a special role: a number multiplied with 1 remains the same. In matrix multiplication, the *identity matrix* plays the same role. The 3x3 identity matrix is

$$\mathbf{I} = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}$$

and the pattern is the same for any size of the matrix; the *diagonal* of the matrix contains 1's and all other elements are 0.

> **Exercise:** Verify that $\mathbf{Ix} = \mathbf{x}$ for any vector $\mathbf{x}$ (assuming of course that the size of the identity matrix corresponds to the vector).
>
> **Exercise:** Verify that $\mathbf{IA} = \mathbf{AI} = \mathbf{A}$ (the identity matrix commutes with any other matrix; this is an exception from the general rule that matrix multiplication is not commutative).

There is no "matrix division". Analogously to $a^{-1}a = \frac{1}{a} \cdot a = 1$, we can however define the *inverse matrix* as the matrix $\mathbf{A}^{-1}$ such that if multiplied with the original matrix $\mathbf{A}$, the product is the identity matrix:

$$\mathbf{A}^{-1}\mathbf{A} = \mathbf{A}\mathbf{A}^{-1} = \mathbf{I}$$

2.4 Sums of matrices and multiplication with a number

We add matrices element-wise, i.e., by adding their elements in the same positions. With 2x2 matrices, this means

$$\begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} + \begin{bmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{bmatrix} = \begin{bmatrix} a_{11} + b_{11} & a_{12} + b_{12} \\ a_{21} + b_{21} & a_{22} + b_{22} \end{bmatrix}$$

whereas in general,

$$[\mathbf{A} + \mathbf{B}]_{ij} = a_{ij} + b_{ij}$$

Matrices can be added to each other only if they have the same size. The zero matrix is the matrix all elements of which are zeros; adding the zero matrix makes no difference.

> With numbers, we are used to the fact that if $ab = 0$ then a or b is zero. With matrices, this is not so: the product $\begin{bmatrix} 1 & 0 \\ 0 & 0 \end{bmatrix} \begin{bmatrix} 0 & 0 \\ 1 & 0 \end{bmatrix}$ gives the zero matrix $\begin{bmatrix} 0 & 0 \\ 0 & 0 \end{bmatrix}$. Even more surprisingly, multiplying the matrix $\begin{bmatrix} 0 & 0 \\ 1 & 0 \end{bmatrix}$ with itself gives the zero matrix!

Because $2\mathbf{A} = \mathbf{A} + \mathbf{A}$, we must have

$$2\mathbf{A} = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} + \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} = \begin{bmatrix} 2a_{11} & 2a_{12} \\ 2a_{21} & 2a_{22} \end{bmatrix}$$

By analogy, we can multiply a matrix with any number by multiplying each element of the matrix with the number. Hence for a 2x2 matrix and any number k we have

$$k\mathbf{A} = \begin{bmatrix} ka_{11} & ka_{12} \\ ka_{21} & ka_{22} \end{bmatrix}$$

and in general,

$$[k\mathbf{A}]_{ij} = ka_{ij}$$

3 Modelling discrete life cycles and the order of matrices in matrix multiplication

This chapter shows some biological consequences of the fact that in matrix multiplication, the order of matrices matter. Consider a simple metapopulation of an annual organism. There are only two local populations connected by migration. The life cycle consists of two events: each year there is reproduction (in the ith population, every individual produces F_i offspring and dies immediately after reproduction) and there is dispersal (an individual in population j moves to population i with probability m_{ij}). The model is similar to the one in section 1.4 but here we assume no adult survival ($P_i = 0$ for $i = 1, 2$).

In discrete-time models, one has to specify the order of events within a year. Suppose thus that after censusing the population (counting the numbers in the population vector $\mathbf{N}_t$), first there is reproduction and then there is dispersal (Figure 3a). Before constructing the full projection matrix, consider the effect of reproduction separately. After reproduction, the original N_1 individuals in population 1 are replaced by F_1N_1 offspring; and similarly the original N_2 individuals in population 2 are replaced by F_2N_2 offspring. The population after reproduction is thus described by the vector

$$\tilde{\mathbf{N}}_t = \begin{bmatrix} F_1 & 0 \\ 0 & F_2 \end{bmatrix} \begin{bmatrix} N_1 \\ N_2 \end{bmatrix} = \mathbf{F}\mathbf{N}_t$$

where the tilde denotes "after reproduction" (but still within year t) and $\mathbf{F}$ is the diagonal matrix of fecundities.

Next, we turn to the effect of dispersal. After dispersal, a fraction m_{11} of the $\tilde{N}_1$ individuals in population 1 are still in population 1, plus a fraction m_{12} of the $\tilde{N}_2$ individuals in population 2 have moved to population 1. Population 1 thus contains $m_{11}\tilde{N}_1 + m_{12}\tilde{N}_2$ individuals; and an analogous reasoning holds for population 2. The population numbers

after dispersal are the numbers at the next census point, $\mathbf{N}_{t+1}$ (cf. Figure 3a), hence we have

$$\mathbf{N}_{t+1} = \begin{bmatrix} m_{11} & m_{12} \\ m_{21} & m_{22} \end{bmatrix} \begin{bmatrix} \tilde{N}_1 \\ \tilde{N}_2 \end{bmatrix} = \mathbf{M}\tilde{\mathbf{N}}_t$$

Putting the two equations together,

$$\mathbf{N}_{t+1} = \mathbf{M}\tilde{\mathbf{N}}_t = \mathbf{MFN}_t$$

Hence the 1-year projection matrix (which projects $\mathbf{N}_t$ directly into $\mathbf{N}_{t+1}$) is the product

$$\mathbf{MF} = \begin{bmatrix} m_{11} & m_{12} \\ m_{21} & m_{22} \end{bmatrix} \begin{bmatrix} F_1 & 0 \\ 0 & F_2 \end{bmatrix} = \begin{bmatrix} F_1 m_{11} & F_2 m_{12} \\ F_1 m_{21} & F_2 m_{22} \end{bmatrix} \tag{11}$$

Notice that because reproduction precedes dispersal, we have to apply the fecundity matrix $\mathbf{F}$ to the population vector $\mathbf{N}$ before applying the dispersal matrix $\mathbf{M}$. Applying a matrix to a (column) vector means pre-multiplying the vector with the matrix. Hence we must first form the product $\mathbf{FN}$, and then pre-multiply this with $\mathbf{M}$ to obtain $\mathbf{MFN}$. The "literal" order "$\mathbf{M}$", "$\mathbf{F}$" in $\mathbf{MFN}$ is just the opposite of the real order of operations! The product $\mathbf{MFN}$ means that the vector $\mathbf{N}$ is first (pre-)multiplied with $\mathbf{F}$ and then the result of this is (pre-)multiplied with $\mathbf{M}$.

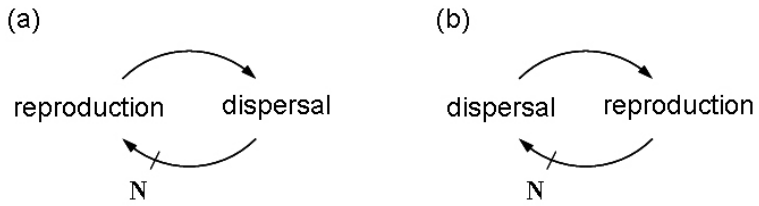

Figure 3: Life cycles with two events within a year.

Let us now compare the above model with the same except that the order of events is the opposite: we now assume that after census, there is first dispersal and then reproduction (Figure 3b). In this case, the population vector $\mathbf{N}$ is first multiplied with the dispersal matrix $\mathbf{M}$ to obtain $\mathbf{MN}$; and then this product is (pre-)multiplied with the fecundity matrix $\mathbf{F}$. This results in

$$\mathbf{N}_{t+1} = \mathbf{FMN}_t$$

i.e., the 1-year projection matrix is

$$\mathbf{FM} = \begin{bmatrix} F_1 & 0 \\ 0 & F_2 \end{bmatrix} \begin{bmatrix} m_{11} & m_{12} \\ m_{21} & m_{22} \end{bmatrix} = \begin{bmatrix} F_1 m_{11} & F_1 m_{12} \\ F_2 m_{21} & F_2 m_{22} \end{bmatrix} \tag{12}$$

Compare the results in equations (11) and (12): the different order of events resulted in different projection matrices. The order of events matters because the order of matrices matters in matrix multiplication.

It might be noticed that with only two events in the life cycle (reproduction, dispersal), we could change the point of census such that the above two models become identical. For example in Figure 3b, we could move the census from before dispersal to after dispersal, and then the life cycle would be identical to Figure 3a. The choice of the census point is of course arbitrary. The above two models are therefore models of the same population censused at different points in the life cycle. The numbers in the population vectors of the two models are different because they are counted at different points, but all qualitative properties of the two models are the same (such as the speed of population growth or the convergence to a stable state). With three or more events within a year, however, moving the census point will not account for the differences in the order of events!

Exercise: Compare the matrix models of metapopulations where the order of events is either reproduction-survival-dispersal or reproduction-dispersal-survival. Both metapopulations are censused before reproduction. Reproduction and dispersal are as above. During survival, individuals in population 1 survive with probability s_1 and individuals in population 2 survive with probability s_2.

4 Systems of linear equations and the determinant

In matrix population models, we calculate the new population vector from the previous population vector according to $\mathbf{N}_{t+1} = \mathbf{A}\mathbf{N}_t$, or, equivalently,

$$\mathbf{N}_t = \mathbf{A}\mathbf{N}_{t-1} \tag{13}$$

But can we figure out the past if we know the present, i.e., can we find $\mathbf{N}_{t-1}$ if we know $\mathbf{N}_t$?

A similar question cencerns equilibria of matrix models. In section 1.1, we set up a model for the dynamics of allele frequencies under mutation,

$$\mathbf{p}_{t+1} = \mathbf{Q}\mathbf{p}_t$$

To find the equilibrium allele frequencies, we must find the frequency vector $\mathbf{p}$ such that if the current frequencies are given by this vector ($\mathbf{p}_t = \mathbf{p}$), then there is no change after mutation such that also the next frequencies are given by the same vector ($\mathbf{p}_{t+1} = \mathbf{p}$). In other words, we must solve the equation

$$\mathbf{p} = \mathbf{Q}\mathbf{p}$$

for the unknown equilibrium vector $\mathbf{p}$. As with numbers, first we collect all terms with the unknown to one side of the equation:

$$\mathbf{0} = \mathbf{Q}\mathbf{p} - \mathbf{p}$$

where $\mathbf{0}$ is a vector of zeros. To factor out $\mathbf{p}$ from the two terms on the right hand side, recall that $\mathbf{p} = \mathbf{I}\mathbf{p}$ (the identity matrix does not change the vector) and therefore we can

write $\mathbf{Qp}-\mathbf{p}=\mathbf{Qp}-\mathbf{Ip}=(\mathbf{Q}-\mathbf{I})\mathbf{p}$, where the difference is formed between two matrices $(\mathbf{Q}-\mathbf{I})$ and the order of multiplication is unchanged ($\mathbf{p}$ is factored out to the right). With this, we can write the equilibrium equation as

$$(\mathbf{Q}-\mathbf{I})\mathbf{p}=\mathbf{0} \tag{14}$$

The two equations in (13) and (14) have the same structure: a known matrix ($\mathbf{A}$ or $\mathbf{Q}-\mathbf{I}$) is multiplied with an unknown vector ($\mathbf{N}_{t-1}$ or $\mathbf{p}$) to yield a known vector ($\mathbf{N}_t$ or $\mathbf{0}$). In general, problems of this sort can be written as

$$\mathbf{Ax}=\mathbf{r} \tag{15}$$

where $\mathbf{A}$ is an arbitrary known matrix, $\mathbf{r}$ is a known vector, and $\mathbf{x}$ is the unknown vector. Such a matrix equation represents a *system of linear equations*. Indeed, if we write out the matrix-vector multiplication, we arrive at the equations

$$\begin{aligned}
&a_{11}x_1+a_{12}x_2+\ldots+a_{1n}x_n=r_1\\
&a_{21}x_1+a_{22}x_2+\ldots+a_{2n}x_n=r_2\\
&\vdots\\
&a_{n1}x_1+a_{n2}x_2+\ldots+a_{nn}x_n=r_n
\end{aligned}$$

where $x_1,\ldots,x_n$ are the unknowns.

