PRIMER 2

Linear Algebra

The mathematical field of linear algebra provides many useful techniques for analyzing dynamical models. Linear algebra can be thought of as a series of bookkeeping techniques for linear equations. An advantage of these techniques is that complicated equations involving more than one variable can be written in a pleasantly compact form. An even more important advantage is that we can use theorems from linear algebra to prove certain facts about the behavior of our models.

P2.1 An Introduction to Vectors and Matrices

Linear algebra describes mathematical operations on *lists of information*. Each element of a list may be a number, a parameter, a function, or a variable. A *vector* represents a list of elements arranged in one of two ways. A "column vector" arranges elements from top to bottom:

A ***vector*** is a list of elements.

$$\begin{pmatrix} 12 \\ 19 \end{pmatrix} \quad \begin{pmatrix} 1 \\ 5 \\ 9 \\ 7 \end{pmatrix} \quad \begin{pmatrix} x \\ y \end{pmatrix} \quad \begin{pmatrix} x \\ y \\ z \end{pmatrix} \quad \begin{pmatrix} n_1 \\ n_2 \\ \vdots \\ n_d \end{pmatrix}.$$

A "row vector" arranges elements from left to right:

$$(12,\ 19) \qquad (1,\ 5,\ 9,\ 7) \qquad (x,\ y) \qquad (x,\ y,\ z) \qquad (n_1,\ n_2,\ \ldots\ n_d).$$

Row vectors can be written with large spaces rather than commas separating each element, e.g., (12 19) instead of (12, 19). Vectors are sometimes written in curly brackets { } or in square brackets [ ], but this is a matter of preference. The number of elements in a vector indicates its "dimensionality." For example, the vector $\binom{x}{y}$ is a two-dimensional column vector, while (x, y) is a two-dimensional row vector.

There is a simple, but very important, graphical interpretation of vectors. We can visualize a vector with two elements as a line on a plane, starting at the origin and ending at the point whose x and y coordinates are given by the elements of the vector $\binom{x}{y}$ (Figure P2.1). Similarly, a vector with three elements can be visualized as a line in three dimensions (Figure P2.2). This interpretation holds for higher dimensions as well, although visualizing the vector becomes problematic! This graphical interpretation indicates that a d-dimensional vector can be thought of as a line with a certain length and direction in d-dimensional space. For example, the length of a two-dimensional vector $\binom{a}{b}$ can be calculated using the Pythagorean theorem for a triangle: $\sqrt{a^2 + b^2}$ (Figure P2.1).

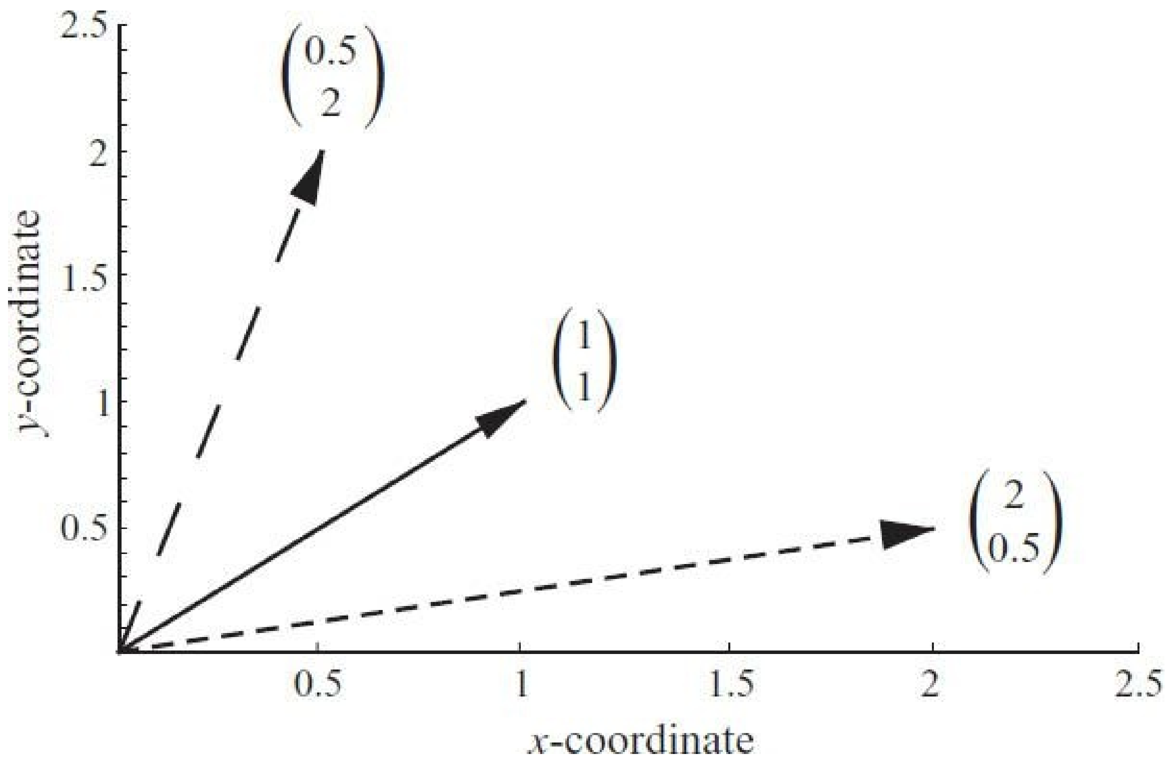


Figure P2.1: Vectors represented as arrows on a two-dimensional plot. A vector is plotted by starting at the origin and ending at the point whose x- and y-coordinates are given by the vector $\binom{x}{y}$. Thus, each vector represents a line pointing in a particular direction with a particular length. For example, the vector $\binom{x}{y} = \binom{2}{0.5}$ points in a direction that is arctan(y/x) = 14° above the horizontal axis and $\sqrt{x^2 + y^2} = 2.06$ units in length.