Formally, we can solve the system of linear equations by pre-multiplying both sides of equation (15) with the inverse of $\mathbf{A}$:

$$\begin{aligned}
\mathbf{A}^{-1}\mathbf{Ax} &= \mathbf{A}^{-1}\mathbf{r}\\
\mathbf{x} &= \mathbf{A}^{-1}\mathbf{r}
\end{aligned} \tag{16}$$

(because $\mathbf{A}^{-1}\mathbf{A}=\mathbf{I}$ and the identity matrix does not change $\mathbf{x}$), but to calculate $\mathbf{x}$, we must know the inverse matrix $\mathbf{A}^{-1}$. In this chapter, we study how to obtain the solution in practice; how to obtain the inverse matrix (if we must); and most importantly, whether there exists a solution in the first place.

4.1 Two equations with two unknowns

For illustration, let us start with a 2x2 matrix $\mathbf{A}$. The system of equations is then

$$a_{11}x_1+a_{12}x_2=r_1 \tag{17a}$$
$$a_{21}x_1+a_{22}x_2=r_2 \tag{17b}$$

To obtain the unknown x_1, we eliminate x_2 from the equations. Firstly, multiply the first equation with a_{22} and the second equation with a_{12}; the goal of this step is to get the same factors in the x_2 terms of the two equations:

$$\begin{aligned}
a_{11}a_{22}x_1+a_{12}a_{22}x_2&=a_{22}r_1\\
a_{12}a_{21}x_1+a_{12}a_{22}x_2&=a_{12}r_2
\end{aligned}$$

Secondly, subtract the second equation from the first; because the x_2 terms are the same, they cancel:

$$a_{11}a_{22}x_1 - a_{12}a_{21}x_1 = a_{22}r_1 - a_{12}r_2$$

Finally, solve the above single equation for x_1:

$$x_1 = \frac{a_{22}r_1 - a_{12}r_2}{a_{11}a_{22} - a_{12}a_{21}} \tag{18}$$

Once we have x_1, we can substitute it into one of the original equations and solve it for the remaining unknown x_2.

Exercise: Show that $x_2 = \frac{a_{11}r_2 - a_{21}r_1}{a_{11}a_{22} - a_{12}a_{21}}$.

This derivation implies that the solution can always be obtained, except in one case: if $a_{11}a_{22} - a_{12}a_{21}$ happens to be zero (because then we would divide with zero). As we shall see later, the quantity $a_{11}a_{22} - a_{12}a_{21}$ is the determinant of the 2x2 matrix $\mathbf{A}$.

It is helpful to illustrate graphically when equations (17) have a solution and when they have not. In Figure 4(a), the two straight lines correspond to the two equations in (17) as follows. Rearranging equation (17a), we obtain $x_2 = (r_1 - a_{11}x_1)/a_{12}$, which gives x_2 as a linear function of x_1; this linear function is plotted as the straight line corresponding to equation 1. The line corresponding to equation (17b) is plotted analogously. The first equation is satisfied by all combinations of x_1 and x_2 on the first line and the second equation is satisfied by all combinations of x_1 and x_2 on the second line. To satisfy both equations simultaneously, the solution must be on both lines. There is only one point that is on both lines, the intersection point of the lines. Hence the intersection point gives the solution (x_1, x_2) graphically.

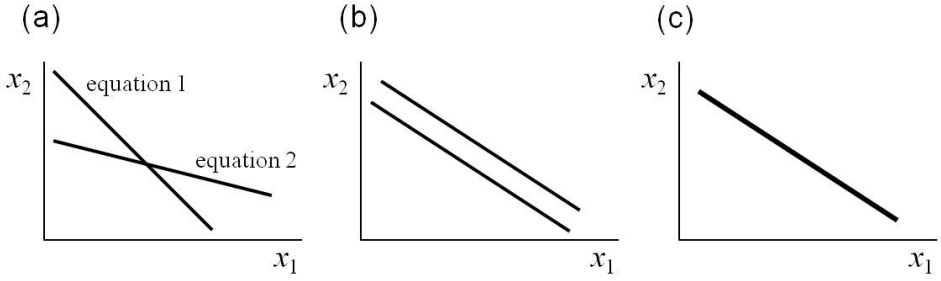

Figure 4: Graphical representation of a system of two linear equations. On each line, one of the equations holds. The solution to both equations is the intersection point of the lines in (a). There is no solution if the lines do not intersect as in (b); and all points on the line are solutions if the lines coincide as in (c).

Figure 4(b) and (c) show how things can go wrong. There is no solution if the lines are parallel (so that they never intersect); and there are infinitely many solutions if the

two lines coincide (all points on the line are on both lines). It follows immediately that equations (17) have either one solution, or no solution, or infinitely many solutions; no other cases are possible.

> In case of a 3x3 matrix, the unknown vector has 3 elements and the analogue of Figure 4 is three dimensional. Each of the three equations correspond to a plane in three-dimensional space. Two of the planes intersect in a line; and this line intersects the third plane in a point, which is the solution. There is no solution if the line is parallel to the third plane or if all three planes are parallel (and no line exists). There are infinitely many solutions if the line is in the third plane or if all three planes are the same. It remains true also in all higher dimensions that a system of linear equations has either one solution or no solution of infinitely many solutions.

If the equations have exactly one solution (as in Figure 4a), we say that there is a *unique solution*. In practice, that is what we hope to have: a unique solution, which is then "the solution" of the problem. To explore whether equations (17) have a unique solution or happen to represent one of the "problem cases" in Figure 4b,c where there is no unique solution, a numerical example will be most useful. Compare the left hand sides of the following equations:

$$x_1 + 2x_2 = 5 \tag{19a}$$
$$3x_1 + 6x_2 = 7 \tag{19b}$$

Obviously, the left hand side of the second equation is just 3 times that of the first equation. The right hand sides however do not agree: 7 is not 3 times 5. It is simply not possible that a quantity $(x_1 + 2x_2)$ equals 5 and its triple, $3(x_1 + 2x_2) = 3x_1 + 6x_2$, equals 7. These two equations contradict each other and therefore the system of equations has no solution. This is the case of Figure 4b.

> Indeed, the two lines corresponding to equations (19) are given by $x_2 = (5 - x_1)/2 = \frac{5}{2} - \frac{1}{2}x_1$ and $x_2 = (7 - 3x_1)/6 = \frac{7}{6} - \frac{1}{2}x_1$. These two lines have the same slope $(-\frac{1}{2})$ but different intercepts ($\frac{5}{2}$ and $\frac{7}{6}$, respectively). Hence the two equations correspond to two parallel lines as shown in Figure 4b.

If we change the right hand sides of equations (19) such that now also the right hand side of the second equation is 3 times that of the first equation,

$$x_1 + 2x_2 = 5 \tag{20a}$$
$$3x_1 + 6x_2 = 15 \tag{20b}$$

then the two equations say precisely the same; dividing both sides of $3x_1 + 6x_2 = 15$ with 3, it simplifies to $x_1 + 2x_2 = 5$. The second equation thus contains no new information. These equations correspond to the coinciding lines of Figure 4c.

Comparing the two examples in equations (19) and (20) it should be clear that the problem in both cases is that the left hand side of the second equation is just 3 times that of the first equation. This means that in the corresponding matrix,

$$\mathbf{A} = \begin{bmatrix} 1 & 2 \\ 3 & 6 \end{bmatrix}$$

the second row is 3 times the first row. Hence we can see directly from the matrix that this is a "problem case" that has no unique solution. Whether the equations $\mathbf{Ax} = \mathbf{r}$ have infinitely many solutions or have no solution depends on whether the right hand sides of the equations (given in vector $\mathbf{r}$) agree with the matrix or not (in our example, whether r_2 is 3 times r_1 or not). But the upshot is, the matrix alone determines whether there is a unique solution. With 2x2 matrices, the equations have no unique solution if one row of the matrix can be obtained by multiplying the other row with a certain number (in our example, the second row is 3 times the first, or the first row is $\frac{1}{3}$ times the second).

4.2 Larger systems of equations

To generalize the above conclusions to larger systems, let us take one more example, now with three unknowns. Let the matrix be

$$\mathbf{A} = \begin{bmatrix} 1 & 2 & 6 \\ 1 & -1 & 4 \\ 2 & 1 & 10 \end{bmatrix}$$

No row can be expressed as a number times another row of $\mathbf{A}$, yet one of the rows can be expressed using the other two rows: as the reader will notice, the last row is just the sum of the first two. If we write out the product $\mathbf{Ax}$ (which is the left hand side of the equations), then the last expression is the sum of the first two:

$$\begin{aligned} x_1 + 2x_2 + 6x_3 \\ x_1 - x_2 + 4x_3 \\ 2x_1 + x_2 + 10x_3 \end{aligned}$$

If the right hand sides agree with this pattern (the last is the sum of the first two), then one of the equations will contain no new information. For example, in the system

$$\begin{aligned} x_1 + 2x_2 + 6x_3 &= 8 \\ x_1 - x_2 + 4x_3 &= 5 \\ 2x_1 + x_2 + 10x_3 &= 13 \end{aligned}$$

the last equation does not say anything new; if the first two equations hold, then the last one holds automatically because it is just the sum of the first two. This system of equations has three unknowns but only two useful equations. Hence one of the unknowns

(e.g. x_3) can be chosen arbitrarily; the first two equations can be solved for the remaining unknowns (x_1 and x_2) and so a valid solution is obtained for any value of the arbitrary unknown (x_3). This system has infinitely many solutions. To the contrary, if the right hand sides do not agree with the pattern of the left hand sides (in this example, the last is not the sum of the first two), then the last equation will contradict the first two and the system has no solution. It is for example impossible to satisfy the system

$$\begin{aligned} x_1 + 2x_2 + 6x_3 &= 8 \\ x_1 - x_2 + 4x_3 &= 5 \\ 2x_1 + x_2 + 10x_3 &= 10 \end{aligned}$$

because whenever the first two equations hold, the last one certainly does not.

We can summarize the examples in the following statement: the system of equations has a unique solution if and only if the rows of the matrix are *linearly independent*. "Linearly independent" means that a row cannot be expressed with other rows using multiplication with a number and addition/subtraction. For example, the rows of the matrix

$$\mathbf{B} = \begin{bmatrix} 1 & 2 & 3 \\ 1 & 1 & 1 \\ 3 & 4 & 5 \end{bmatrix}$$

are not linearly independent because the last row is the first row plus twice the second row.

Denote the ith row of an $n \times n$ matrix $\mathbf{A}$ with $\mathbf{a_i}^T$ (where I use the transpose because $\mathbf{a_i}^T$ is a row vector). $\mathbf{a_n}^T$ can be expressed using the other rows if we can find appropriate numbers $c_1, \ldots, c_{n-1}$ such that $\mathbf{a_n}^T = c_1\mathbf{a_1}^T + c_2\mathbf{a_2}^T + \ldots + c_{n-1}\mathbf{a_{n-1}}^T$. With $c_n = -1$, this is equivalent to

$$c_1\mathbf{a_1} + c_2\mathbf{a_2} + \ldots + c_n\mathbf{a_n} = \mathbf{0}$$

The expression $c_1\mathbf{a_1} + c_2\mathbf{a_2} + \ldots + c_n\mathbf{a_n}$ is called a *linear combination* of the vectors $\mathbf{a_i}$. The vectors are not linearly independent if there is a linear combination of them that equals the zero vector.

Exercise: Take matrix $\mathbf{B}$ as given above, and give examples for the vector $\mathbf{r}$ such that the system $\mathbf{Bx} = \mathbf{r}$ has (i) no solution; (ii) infinitely many solutions.

4.3 Singular matrices

When the rows[4] of a matrix are not linearly independent, we say that the matrix is *singular*. A system of linear equations does not have a unique solution if the corresponding

[4]For a square matrix, the columns are linearly independent precisely when the rows are linearly independent; hence we could define a singular matrix also in terms of its columns, without any difference from the definition in terms of its rows.

matrix is singular. This is of course an exceptional case (cf. Figure 4), but this exceptional case will be of great importance.

If matrix $\mathbf{A}$ is singular, then it cannot be inverted ($\mathbf{A}^{-1}$ does not exist). Therefore the solution to $\mathbf{Ax} = \mathbf{r}$ cannot be obtained as $\mathbf{x} = \mathbf{A}^{-1}\mathbf{r}$ (cf. equation (16)); a unique solution does not exist.

To illustrate this fact graphically, let's consider the matrix

$$\begin{bmatrix} 1 & 0 \\ 0 & 0 \end{bmatrix}$$

This matrix is obviously singular; the second row is 0 times the first row (and notice that for the same reason, any matrix that contains a row (or column) of zeros is singular). Applying this matrix to any vector,

$$\begin{bmatrix} 1 & 0 \\ 0 & 0 \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix} = \begin{bmatrix} x_1 \\ 0 \end{bmatrix}$$

it retains the first element of the vector but replaces the second element with zero. Graphically, this means that the matrix projects every vector to the x_1-axis (Figure 5a). The second element of the original vector, x_2, is "forgotten": there is no way one could reconstruct the value of x_2 from the result vector.

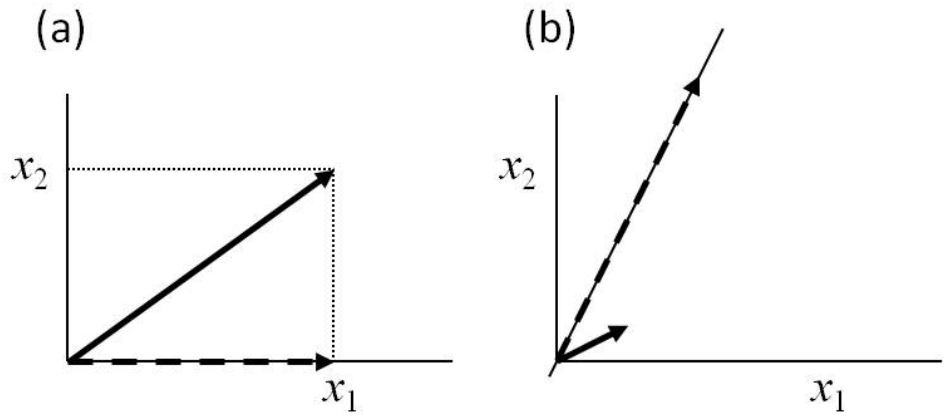

Figure 5: What a singular matrix does to a vector. In (a), any original vector with coordinates x_1 and x_2 (bold arrow) is projected onto the x_1-axis, i.e., its x_1-coordinate is retained but its x_2 coordinate is replaced with 0 (dashed arrow). In (b), any original vector (bold arrow) is stretched and rotated into a result vector (dashed arrow) that is on the line $x_2 = 2x_1$ (thin line).

Another example is the singular matrix

$$\begin{bmatrix} 1 & 2 \\ 2 & 4 \end{bmatrix}$$

the second row of which is twice the first row. Applying this matrix to an arbitrary vector,

$$\begin{bmatrix} 1 & 2 \\ 2 & 4 \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix} = \begin{bmatrix} x_1 + 2x_2 \\ 2x_1 + 4x_2 \end{bmatrix}$$

the second element of the result is always twice the first element. Graphically, the x_2 coordinate of the result vector is always twice its x_1 coordinate; hence this matrix rotates every vector such that it lands on the $x_2 = 2x_1$ line (see Figure 5b).

In both examples, we can start with any vector in a plane (of the coordinate system in Figure 5), and the multiplication with the singular matrix results in a vector on a line (on the x_1 axis or on the line $x_2 = 2x_1$). A singular matrix therefore collapses the vectors into less dimensions than the original (a plane is collapsed onto a line). From knowing the vector $\mathbf{Ax}$, we cannot figure out the original vector $\mathbf{x}$, because information is lost when the dimensions are collapsed. Saying that from knowing the vector $\mathbf{Ax}$ we cannot figure out the original vector $\mathbf{x}$ is the same as saying that the equation $\mathbf{Ax} = \mathbf{r}$ cannot be solved. If the vector $\mathbf{r}$ is in the dimensions retained by the matrix (e.g. on the line onto which the matrix collapses every vector) then many vectors $\mathbf{x}$ are collapsed into this same vector $\mathbf{r}$ and there are infinitely many solutions to the equation; and if $\mathbf{r}$ is not in the dimensions retained by the matrix, then there is no solution.

We started this chapter with asking if it is possible to project a population vector backwards in time; i.e., if it is possible to tell the previous population vector $\mathbf{N}_{t-1}$ if we know the present population vector $\mathbf{N}_t$. To tell $\mathbf{N}_{t-1}$, we have to find a unique solution to the equation

$$\mathbf{N}_t = \mathbf{A}\mathbf{N}_{t-1}$$

(cf. equation (13)). Now we can answer the question as follows: it is possible to project backward provided that the projection matrix $\mathbf{A}$ is not singular. If $\mathbf{A}$ is singular, then information is lost, such that it is not possible to reconstruct $\mathbf{N}_{t-1}$ from $\mathbf{N}_t$.

4.4 The determinant

If a matrix is small and contains "simple" numbers (e.g. integers), then it might be obvious when it is singular (as it was in the preceding examples). But how do we tell whether a large matrix is singular or not? To this end, we need to define the *determinant* of a matrix. A determinant is a number that is calculated from the elements of the matrix; and if the determinant is zero, then the matrix is singular. In this section, we proceed with first showing how to calculate the determinant and then discussing the link between the matrix being singular and its determinant being zero.

4.4.1 2×2 matrices

The determinant of the 2x2 matrix

$$\mathbf{A} = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}$$

is given by the formula

$$|\mathbf{A}| = a_{11}a_{22} - a_{12}a_{21} \tag{21}$$

The vertical lines in $|\mathbf{A}|$ denote the determinant. The determinant of $\mathbf{A}$ can also be denoted as $\det(\mathbf{A})$.

Notice that the determinant of the 2×2 matrix appears as the denominator in the solution of a system of two equations, given in (18). If the determinant is zero, then the solution cannot be obtained; this already hints that a zero determinant signals a singular matrix.

4.4.2 $n \times n$ matrices

For larger matrices, the calculation of the determinant can be done through the calculation of smaller determinants as follows. Suppose we want to calculate the determinant of a 3×3 matrix,

$$\begin{vmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{vmatrix}$$

To start, assign a "+" or a "−" sign to each element of the determinant as on a chessboard (starting with "+" in the first element of the first row):

$$\begin{vmatrix} + & - & + \\ - & + & - \\ + & - & + \end{vmatrix}$$

Then take the first element of a row (e.g. take a_{11}); keep its original sign if the chessboard pattern assigns "+" to this element and change its sign if the chessboard pattern assigns "−"; and multiply this with the determinant of the matrix after deleting the row and the column where the element is. For the element a_{11}, this means

$$a_{11} \begin{vmatrix} a_{22} & a_{23} \\ a_{32} & a_{33} \end{vmatrix}$$

(note the "+" sign and that the first row and first column are left out from the determinant). The 2×2 determinant in this expression can be calculated as shown above. Do this same procedure while going through the entire row of the matrix, and add up the results to obtain the determinant of the 3×3 matrix:

$$\begin{vmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{vmatrix} = a_{11} \begin{vmatrix} a_{22} & a_{23} \\ a_{32} & a_{33} \end{vmatrix} - a_{12} \begin{vmatrix} a_{21} & a_{23} \\ a_{31} & a_{33} \end{vmatrix} + a_{13} \begin{vmatrix} a_{21} & a_{22} \\ a_{31} & a_{32} \end{vmatrix}$$

In this example, we expanded the determinant using its first row; but it can be done (and gives the same result) using any row or any column. The important things are to follow the chessboard pattern of signs; to go fully through one row or one column; and at every step, to delete the row and the column where the current element is. So the same determinant may also be calculated using the second row of the matrix:

$$\begin{vmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{vmatrix} = -a_{21} \begin{vmatrix} a_{12} & a_{13} \\ a_{32} & a_{33} \end{vmatrix} + a_{22} \begin{vmatrix} a_{11} & a_{13} \\ a_{31} & a_{33} \end{vmatrix} - a_{23} \begin{vmatrix} a_{11} & a_{12} \\ a_{31} & a_{32} \end{vmatrix}$$

The determinants of larger matrices are expanded analogously. The expansion of a 4×4 matrix results in an expression containing four 3×3 determinants, each of which is reduced to three 2×2 determinants as above. The procedure described here is known as the Laplace expansion of determinants.

4.4.3 Properties of determinants

I discuss the following properties of determinants for two reasons. First, it is easy to see why these properties hold; and therefore they can be seen as exercises about determinants. Second, I shall use these properties in the next section to prove that singular matrices have zero determinant. If however the reader is content with understanding only the fact (not the proof) that the determinant of a singular matrix is zero, then this section may be skipped.

(i) If we exchange two rows (or two columns) of a matrix, then it's determinant changes sign.

Denote the original matrix with $\mathbf{A}$ and let $\tilde{\mathbf{A}}$ be the same matrix except that the first and the second rows are exchanged. For example with 3×3 matrices, we have

$$|\mathbf{A}| = \begin{vmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{vmatrix} \quad \text{and} \quad |\tilde{\mathbf{A}}| = \begin{vmatrix} a_{21} & a_{22} & a_{23} \\ a_{11} & a_{12} & a_{13} \\ a_{31} & a_{32} & a_{33} \end{vmatrix}$$

Expand $|\mathbf{A}|$ using its first row and $|\tilde{\mathbf{A}}|$ using its second row. The numbers obtained during the expansion are exactly the same, except that due to the chessboard rule, all numbers in the expansion of $|\tilde{\mathbf{A}}|$ get a negative sign. Hence $|\tilde{\mathbf{A}}| = -|\mathbf{A}|$ as stated. The same applies if we exchange any two consecutive rows (e.g. the second and the third rows).

Suppose now that the first and the third rows are to be exchanged. This we can achieve by exchanging consecutive rows three times. Label the original rows of the matrix with 1,2,3 and exchange them as follows: (1,2,3) $\rightarrow$ (2,1,3) $\rightarrow$ (2,3,1) $\rightarrow$ (3,2,1). At each of these exchanges, the determinant changes sign; and because we have had an odd number of exchanges, the final determinant has the opposite sign to the original. It can be seen that exchanging two arbitrary rows can be achieved by an odd number of exchanges between consecutive rows. Hence in every case, the determinant changes sign.

(ii) If we multiply one row (or column) of a matrix with a number c, then the determinant is also multiplied with c.

Expand the determinant using the row (column) that has been multiplied with c; each term of the expansion is then multiplied with c.

(iii) If a row (or column) of a matrix contains sums of two terms, then the determinant is the sum of two determinants, where one determinant contains only the first terms and the other contains only the second terms in that row (or column).

The statement is far easier to understand if we write an example:

$$\begin{vmatrix} b_1+c_1 & b_2+c_2 & b_3+c_3 \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{vmatrix} = \begin{vmatrix} b_1 & b_2 & b_3 \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{vmatrix} + \begin{vmatrix} c_1 & c_2 & c_3 \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{vmatrix}$$

To see why this is true, expand the determinant using its row (column) where the sums are.

4.4.4 The determinant of a singular matrix

We introduced the concept of the determinant to be able to tell if a matrix is singular or not. So now we formulate the most important fact about singular matrices as the following theorem:

> **Theorem.** If a matrix is singular, then its determinant is zero; and conversely, if the determinant of a matrix is zero, then the matrix is singular.

To make the above statement briefer, we can say that a matrix is singular *if and only if* its determinant is zero. Here "if" means that the zero determinant is sufficient to make sure that the matrix is singular (i.e., all matrices with zero determinant are singular); and "only if" means that the zero determinant is necessary to make sure that the matrix is singular (i.e., only those matrices are singular that have zero determinant). The relationship "if and only if" between two properties mean that the two are equivalent; here a matrix being singular is equivalent to its determinant being zero. "If and only if" is sometimes abbreviated as "iff".

> **Proof.** First we prove the first half of the theorem: if a matrix is singular, then its determinant is zero. In a singular matrix, the rows are not linearly independent, i.e., one of the rows can be written as a linear combination of the others (see section 4.3). The simplest case is if two rows of the matrix are the same. In this case, we exchange these two rows, which makes no difference to the matrix and hence to its determinant. Exchanging two rows, however, changes the sign of the determinant by property (i) discussed in the previous section. There is only one number that does not change if its sign is changed to the opposite: zero. Hence the determinant of a matrix with two identical rows must be zero.
>
> Now we can consider the general case when no two rows are identical, but one of them is a linear combination of the others. Without loss of generality, we take the last row as a linear combination of the others. I write the reasoning for a 3×3 matrix, but it should be clear that the same argument holds for any size. Thus we start with the matrix
>
> $$\mathbf{A} = \begin{bmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ \alpha a_{11} + \beta a_{21} & \alpha a_{12} + \beta a_{22} & \alpha a_{13} + \beta a_{23} \end{bmatrix}$$
>
> where the last row is written as α times the first row plus β times the second row (a linear combination of the first two rows). The last row of the matrix contains sums, hence use property (iii) in the preceding section to write the determinant of $\mathbf{A}$ as
>
> $$|\mathbf{A}| = \begin{vmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ \alpha a_{11} & \alpha a_{12} & \alpha a_{13} \end{vmatrix} + \begin{vmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ \beta a_{21} & \beta a_{22} & \beta a_{23} \end{vmatrix}$$

Now both determinants on the right hand side have their last row multiplied with a number. Applying property (ii) in the previous section we obtain

$$|\mathbf{A}| = \alpha \begin{vmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{11} & a_{12} & a_{13} \end{vmatrix} + \beta \begin{vmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{21} & a_{22} & a_{23} \end{vmatrix}$$

Notice now that in the first determinant, the last row is the same as the first; and in the second determinant, the last row is the same as the second. Hence both determinants are zero because they contain identical rows, and we arrive at

$$|\mathbf{A}| = \alpha \cdot 0 + \beta \cdot 0 = 0$$

If the matrix is of size $n \times n$, then the same logic applies except that one of the rows is written as the sum of $n-1$ other rows, and hence in the first step of the expansion (using property (iii)) we get a sum of $n-1$ determinants. Each determinant is then shown to be zero as above.

We still have to prove the converse theorem, i.e., that every matrix that has zero determinant is singular. This we shall do at the end of the next section.

4.4.5 Cramer's rule

This entire section is "small print" and may be skipped. As a further exercise to determinants, here we obtain a simple formula to solve a system of linear equations of any size. In practice, however, this formula is rarely used; instead, systems of linear equations are solved by eliminating unknowns as we did at the beginning of section 4.1. We shall use this formula to complete the (optional) proof in the previous section.

Suppose we have a system of linear equations, $\mathbf{Ax} = \mathbf{r}$. Construct a new matrix $\mathbf{A}_i$ by replacing the ith column of $\mathbf{A}$ with the vector $\mathbf{r}$. For example, in the 3×3 case and $i = 2$ we have

$$\mathbf{A}_2 = \begin{bmatrix} a_{11} & r_1 & a_{13} \\ a_{21} & r_2 & a_{23} \\ a_{31} & r_3 & a_{33} \end{bmatrix}$$

For brevity, let the vector $\mathbf{a}_j$ be the jth column of the matrix. With this notation, the original matrix is

$$\mathbf{A} = \begin{bmatrix} \mathbf{a}_1 & \mathbf{a}_2 & \mathbf{a}_3 \end{bmatrix}$$

and the example we gave above is

$$\mathbf{A}_2 = \begin{bmatrix} \mathbf{a}_1 & \mathbf{r} & \mathbf{a}_3 \end{bmatrix}$$

Because $\mathbf{Ax} = \mathbf{r}$, we can put $\mathbf{Ax}$ into the matrix in place of $\mathbf{r}$:

$$\mathbf{A}_2 = \begin{bmatrix} \mathbf{a}_1 & \mathbf{Ax} & \mathbf{a}_3 \end{bmatrix}$$

By the matrix-vector multiplication, $\mathbf{Ax} = \sum_j x_j \mathbf{a}_j$ (verify this!). Substituting this into $\mathbf{A}_2$ we obtain

$$\mathbf{A}_2 = \begin{bmatrix} \mathbf{a}_1 & \sum_j x_j \mathbf{a}_j & \mathbf{a}_3 \end{bmatrix} = \begin{bmatrix} \mathbf{a}_1 & x_2\mathbf{a}_2 + \sum_{j \neq 2} x_j \mathbf{a}_j & \mathbf{a}_3 \end{bmatrix}$$

Now we calculate the determinant of $\mathbf{A}_2$ applying property (iii) of determinants (see section 4.4.3) to the second column:

$$|\mathbf{A}_2| = \left| \begin{array}{ccc} \mathbf{a}_1 & x_2\mathbf{a}_2 & \mathbf{a}_3 \end{array} \right| + \left| \begin{array}{ccc} \mathbf{a}_1 & \sum_{j\neq 2} x_j\mathbf{a}_j & \mathbf{a}_3 \end{array} \right|$$

By property (ii), the first determinant on the right hand side is $x_2|\mathbf{A}|$. In the second determinant, the second column is a linear combination of the other columns and therefore the determinant is zero. Therefore we arrive at $|\mathbf{A}_2| = x_2|\mathbf{A}|$, or

$$x_2 = \frac{|\mathbf{A}_2|}{|\mathbf{A}|}$$

We used the example of $\mathbf{A}_2$ throughout, but it should be clear that the same logic applies to any column of $\mathbf{A}$; and hence we can obtain any element of the solution vector $\mathbf{x}$ by the formula

$$x_i = \frac{|\mathbf{A}_i|}{|\mathbf{A}|} \tag{22}$$

This formula is called *Cramer's rule*.

Exercise: Show that the solution in equation (18) that we obtained for a 2×2 matrix is an example for Cramer's rule.

Cramer's rule gives the unique solution of the system $\mathbf{Ax} = \mathbf{r}$, provided that the formula in (22) is valid, i.e., if its denominator, $|\mathbf{A}|$, is not zero. If the determinant of matrix $\mathbf{A}$ is zero, then according to Cramer's rule, the unique solution of $\mathbf{Ax} = \mathbf{r}$ does not exist. As we have seen (section 4.3), a unique solution does not exist when the rows (columns) of $\mathbf{A}$ are not linearly independent, or, in other words, if the matrix is singular.

4.5 The inverse matrix

This section is again optional. Here we discuss how the inverse matrix $\mathbf{A}^{-1}$ can be obtained; it however turns out that we rarely need to calculate $\mathbf{A}^{-1}$ in practice.

Recall that in a matrix multiplication

$$\mathbf{AB} = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} \begin{bmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{bmatrix}$$

the first column of the result is obtained using only the first column of $\mathbf{B}$. Solve the equation

$$\mathbf{Ab}_1 = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} \begin{bmatrix} b_{11} \\ b_{21} \end{bmatrix} = \begin{bmatrix} 1 \\ 0 \end{bmatrix} \tag{23}$$

for the unknown vector $\mathbf{b}_1 = \begin{bmatrix} b_{11} \\ b_{21} \end{bmatrix}$. If we insert this vector as the first column of $\mathbf{B}$, then the first column of the product $\mathbf{AB}$ will be the first column of the identity matrix as shown above. We can repeat this trick with the second column. Solve the equation

$$\mathbf{Ab}_2 = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} \begin{bmatrix} b_{12} \\ b_{22} \end{bmatrix} = \begin{bmatrix} 0 \\ 1 \end{bmatrix} \tag{24}$$

for the unknown vector $\mathbf{b}_2 = \begin{bmatrix} b_{12} \\ b_{22} \end{bmatrix}$. Inserting the solution as the second column of $\mathbf{B}$ makes sure that the second column of $\mathbf{AB}$ will equal the second column of the identity

matrix. With a 2×2 matrix $\mathbf{A}$, hence we can assemble the inverse matrix from the columns obtained from equations (23) and (24):

$$\mathbf{A}^{-1} = \begin{bmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{bmatrix}$$

and by the construction, we have that

$$\mathbf{A}\mathbf{A}^{-1} = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} \begin{bmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{bmatrix} = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$$

The method is the same for larger matrices.

If $\mathbf{A}$ is singular, then equations (23) and (24) don't have unique solutions and hence $\mathbf{A}^{-1}$ cannot be constructed; the inverse of a singular matrix does not exist.

5 Long-term behaviour of matrix models

In this section, we consider an arbitrary matrix model

$$\mathbf{N}(t+1) = \mathbf{A}\mathbf{N}(t)$$

and ask what its long-term behaviour looks like. In this chapter, we shall use the above notation that is typical for ecological models of age- or stage-structured or spatially structured populations. However, the same principles apply to all matrix models.

To project the population from an arbitrary initial vector $\mathbf{N}_0$ for an arbitrarily long period of time t, we can write

$$\begin{aligned} \mathbf{N}(1) &= \mathbf{A}\mathbf{N}(0) \\ \mathbf{N}(2) &= \mathbf{A}\mathbf{N}(1) = \mathbf{A}\mathbf{A}\mathbf{N}(0) \equiv \mathbf{A}^2\mathbf{N}(0) \\ \mathbf{N}(3) &= \mathbf{A}\mathbf{N}(2) = \mathbf{A}^3\mathbf{N}(0) \\ &\vdots \\ \mathbf{N}(t) &= \mathbf{A}^t\mathbf{N}(0) \end{aligned} \tag{25}$$

The last of these equations lets us calculate $\mathbf{N}(t)$ directly from any initial population vector $\mathbf{N}(0)$, but at a huge computational cost: obtaining the matrix $\mathbf{A}^t$ involves $t-1$ matrix multiplications[5] (where t could be thousands). Even worse, such large computations offer little insight into what happens in the model and why.

Nonetheless, it is worthwhile to gain *some* experimental evidence about how a matrix model behaves. Therefore we start with a few computational experiments, and then turn to analytic techniques to explain why certain behaviours have been observed and how generally they occur.

[5]If only one specific initial vector is of interest, then $\mathbf{N}(t)$ can be obtained by t matrix-vector multiplications as $\mathbf{N}(1) = \mathbf{A}\mathbf{N}(0)$, ..., $\mathbf{N}(t) = \mathbf{A}\mathbf{N}(t-1)$. This amounts to less computations than calculating $\mathbf{A}^t$. However, the entire calculation has to be done again if we wish to try with a different initial vector.

5.1 Numerical experiments

5.1.1 An age-structured population

Figure 6 shows the behaviour of an age-structured population described by the Leslie matrix

$$\mathbf{L} = \begin{bmatrix} 0.7 & 1 & 2 & 2 & 1 \\ 0.25 & 0 & 0 & 0 & 0 \\ 0 & 0.4 & 0 & 0 & 0 \\ 0 & 0 & 0.6 & 0 & 0 \\ 0 & 0 & 0 & 0.5 & 0 \end{bmatrix} \tag{26}$$

Each histogram shows the fractions of individuals who belong to age classes 1-5. The first panel is the initial population, this was chosen arbitrarily. The subsequent histograms were obtained by projecting the population to the next year using $\mathbf{N}(t) = \mathbf{L}\mathbf{N}(t-1)$ and calculating the fractions $N_i(t)/\sum_j N_j(t)$ of individuals in age class i. The bottom panel of the figure shows how the population growth factor changed in time. The population growth factor is the total number of individuals in a given year divided with the total number in the previous year ($\sum_j N_j(t)/\sum_j N_j(t-1)$). It is commonly called the annual growth "rate" (note however that this quantity is not a rate!).

> **Exercise:** Reproduce the histograms shown in Figure 6 by projecting the initial population $\mathbf{N}(0) = [0, 1, 1, 1, 0]^T$ with the Leslie matrix above. Experiment with different initial vectors.

The histograms of Figure 6 change in the first few years; for example, the initial population had no 1-year olds, and consequently the population in year $t = 1$ has no 2-year olds. However, the changes diminish with time. The population converges to a *stable age structure*; after the transient has died out, the population consists of a fixed fraction of 1-year olds, 2-year olds, etc. Simultaneously with the stabilization of the age structure, also the population growth factor converges to a constant value. (Note that this constant value is not 1, which means that the population grows exponentially. The elements of $\mathbf{N}(t)$ hence increase with time, but the ratios or relative sizes of the elements, shown by the histograms in Figure 6, become constant.)

> The latter fact is easy to understand. Once the age structure has stabilized, each year the same fraction of individuals produces F_1 (and $F_2, ..., F_n$) offspring; and the same fraction of individuals is subject to mortality $1 - P_1$ (and $1 - P_2, ..., 1 - P_{n-1}$). Hence the *per capita* population growth is the same in each year.

The behaviour observed in Figure 6 is *typical* for almost all matrix models. The following exercise however shows that there are some exceptions.

> **Exercise:** Explore the long-term dynamics of biennial plants given by the Leslie matrix

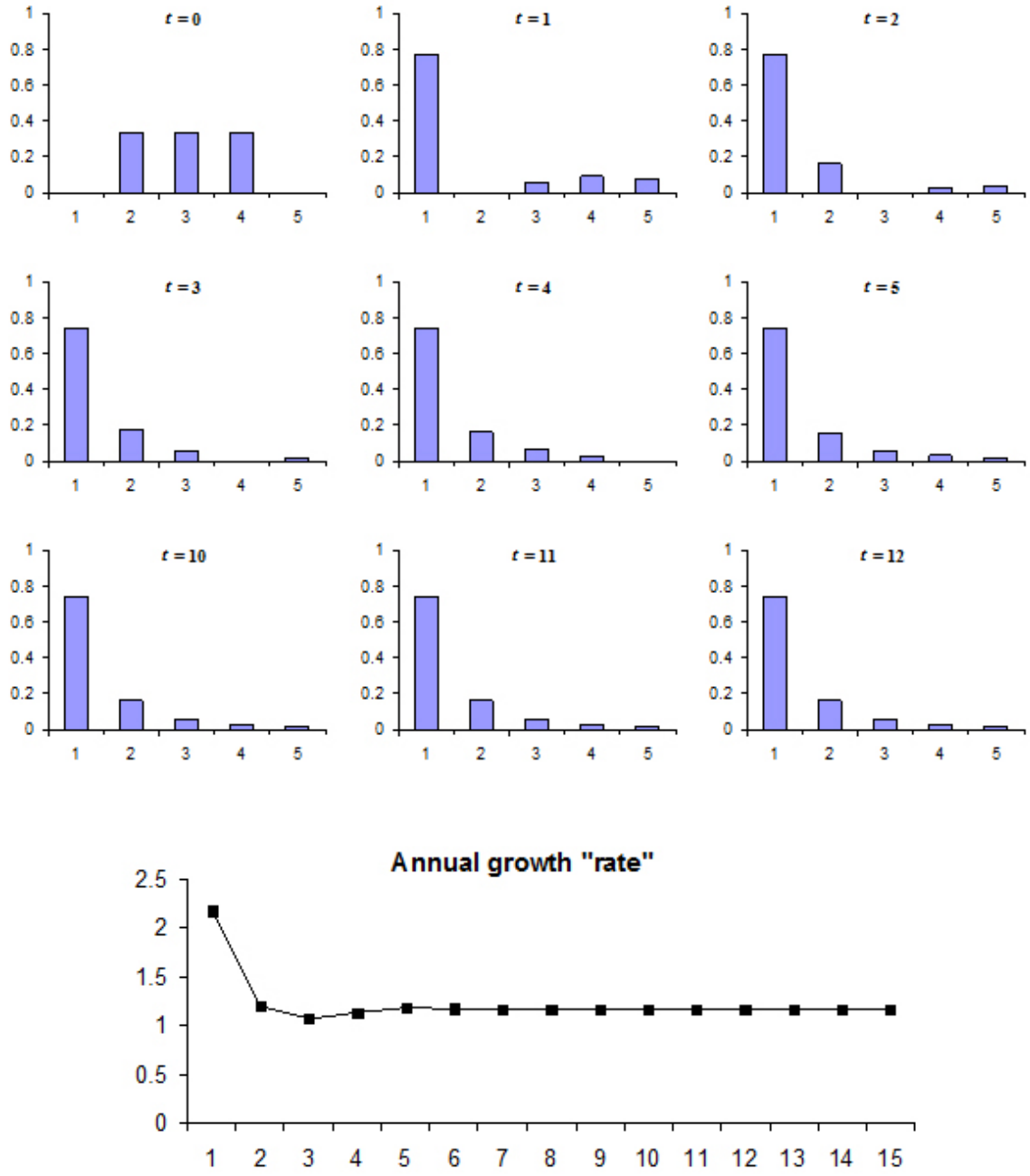

Figure 6: Changes of the age distribution and of the annual growth "rate" under the Leslie matrix given in (26). The initial distribution is shown in the top first panel. Initially the age distribution exhibits transient changes (top two rows) but later it stabilizes (last row of panels). The bottom panel shows the annual growth "rate" as a function of time.

$$\mathbf{L} = \begin{bmatrix} 0 & F \\ P & 0 \end{bmatrix} \tag{27}$$

where F is the fecundity of reproductive plants and P is the probability that a vegetative plant survives to be reproductive (choose the numbers arbitrarily). Monitor the age structure and the annual growth factor while projecting the population forward in time; show that these do not converge to fixed values but maintain 2-year oscillations. To interpret the results, it is helpful to consider an initial population of only 1-year old plants; and an initial population of only 2-year old plants. Any initial population is the mixture of these two.

5.1.2 Allele frequencies under mutation

In section 1.1, we set up a model to project the frequencies of alleles under mutation,

$$\mathbf{p}(t+1) = \mathbf{Q}\mathbf{p}(t)$$

This is a typical example for all models where frequencies are projected using a matrix of transition probabilities. Figure 7 shows the long-term behaviour of this model with the transition probability matrix

$$\mathbf{Q} = \begin{bmatrix} 0.8 & 0.2 & 0.15 \\ 0.06 & 0.7 & 0.1 \\ 0.14 & 0.1 & 0.75 \end{bmatrix} \tag{28}$$

Once again, the frequency vector $\mathbf{p}(t)$ converges to a stable distribution as t becomes large. The only difference from Figure 6 is in the annual growth factor. Because the elements of $\mathbf{p}(t)$ must add up to 1 in every year t, the total remains the same each year; and hence the annual growth factor is constant at value 1.

This is a direct consequence of the matrix being a stochastic matrix. Stochastic matrices represent transitions between states with no loss or gain of individuals; this is evident from the matrix as each of its columns sums to 1 (cf. section 1.1) and implies that the growth factor is always 1. Stochastic projection matrices are thus a special case of all projection matrices.

Exercise: Construct an example for a transition probability matrix under which $\mathbf{p}(t)$ does not converge to a stable distribution (a simple 2x2 example suffices).

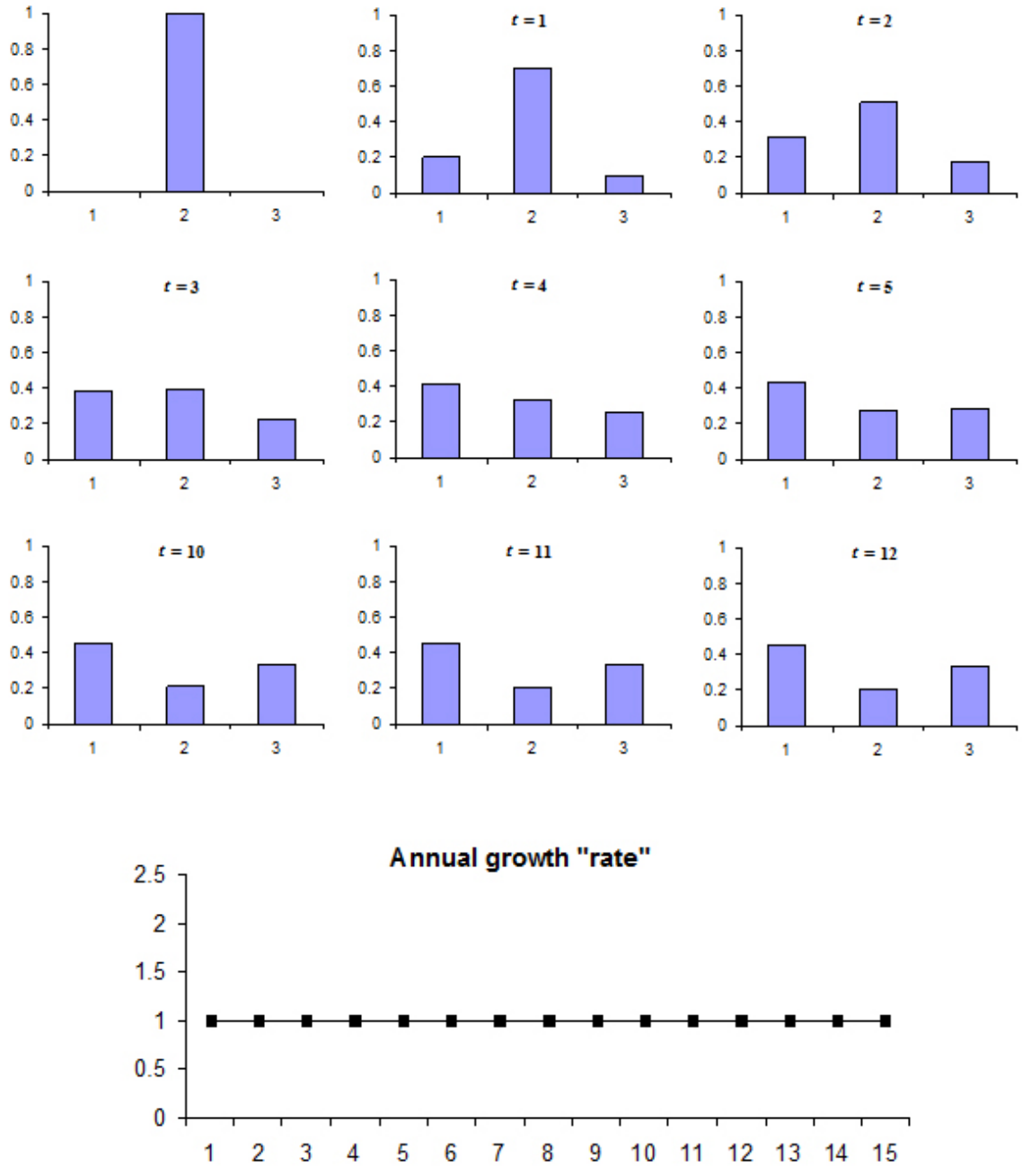

Figure 7: Changes of the state distribution and of the annual growth "rate" under the stochastic matrix given in (28). The initial distribution is shown in the top first panel.

5.2 Eigenvalues and eigenvectors

We begin the analysis of matrix models with seeking the equilibrium population structure observed in typical numerical experiments as in Figures 6 and 7. Once the equilibrium structure is established, the population grows each year by a constant factor λ, the annual growth factor, while preserving the ratios between the elements of the population vector. Hence each element of the population vector must grow by the same factor λ, and we have

$$\mathbf{N}(t+1) = \lambda \mathbf{N}(t)$$

As always, $\mathbf{N}(t+1) = \mathbf{A}\mathbf{N}(t)$. When the population has reached its equilibrium structure, then we have

$$\mathbf{A}\mathbf{N}(t) = \lambda \mathbf{N}(t)$$

In general, any vector $\mathbf{u}$ that satisfies the equation

$$\mathbf{A}\mathbf{u} = \lambda \mathbf{u} \tag{29}$$

is called an *eigenvector* of matrix $\mathbf{A}$, and the number λ is called an *eigenvalue*. The equilibrium structure of a population is therefore given by an eigenvector of the projection matrix, and the annual growth factor is an eigenvalue. To determine the equilibrium structure and the annual growth facto of a population, we must determine the eigenvector and the eigenvalue of its projection matrix $\mathbf{A}$.

Pretend for a moment that we know the eigenvalue λ; we could then solve equation (29) for the unknown vector $\mathbf{u}$. Rearranging equation (29), we obtain

$$\mathbf{A}\mathbf{u} - \lambda \mathbf{u} = (\mathbf{A} - \lambda \mathbf{I})\mathbf{u} = \mathbf{0} \tag{30}$$

But this equation has an obvious solution: if $\mathbf{u}$ is the zero vector, then this equation holds for any λ. (Write out the system of linear equations from (30) to see that every term in the left hand sides of the equations contains an element of $\mathbf{u}$. If all elements of $\mathbf{u}$ are zero, then the left hand side of each equation equals zero, precisely as required by (30)). $\mathbf{u} = \mathbf{0}$ is a trivial solution of equation (30), but it is also a useless solution because it corresponds to a nonexisting population.

Equation (30) represents a system of linear equations, and therefore has generically only one solution: the trivial solution. To find any other solution, the matrix $\mathbf{A} - \lambda \mathbf{I}$ must be singular (cf. sections 4.1 - 4.3).

This fact gives us the key to determine the eigenvalue λ. Because $\mathbf{A} - \lambda \mathbf{I}$ must be singular, its determinant must be zero; hence we have the equation

$$|\mathbf{A} - \lambda \mathbf{I}| = 0 \tag{31}$$

that we can solve for λ. This equation is called the *characteristic equation*.

Finding eigenvalues and eigenvectors is a two-step process: first solve the characteristic equation for λ; then solve equation (29) (or equivalently equation (30)) for $\mathbf{u}$. I detail these two steps below, and in the next section I show a worked example for the calculations.

1. Solve the characteristic equation. To start with, one has to expand the determinant in the characteristic equation; the expansion is described in section 4.4. In case of a 2x2 matrix $\mathbf{A}$, the characteristic equation becomes

$$\begin{vmatrix} a_{11}-\lambda & a_{12} \\ a_{21} & a_{22}-\lambda \end{vmatrix} = \lambda^2 - (a_{11}+a_{22})\lambda + a_{11}a_{22} - a_{12}a_{21} = 0$$

   The elements of $\mathbf{A}$ are known, the characteristic equation is thus a quadratic equation for λ. The quadratic equation has two solutions (λ_1, λ_2)[6], both are eigenvalues of matrix $\mathbf{A}$.

   If $\mathbf{A}$ is of size $n \times n$, then its characteristic equation is of degree n (this is easily seen from the expansion). Solving equations of high degrees is possible only numerically. In practice, it is best to plot the left hand side of the characteristic equation as a function of λ and determine the approximate eigenvalues from the graph[7].

2. Find the eigenvector for each eigenvalue. To find the eigenvector, we need to solve the equation that defines the eigenvector, $\mathbf{Au} = \lambda\mathbf{u}$ (or, equivalently, $(\mathbf{A}-\lambda\mathbf{I})\mathbf{u} = \mathbf{0}$). Each eigenvalue has its own eigenvector, hence we must do this step n times: First use λ_1 for λ to find its corresponding eigenvector $\mathbf{u}_1$; then use λ_2 to find $\mathbf{u}_2$; etc.

   In the system of linear equations that determine the elements of $\mathbf{u}$,

$$\begin{aligned} a_{11}u_1 + a_{12}u_2 + ... + a_{1n}u_n &= \lambda u_1 \\ a_{21}u_1 + a_{22}u_2 + ... + a_{2n}u_n &= \lambda u_2 \\ &\vdots \\ a_{n1}u_1 + a_{n2}u_2 + ... + a_{nn}u_n &= \lambda u_n \end{aligned}$$

   one of the equations is not independent of the others and thus gives no information. This is no surpise; this is because the matrix $\mathbf{A} - \lambda\mathbf{I}$ is singular (cf. step 1). We simply throw away one of the equations, and solve the rest. But because we have

[6]Recall that the solutions of the quadratic equation $ax^2 + bx + c = 0$ are $x_{1,2} = \frac{-b \pm \sqrt{b^2-4ac}}{2a}$. The two solutions may be complex (when $b^2 - 4ac < 0$ so that the square root gives a complex number) or exceptionally the two solutions may coincide yielding a multiple root (when $b^2 - 4ac = 0$). Accordingly, a matrix may have complex eigenvalues or multiple eigenvalues; we deal with these complications later.

[7]These approximate values can be made much more precise with numerical algorithms such as the bisection method or the Newton-Raphson method, which are implemented in many software packages. Complex eigenvalues cannot be obtained graphically, but we shall actually not need them here.

now one more unknown element of $\mathbf{u}$ than the number of useful equations, we cannot obtain a full solution. Instead, we can choose one of the elements arbitrarily, and solve the above equations for the rest. For example, if we choose a value for u_1, then all other elements of $\mathbf{u}$ follow. But if we increase the chosen value of u_1 k-fold, then also all other elements of $\mathbf{u}$ increase k-fold.

In other words, if $\mathbf{u}$ is an eigenvector, then $k\mathbf{u}$ is also an eigenvector. This is easily seen also from the definition of an eigenvector: if the equation $\mathbf{Au} = \lambda\mathbf{u}$ holds, then also $\mathbf{A}(k\mathbf{u}) = \lambda(k\mathbf{u})$ holds. Eigenvectors are determined only up to a constant.

Because $(\mathbf{A} - \lambda\mathbf{I})\mathbf{u} = \mathbf{0}$, the singular matrix $\mathbf{A} - \lambda\mathbf{I}$ collapses the eigenvector $\mathbf{u}$ into the origin. But if a matrix collapses a vector into the origin, then it collapses also every other vector that are on the same line; hence all vectors on a line are eigenvectors.

By determining the eigenvalues and eigenvectors, we have candidate solutions for the annual growth factor and the equilibrium population structure. We shall investigate in section 5.4 which of the eigenvalue-eigenvector pairs represent the annual growth factor and the stable structure.

5.3 A worked example

Let me illustrate the calculation of eigenvalues and eigenvectors with the example of an age-structured population given by the Leslie matrix

$$\mathbf{L} = \begin{bmatrix} 1 & 1 \\ 0.75 & 0 \end{bmatrix} \tag{32}$$

First we write down the characteristic equation. From $|\mathbf{L} - \lambda\mathbf{I}| = 0$, we obtain

$$\begin{vmatrix} 1-\lambda & 1 \\ 0.75 & -\lambda \end{vmatrix} = \lambda^2 - \lambda - 0.75 = 0$$

The solutions of this quadratic equation are

$$\lambda_{1,2} = \frac{1 \pm \sqrt{1 + 4 \cdot 0.75}}{2}$$

which gives

$$\lambda_1 = 1.5 \quad \text{and} \quad \lambda_2 = -0.5$$

In order to determine the eigenvector belonging to the first eigenvalue $\lambda_1 = 1.5$, we use $\mathbf{Lu} = \lambda\mathbf{u}$ with $\lambda_1 = 1.5$ as eigenvalue:

$$\begin{bmatrix} 1 & 1 \\ 0.75 & 0 \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} = 1.5 \begin{bmatrix} u_1 \\ u_2 \end{bmatrix}$$

and write this out as a system of equations for the unknown elements of the eigenvector, u_1, u_2:

$$\begin{aligned} u_1 + u_2 &= 1.5u_1 \\ 0.75u_1 &= 1.5u_2 \end{aligned}$$

From the second equation, we get $u_2 = \frac{1}{2}u_1$. We do not expect the first equation to give any more information; indeed, solving the first equation for u_2 gives the same result, $u_2 = \frac{1}{2}u_1$. We can thus neglect one of the two equations. As always, the eigenvector is determined only up to a constant, so that we can choose any vector where the second element is half of the first,

$$\mathbf{u}_1 = \begin{bmatrix} 2 \\ 1 \end{bmatrix} \quad \text{or} \quad \begin{bmatrix} 1 \\ 1/2 \end{bmatrix} \quad \text{or} \quad \begin{bmatrix} 2/3 \\ 1/3 \end{bmatrix} \quad \text{or} \ldots$$

In any case, the eigenvector shows that there are twice as many 1-year old individuals as 2-year olds.

In this example, the second eigenvalue, $\lambda_2 = -0.5$, clearly can not be the annual growth factor of the population, because the number of individuals cannot become negative. If nevertheless necessary, one can determine $\mathbf{u}_2$, the eigenvector corresponding to $\lambda_2 = -0.5$, in the same way as above. The equations

$$\begin{aligned} u_1 + u_2 &= -0.5u_1 \\ 0.75u_1 &= -0.5u_2 \end{aligned}$$

give $u_2 = -2u_1$, i.e., the vectors

$$\mathbf{u}_2 = \begin{bmatrix} 1 \\ -2 \end{bmatrix} \quad \text{or} \quad \begin{bmatrix} 2 \\ -4 \end{bmatrix} \quad \text{or} \quad \begin{bmatrix} 1/3 \\ -2/3 \end{bmatrix} \quad \text{or} \ldots$$

are all eigenvectors, as are infinitely many more vectors where the second component is (-2) times the first.

We can conclude that the equilibrium structure of this age-structured population is such that there are twice as many 1-year olds than 2-year olds (cf. $\mathbf{u}_1$), and if this structure is attained, then the population grows $\lambda_1 = 1.5$-fold every year.

> The lifetime reproductive success of this population is $R_0 = 1 + 0.75 = 1.75$, because all 1-year old individuals produce one offspring and the fraction 0.75 who survive till age 2 produce another offspring. Both $\lambda_1 = 1.5 > 1$ and $R_0 = 1.75 > 1$ indicate that the population is growing, but R_0 is less than λ_1. This is because the lifetime number of offspring is realized in 2 years, whereas λ_1 shows growth over 1 year. The offspring produced at age 1 start reproducing a year earlier than the offspring produced at age 2. Because the latter lose a year of reproduction, they contribute less to the long-term growth of the population.

Exercise: Determine the annual growth factor and the equilibrium age distribution of a population with a Leslie matrix similar to (32), except that each age class produces 2 offspring rather than 1. Compare the results with those above.

Exercise: Examine the effect of delayed reproduction by determining the annual growth factor and equilibrium age distribution of a population where the 1-year old individuals do not reproduce but survive to age 2 with probability 1, and thereafter the 2- and 3-year olds behave respectively as the 1- and 2-year olds in (32). Because the projection matrix is now 3x3, the eigenvalues must be determined numerically. (In reality, the probability of survival between ages 1 and 2 is less then 1; this will obviously decrease the population growth factor.)

Exercise: Consider a population with Leslie matrix as in (32), except that both offspring are produced at age 1. 75% of the individuals do survive to age 2, but do not reproduce then. Calculate both eigenvalues and eigenvectors. Can both eigenvalues represent annual growth factors in this model? Can you think of an initial population that goes extinct rather than grows with factor λ_1?

5.4 The dominant eigenvalue

Suppose that we have determined all eigenvalues of a projection matrix. Let us label the eigenvalues such that the first eigenvalue is the greatest in absolute value:

$$|\lambda_1| > |\lambda_2|, ...|\lambda_n| \tag{33}$$

The eigenvalue greatest in absolute value, λ_1, is called the *dominant eigenvalue* (or *leading eigenvalue*). The corresponding eigenvector, $\mathbf{u}_1$, is the *dominant eigenvector*. In this section, I explain as quickly as possible why, in almost all models, the dominant eigenvalue is the population growth factor and the dominant eigenvector gives the stable structure. The exceptions we shall treat later (see section 5.6), but the typical behaviour is this: after attaining the stable structure given by $\mathbf{u}_1$, the population grows exponentially with growth factor λ_1.

To investigate the long-term behaviour of a matrix model, we need to evaluate

$$\mathbf{N}(t) = \mathbf{A}^t\mathbf{N}(0) \tag{34}$$

(cf. equation (25)). The trick is to put the initial vector $\mathbf{N}(0)$ together of components of eigenvectors. This will be useful because multiplying many times an *eigenvector* with the matrix is much easier than multiplying any other vector. Since $\mathbf{Au} = \lambda\mathbf{u}$, each multiplication with $\mathbf{A}$ simply multiplies the eigenvector with the eigenvalue; and therefore

$$\mathbf{A}^t\mathbf{u} = \lambda^t\mathbf{u} \tag{35}$$

How to put the initial vector together from components of eigenvectors is easiest understood via a numerical example. Suppose that the eigenvectors are

$$\mathbf{u}_1 = \begin{bmatrix} 1 \\ 2 \end{bmatrix} \quad \text{and} \quad \mathbf{u}_2 = \begin{bmatrix} 0 \\ -1 \end{bmatrix}$$

and the initial vector is

$$\mathbf{N}(0) = \begin{bmatrix} 10 \\ 5 \end{bmatrix}$$

We can then write the initial vector as

$$\mathbf{N}(0) = 10\mathbf{u}_1 - 15\mathbf{u}_2$$

In general, we can (almost always) write the initial vector as

$$\mathbf{N}(0) = \alpha_1\mathbf{u}_1 + \alpha_2\mathbf{u}_2$$

or, in case of an $n \times n$ matrix, as

$$\mathbf{N}(0) = \alpha_1\mathbf{u}_1 + \alpha_2\mathbf{u}_2 + ... + \alpha_n\mathbf{u}_n \tag{36}$$

with some suitable numbers $\alpha_1, ..., \alpha_n$.

> Since the initial vector $\mathbf{N}(0)$ and the eigenvectors $\mathbf{u}_1, ..., \mathbf{u}_n$ are known, (36) represents a system of n linear equations for the n unknown numbers $\alpha_1, ..., \alpha_n$. These equations can be solved to obtain the values of $\alpha_1, ..., \alpha_n$; but we shall not need it in this section.

In equation (36), we have the initial vector built up from components of eigenvectors. Now we substitute this into the long-term projection (34) and use (35):

$$\begin{aligned} \mathbf{N}(t) &= \mathbf{A}^t\mathbf{N}(0) = \\ &= \mathbf{A}^t(\alpha_1\mathbf{u}_1 + \alpha_2\mathbf{u}_2 + ... + \alpha_n\mathbf{u}_n) = \\ &= \alpha_1\mathbf{A}^t\mathbf{u}_1 + \alpha_2\mathbf{A}^t\mathbf{u}_2 + ... + \alpha_n\mathbf{A}^t\mathbf{u}_n = \\ &= \alpha_1\lambda_1^t\mathbf{u}_1 + \alpha_2\lambda_2^t\mathbf{u}_1 + ... + \alpha_n\lambda_n^t\mathbf{u}_n = \\ &= \lambda_1^t\Big[\alpha_1\mathbf{u}_1 + \alpha_2\Big(\frac{\lambda_2}{\lambda_1}\Big)^t\mathbf{u}_2 + ... + \alpha_n\Big(\frac{\lambda_n}{\lambda_1}\Big)^t\mathbf{u}_n\Big] \end{aligned} \tag{37}$$

Because λ_1 is greater in absolute value than any of the other eigenvalues (cf. (33)), the ratios $\frac{\lambda_2}{\lambda_1}, ..., \frac{\lambda_n}{\lambda_1}$ are all less than 1 in absolute value. Raising these numbers to high powers gives *very* small values; for example, $\frac{\lambda_2}{\lambda_1} = 0.95$ raised to power $t = 200$ is only 0.000035. This means that all but the first term in (37) become negligibly small as t becomes large. We thus have

$$\mathbf{N}(t) \approx \lambda_1^t\alpha_1\mathbf{u}_1 \tag{38}$$

where the approximation is excellent for large t and improving ever more as t increases. The result in (38) says that $\mathbf{N}(t)$ is a number times the dominant eigenvector $\mathbf{u}_1$ (the product itself is the dominant eigenvector, because eigenvectors are determined only up to a constant); hence in the long term, the population structure becomes the structure of $\mathbf{u}_1$. Each time t increases by one, $\mathbf{N}(t)$ grows λ_1-fold; hence λ_1 is the population growth factor. By (38), we have shown that the population eventually grows with the dominant eigenvalue of its projection matrix and its structure converges to the dominant eigenvector.

5.5 Diagonalization

In this section, we formulate the above ideas in a somewhat more technical way that eventually leads to more biological insight. This is however not indispensable, and hence the reader may skip this section and proceed directly to the next.

This section will make use of diagonal matrices. A diagonal matrix is a matrix where the only non-zero elements are in the diagonal:

$$\mathbf{\Lambda} = \begin{bmatrix} \lambda_1 & 0 & \dots & 0 \\ 0 & \lambda_2 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & \lambda_n \end{bmatrix} \tag{39}$$

The next three exercises explore the properties of diagonal matrices, which will be used at crucial points in this section.

Exercise: Show that a diagonal matrix can easily be raised to any power as

$$\mathbf{\Lambda}^t = \begin{bmatrix} \lambda_1^t & 0 & \dots & 0 \\ 0 & \lambda_2^t & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & \lambda_n^t \end{bmatrix} \tag{40}$$

Exercise: Show that pre-multiplying any matrix $\mathbf{A}$ with a diagonal matrix $\mathbf{\Lambda}$ multiplies the rows of $\mathbf{A}$ with the numbers λ_i:

$$\mathbf{\Lambda A} = \begin{bmatrix} \lambda_1 a_{11} & \lambda_1 a_{12} & \dots & \lambda_1 a_{1n} \\ \lambda_2 a_{21} & \lambda_2 a_{22} & \dots & \lambda_2 a_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ \lambda_n a_{n1} & \lambda_n a_{n2} & \dots & \lambda_n a_{nn} \end{bmatrix} \tag{41}$$

Exercise: Show that post-multiplying any matrix $\mathbf{A}$ with a diagonal matrix $\mathbf{\Lambda}$ multiplies the columns of $\mathbf{A}$ with the numbers λ_i:

$$\mathbf{A\Lambda} = \begin{bmatrix} \lambda_1 a_{11} & \lambda_2 a_{12} & \dots & \lambda_n a_{1n} \\ \lambda_1 a_{21} & \lambda_2 a_{22} & \dots & \lambda_n a_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ \lambda_1 a_{n1} & \lambda_2 a_{n2} & \dots & \lambda_n a_{nn} \end{bmatrix} \tag{42}$$

The number of eigenvectors. The characteristic equation of an $n \times n$ matrix is an nth degree equation for the eigenvalue λ. Such an equation has n solutions, and therefore the matrix has n eigenvalues. There are however two possible complications. First, some of the eigenvalues may be complex numbers. One can do all necessary calculations also with complex eigenvalues and eigenvectors; and in biologically meaningful models, the predicted population vectors will (obviously) turn out to be real, not complex. The second complication is more serious: some of the solutions of the characteristic equation may coincide with each other. Such coinciding solutions are called *multiple roots*. Figure 8 shows the roots of the simple quadratic equation $x^2 - a = 0$. If a is positive (Figure 8a), then there are two roots, $x_{1,2} = \pm\sqrt{a}$, as shown in the figure. If a is negative, then there are again two different roots, $x_{1,2} = \pm\sqrt{a}$, which are complex numbers (because we are taking the square root of a negative number). These roots cannot be seen in the figure, but can nevertheless be calculated and used. The critical case is when $a = 0$. In this case, both solutions are the same number, $x_{1,2} = \pm 0 = 0$. As Figure 8 suggests, the two roots $x_{1,2}$ get closer and closer to each other as a approaches 0, and coincide only when a is exactly 0. Multiple roots are therefore exceptional (the technical term is "degenerate").

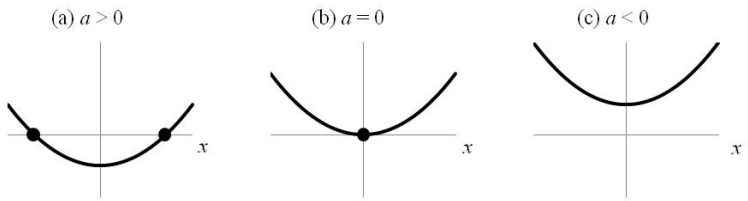

Figure 8: The graph of $x^2 - a$. In (a), the two roots $x_{1,2} = \pm\sqrt{a}$ are marked with dots. In (b), the two roots coincide, whereas in (c), the roots are complex and therefore cannot be seen.

Different eigenvalues always have their own eigenvectors, so if the matrix has n different eigenvalues (what is almost always the case) then it has n different eigenvectors that are linearly independent of each other. In case of a multiple root, however, we may or may not find as many different eigenvectors corresponding to the multiple root as the number of coinciding eigenvalues; and if there are fewer eigenvectors, then the total number of eigenvectors is less than n. In the remainder of this section, we shall assume that the matrix does have n different eigenvectors. Such matrices are called *diagonalizable*, i.e., we assume that the projection matrix we are concerned with is diagonalizable. All matrices that are not diagonalizable have multiple eigenvalues, and therefore represent exceptional (degenerate) cases that we do not pursue in this course.

Transforming the projection matrix. Assume thus that matrix $\mathbf{A}$ has n different eigenvectors. Collect these n eigenvectors into a matrix

$$\mathbf{C} = \begin{bmatrix} | & | & & | \\ \mathbf{u}_1, & \mathbf{u}_2, & \ldots, & \mathbf{u}_n \\ | & | & & | \end{bmatrix}$$

such that the eigenvectors are the columns of matrix $\mathbf{C}$. The product $\mathbf{AC}$ is easy to compute: treating $\mathbf{C}$ column-wise (cf. section 2.1) and using $\mathbf{Au} = \lambda\mathbf{u}$, we obtain

$$\mathbf{AC} = [\mathbf{Au}_1, \mathbf{Au}_2, \ldots, \mathbf{Au}_n] = [\lambda_1\mathbf{u}_1, \lambda_2\mathbf{u}_2, \ldots, \lambda_n\mathbf{u}_n]$$

In the product $\mathbf{AC}$, the columns of $\mathbf{C}$ are multiplied with the eigenvalues. As we have seen in equation (42), the same result can also be obtained from the multiplication

$$\mathbf{C\Lambda} = [\lambda_1\mathbf{u}_1, \lambda_2\mathbf{u}_2, \ldots, \lambda_n\mathbf{u}_n]$$

where $\mathbf{\Lambda}$ is the diagonal matrix containing the eigenvalues. Hence we can write

$$\mathbf{AC} = \mathbf{C\Lambda}$$

Because matrix $\mathbf{C}$ has n linearly independent columns (the eigenvectors are all different), it can be inverted ($\mathbf{C}^{-1}$ exists).By post-multiplying both sides of the above equation with ($\mathbf{C}^{-1}$, we can express $\mathbf{A}$ as

$$\mathbf{A} = \mathbf{C\Lambda C}^{-1} \tag{43}$$

Fast matrix powers. For projecting the population vector according to the matrix model $\mathbf{N}(t) = \mathbf{A}^t\mathbf{N}(0)$, we need to calculate high powers of matrix $\mathbf{A}$. The transformation in (43) is the key to do this. With (43), we obtain

$$\mathbf{A}^t = \mathbf{C\Lambda C}^{-1}\mathbf{C\Lambda C}^{-1}\ldots\mathbf{C\Lambda C}^{-1} = \mathbf{C\Lambda}\ldots\mathbf{\Lambda C}^{-1} = \mathbf{C\Lambda}^t\mathbf{C}^{-1} \tag{44}$$

because the products $\mathbf{C}^{-1}\mathbf{C}$ give the identity matrix and therefore are cancelled. Raising a *diagonal* matrix to a high power is easy (see (40)), so that we can calculate $\mathbf{A}^t$ efficiently if we know all its eigenvalues (for matrix $\mathbf{\Lambda}$) and eigenvectors (for matrix $\mathbf{C}$). The only remaining hurdle is to calculate the inverse matrix $\mathbf{C}^{-1}$. As we show in the next step, the rows of $\mathbf{C}^{-1}$ also have an intimate relationship with the original matrix $\mathbf{A}$.

Left eigenvectors. To figure out what matrix $\mathbf{C}^{-1}$ contains, pre-multiply both sides of equation (43) with $\mathbf{C}^{-1}$. This gives

$$\mathbf{C}^{-1}\mathbf{A} = \mathbf{C}^{-1}\mathbf{C\Lambda C}^{-1} = \mathbf{\Lambda C}^{-1} \tag{45}$$

Recall from (41) that in $\mathbf{\Lambda C}^{-1}$, pre-multiplication with the diagonal matrix multiplies the rows of matrix $\mathbf{C}^{-1}$ with the eigenvalues in $\mathbf{\Lambda}$. Let us thus consider matrix $\mathbf{C}^{-1}$ as a collection of rows:

$$\mathbf{C}^{-1} = \begin{bmatrix} — \ \mathbf{v}_1^{\mathrm{T}} — \\ — \ \mathbf{v}_2^{\mathrm{T}} — \\ \vdots \\ — \ \mathbf{v}_n^{\mathrm{T}} — \end{bmatrix}$$

The superscript "T" denotes the transpose (see section 2.2), i.e., makes the vectors row vectors that can be placed in the rows of the matrix. Now we look at the two sides of equation (45). By the rules of matrix multiplication, the ith row of the product $\mathbf{C}^{-1}\mathbf{A}$ is computed by multiplying the ith row of $\mathbf{C}^{-1}$ with matrix $\mathbf{A}$; hence the ith row of the left hand side is given by the vector-matrix product $\mathbf{v}_i^T\mathbf{A}$. On the right hand side of (45) a diagonal matrix pre-multiplies $\mathbf{C}^{-1}$ and hence the ith row of the result is λ_i times the ith row of $\mathbf{C}^{-1}$, which is $\lambda_i\mathbf{v}_i^T$. Combining these results, we have

$$\mathbf{v}_i^T\mathbf{A} = \lambda_i\mathbf{v}_i^T \tag{46}$$

$\mathbf{v}_i^T$ is thus a row vector such that if we multiply it with matrix $\mathbf{A}$, the result is the ith eigenvalue times the original vector $\mathbf{v}_i^T$. This is very similar to the definition of an eigenvector given in equation (29), the only difference is that $\mathbf{v}_i^T$ is a row vector and therefore must be placed before the matrix in order to be able to multiply. $\mathbf{v}_i^T$ is called the *left eigenvector* belonging to eigenvalue λ_i. The "normal" eigenvectors $\mathbf{u}_1, \ldots, \mathbf{u}_n$ are also called right eigenvectors (although if nothing is said, an eigenvector is taken to be the right eigenvector). The set of left eigenvectors, $\mathbf{v}_1^T, \ldots, \mathbf{v}_n^T$ are similar to the right eigenvectors except that they are row vectors and hence the order of matrix-vector multiplication is the opposite. Each eigenvalue λ_i has a (right) eigenvector $\mathbf{u}_i$ and a left eigenvector $\mathbf{v}_i^T$.

Scaling of the left eigenvectors. Like any eigenvector, also the left eigenvectors are undetermined up to a constant, i.e., any number times an eigenvector $\mathbf{v}_i^T$ is also an eigenvector belonging to λ_i. However, we are not as free choosing the left eigenvectors as we are to choose the right eigenvectors. If we want the left eigenvectors to be the rows of $\mathbf{C}^{-1}$, we must make sure that the product $\mathbf{C}^{-1}\mathbf{C}$ will indeed be the identity matrix as it should. The off-diagonal elements will be 0 automatically, but for the diagonal elements of the product to be 1, we must have that the ith row of $\mathbf{C}^{-1}$ times the ith column of $\mathbf{C}$ is 1:

$$\mathbf{v}_i^T \mathbf{u}_i = 1 \quad \text{or, equivalently,} \quad \sum_{j=1}^{n} v_{i,j} u_{i,j} = 1 \tag{47}$$

where $v_{i,j}$ and $u_{i,j}$ denote respectively the jth elements of the ith left and right eigenvectors. In practice, we first choose the scaling of the right eigenvectors as we wish, and then compute the left eigenvectors to obey the scaling given in (47). The scaling equation gives one more equation to those determining the elements of the left eigenvector, so that we have as many independent equations as vector elements and can obtain all elements of the left eigenvector unambiguously.

Long-term population growth and the reproductive value. Now we return to the population model $\mathbf{N}(t) = \mathbf{A}^t \mathbf{N}(0)$. Substituting $\mathbf{A}^t$ from equation (44), the population vector after t years of growth is given by

$$\mathbf{N}(t) = \mathbf{C}\mathbf{\Lambda}^t \mathbf{C}^{-1} \mathbf{N}(0) \tag{48}$$

where all ingredients ($\mathbf{C}$, $\mathbf{\Lambda}$, $\mathbf{C}^{-1}$) are given by the eigenvalues and eigenvectors of the projection matrix $\mathbf{A}$. This equation gives an exact projection of the population for arbitrarily long time t, at the cost of calculating all eigenvlues and (left and right) eigenvectors.

If we are interested in only what happens after sufficiently long time, then we can obtain a good approximation by looking into the matrix $\mathbf{\Lambda}^t$ for large t. Let λ_1 be the dominant eigenvalue (i.e., the one largest in absolute value) and rewrite (40) such that λ_1^t is factored out:

$$\mathbf{\Lambda}^t = \begin{bmatrix} \lambda_1^t & 0 & \ldots & 0 \\ 0 & \lambda_2^t & \ldots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \ldots & \lambda_n^t \end{bmatrix} = \lambda_1^t \begin{bmatrix} 1 & 0 & \ldots & 0 \\ 0 & \left(\frac{\lambda_2}{\lambda_1}\right)^t & \ldots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \ldots & \left(\frac{\lambda_n}{\lambda_1}\right)^t \end{bmatrix}$$

Because the numbers $\frac{\lambda_2}{\lambda_1}, \ldots, \frac{\lambda_n}{\lambda_1}$ are all less than 1 in absolute value, their t-powers become very close to zero when t is large. Hence in the long term, all but the first diagonal element

of $\mathbf{\Lambda}^t$ are negligibly small, and we have

$$\mathbf{\Lambda}^t \approx \lambda_1^t \begin{bmatrix} 1 & 0 & \dots & 0 \\ 0 & 0 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & 0 \end{bmatrix}$$

Substituting this approximation into the exact projection in (48) greatly simplifies the matrix multiplications because $\mathbf{\Lambda}^t$ now contains many zeros. In fact, all but the first column of $\mathbf{C}$ is multiplied with only zeros; and all but the first row of $\mathbf{C}^{-1}$ is multiplied with only zeros. The projection thus simplifies to

$$\mathbf{N}(t) \approx \lambda_1^t \mathbf{u}_1 \mathbf{v}_1^T \mathbf{N}(0) \tag{49}$$

This equation is exactly the same as the approximation we got in equation (38), with the additional information that the number α_1 in (38) is given by $\mathbf{v}_1^T \mathbf{N}(0)$, the scalar product of the dominant left eigenvector and the initial population vector.

Equation (49) gives an important biological interpretation to the dominant left eigenvector. The initial population vector $\mathbf{N}(0)$ influences the long-term projection $\mathbf{N}(t)$ only by a single number, $\mathbf{v}_1^T \mathbf{N}(0) = \sum_j v_{1,j} N_j(0)$. This number is the weighted sum of the initial numbers $N_j(0)$, and the weights are the elements of the dominant left eigenvector. For example, if the first element of the left eigenvector is much greater than the second, then starting a population with individuals in the first state (age group etc.) will give much higher popultion numbers after t years than starting a population with individuals in the second state. The jth element of $\mathbf{v}_1^T$ hence show how "valuable" is a j-state individual for the population far in the future. For example in age-structured populations, pre-reproductive individuals give a lower contribution to population growth because it takes time before they start reproducing (this leaves less time for exponential growth) and may also die before they reach reproduction. As a consequence, the first few elements of $\mathbf{v}_1^T$, which correspond to the pre-reproductive age classes, are smaller than those of the reproductive age classes. Post-reproductive individuals do not contribute to future population growth at all, and the corresponding elements of $\mathbf{v}_1^T$ are zero. In other matrix models, the contribution of various states to long-term population growth may be less intuitively obvious. All these differences are however quantitatively captured in the dominant left eigenvector, the elements of which are called the *reproductive values* of the corresponding states.

5.6 Classification of matrix models and the Perron-Frobenius theorem

In this final section on the analysis of matrix models, we focus on how things can go wrong. This will allow us to formulate the exact conditions that guarantee the "typical" behaviour of exponential growth with a stable population structure. Finally, we describe an enormously useful theorem that allows us to deduce the qualitative behaviour of a matrix model directly from the life cycle graph.

Equation (38) in section 5.4 predicts that the population will eventually grow exponentially at a speed given by the dominant eigenvalue λ_1 and its structure will be given by the dominant eigenvector $\mathbf{u}_1$ (the same is obtained also in equation (49) of section 5.5). There are two steps in the derivation where exceptions may appear.

1. There may be no "dominant" eigenvalue, i.e., no *single* eigenvalue λ_1 that is greatest in absolute value. If there are several eigenvalues of the same absolute value, then all terms corresponding to these in equation (37) are of the same magnitude and cannot be neglected to arrive at the single term in equation (38). This is the case if the largest eigenvalue is a multiple root, or if there are different eigenvalues that equal in absolute value (such as 1 and -1, for example). Both possibilities are degenerate (i.e., exceptional in a mathematical sense), but the latter does show up in interesting biological systems; this will explain the oscillating dynamics of biennial plants, numerically investigated in an exercise of section 5.1.1.

2. The number α_1 in equation (38) may be zero. In this case, the whole term is of course zero rather than being the largest; and therefore some other terms of equation (37) that have been neglected in (38) can in fact be not be neglected. Note however that even a small (but non-zero) α_1 is sufficient for the approximation (38) to be valid, because the powers $\left(\frac{\lambda_2}{\lambda_1}\right)^t$ etc. in equation (37) become overwhelmingly small when t is large.

   The number α_1 depends on the initial population vector $\mathbf{N}(0)$. In some models, α_1 is positive for all possible initial vectors; but in other systems, there are initial vectors that make α_1 zero. An example for the latter is an age-structured population where there are post-reproductive ages, and the initial population contains only individuals who will no longer reproduce. Obviously, this initial population must go extinct even if other initial populations can grow with the same projection matrix. In section 5.5, we saw that α_1 is the weighted sum of the elements of the initial vector $\mathbf{N}(0)$, and the weights are given by the dominant left eigenvector. If the dominant left eigenvector contains only positive numbers, then the weighted sum must also be positive, and therefore α_1 is positive (assuming that at least one element of $\mathbf{N}(0)$ is positive, but otherwise there is no population to start with). If however the dominant left eigenvector contains some zeros, then we can initiate the population with individuals in only those states that have zero elements in the dominant left eigenvector and then α_1 is zero.

To see when we can exclude the above two exceptions from exponential growth with stable population structure, we need to classify the matrix population models into three categories. This classification can be done just by inspecting two properties of the life cycle graph.

- We say that the life cycle graph and the corresponding projection matrix is *irreducible* if it is possible to get from any state to any state following the arrows of the life cycle graph. For example, the life cycle graph of an age-structured population in Figure 9 is *not* irreducible (i.e., it is reducible) because from state 3, it is not possible to get back to state 1 or to state 2. If however we delete the grey part of the figure (by assuming $P_2 = 0$), then the remaining life cycle graph is irreducible.

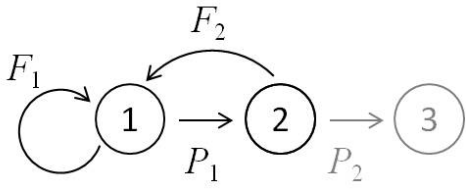

Figure 9: With a post-reproductive age class (age 3), the life cycle graph is reducible. If the grey part of the figure is deleted, then the remainder is irreducible.

- For irreducible graphs, we need to find all "loops" (sequences of arrows along which we get back to the state we started from) and record their length (the number of arrows followed within the loop). Let I denote the greatest common divisor of all loop lengths (I is called the index of imprimitivity). If $I = 1$, then the life cycle graph and the projection matrix is *primitive*; otherwise it is imprimitive ("not primitive"). In the life cycle graph shown in Figure 10, there are three loops: $1 \to 2 \to 1$ (length 2), $1 \to 2 \to 3 \to 4 \to 1$ (length 4), and, in grey, $1 \to 2 \to 3 \to 1$ (length 3). The greatest common divisor of the loop lengths 2, 3, 4 is $I = 1$, hence the life cycle graph is primitive. If however we delete the grey arrow from Figure 10 (by assuming $F_3 = 0$), then the remaining loops are of lengths 2 and 4, the greatest common divisor of which is $I = 2$. Hence without the grey arrow, the life cycle graph is imprimitive.

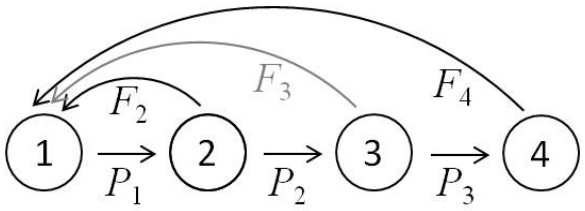

Figure 10: With all arrows present, this age-structured population has a primitive life cycle graph. If however the grey arrow is absent, the life cycle graph is imprimitive.

The above two properties classify all projection matrices into three categories: (i) primitive matrices that are irreducible and have $I = 1$; (ii) irreducible but imprimitive matrices (irreducible but $I > 1$); and (iii) reducible matrices (here I is irrelevant). The *Perron-Frobenius theorem*, which we describe in the remainder of this section, characterizes the eigenvalues and eigenvectors of these three categories of projection matrices. As we have seen above, the eigenvalues and eigenvectors determine in turn the long-term dynamics of matrix population models. The Perron-Frobenius theorem is valid for non-negative matrices, i.e., for matrices all elements of which are positive or zero. Projection matrices of discrete-time matrix models contain life history parameters such as fecundities and probabilities of survival, transition probabilities between various states and

similar quantities that are non-negative by their nature. Hence projection matrices are non-negative matrices and fall under the Perron-Frobenius theorem.

(i) *Primitive matrices.* If the projection matrix is primitive, then it has a dominant eigenvalue which is a strictly positive real number, a simple (not multiple) root of the characteristic equation and strictly larger in absolute value than any other eigenvalue. All elements of the corresponding dominant eigenvector are strictly positive (no zeros), and the same holds also for the dominant left eigenvector.

These facts imply that neither of the two problems described at the beginning of this section can occur. For primitive matrices, there is a single dominant eigenvalue, hence the first exception is excluded; and because the dominant left eigenvector has no zeros but only positive elements, the possibility that α_1 could be zero is also excluded (see the details above).

In summary, if the projection matrix is primitive, then the population vector converges to the stable structure given by the dominant eigenvector and afterwards grows exponentially with the dominant eigenvalue. The convergence occurs for any possible initial population vector that has at least one positive element (otherwise the initial population does not exist). At the stable structure, no state is empty (because all elements of the dominant eigenvector are positive)[8].

(ii) *Irreducible but imprimitive matrices.* Irreducible but imprimitive matrices have a strictly positive eigenvalue such that no eigenvalue is greater in absolute value, but have another $I-1$ eigenvalues that have the same absolute value (with $I > 2$, some of these are complex eigenvalues). The dynamics of these matrix models oscillate with period I; the simplest example is the dynamics of biennial plants, where $I = 2$ and the population exhibits cycles of period 2.

The best way to analyze these models is to follow the dynamics not every year but every I years (i.e., to use $\mathbf{N}(t+I) = \mathbf{A}^I\mathbf{N}(t)$). In this way, we don't see the oscillations (for example if the population has cycles over $I = 2$ years, then odd years are the same and even years are the same; if we census the population in only even years, then we see only one type of years). $\mathbf{A}^I$, the matrix projecting over I years, is primitive such that we can analyze the long-term trends as above, and can "fill in" the oscillations afterwards.

(iii) *Reducible matrices.* With reducible matrices, both exceptions detailed at the beginning of this section can occur. One can try to isolate a part of the life cycle graph

[8]This is sometimes called the *strong ergodic theorem* of matrix models. "Ergodic" means that the dynamics becomes independent of the initial vector. "Strong ergodic" means that it converges to a definite structure, given by the dominant eigenvector; in temporally fluctuating environments, for example, the dynamics still forgets its initial state but because of the fluctuations, there is no single definitive structure to which the dynamics converges.

that is irreducible and there are no arrows pointing inwards from other parts. (Outgoing arrows are no problem because they correspond to losses similar to mortality, but incoming arrows represent an unknown amount of inflow from other parts of the graph.) Such an isolated part can be analyzed separately. For example in Figure 9, we can cut the post-reproductive age 3 and analyze the rest of the graph. Once the dynamics of age classes 1-2 are known, we can calculate the number of 3-year olds simply as the number of survivors from the previous year's 2-year olds.