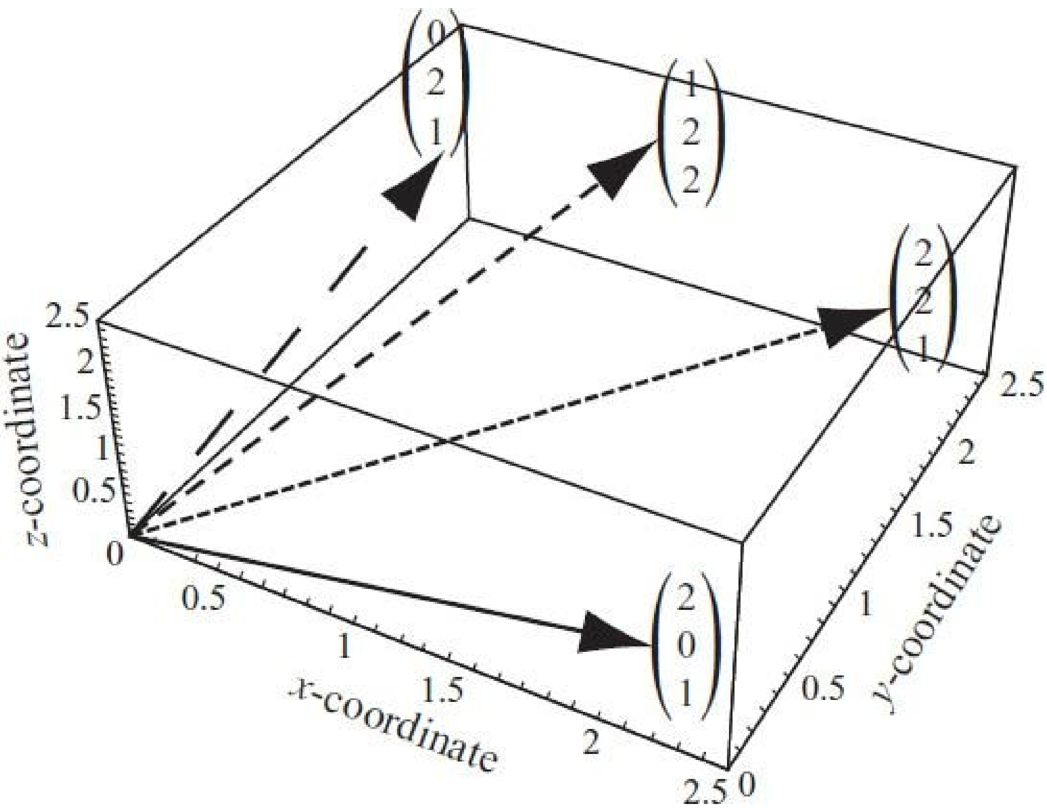


Figure P2.2: Vectors represented as arrows on a three-dimensional plot. A vector is plotted by starting at the origin and ending at the point whose x-, y- and z-coordinates are given by the vector $\begin{pmatrix} x \\ y \\ z \end{pmatrix}$.

While a column vector has only one column and a row vector has only one row, a *matrix* (plural: matrices) represents a more general list that can contain any number of rows and columns:

> A ***matrix*** is a table of elements with r rows and c columns.

$$\begin{pmatrix} 12 & 19 \\ 10 & 23 \end{pmatrix} \quad \begin{pmatrix} 1 & 5 & 9 \\ 7 & 7 & 7 \end{pmatrix} \quad \begin{pmatrix} a & b \\ c & d \\ e & f \end{pmatrix} \quad \begin{pmatrix} m_{11} & m_{12} & \cdots & m_{1c} \\ m_{21} & m_{22} & \cdots & m_{2c} \\ \vdots & \vdots & \vdots & \vdots \\ m_{r1} & m_{r2} & \cdots & m_{rc} \end{pmatrix}.$$

The dimensionality of a matrix is always written as the number of rows by the number of columns (the dimensionality of the above matrices is 2×2, 2×3, 3×2, and $r \times c$). A vector can be thought of as a special case of a matrix; a column vector is a $d \times 1$ matrix and a row vector is a $1 \times d$ matrix. We will use the convention that m_{ij} describes the element in the ith row and jth column of a matrix. That is, we always refer to an element according to its *row first and column second*. We will identify a matrix by assigning it a label using a boldface symbol (e.g., **M**) and a vector by assigning it a label with a "half arrow" above it (e.g., $\vec{x}$).

Matrices also have a graphical interpretation. A matrix can be considered as a way of "transforming" (i.e., moving) a vector. The transformation might rotate or stretch the original vector so that the vector points in a different direction and/or has a different length. As illustrated in Figure P2.3, a 2 × 2 matrix maps the x and y coordinates of a point given by the vector $\begin{pmatrix} x \\ y \end{pmatrix}$ to a new set of x and y coordinates. These new coordinates are determined by matrix multiplication, as described in section P2.4.

Most matrices used in mathematical biology are "square," meaning that the number of rows equals the number of columns (i.e., the matrix has dimensionality $d \times d$). There are several special square matrices that we will encounter often. A *diagonal matrix* contains elements that are all zero except along the diagonal from upper left to lower right:

Definition P2.1:

$$\mathbf{D} = \begin{pmatrix} m_{11} & 0 & \cdots & 0 \\ 0 & m_{22} & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \cdots & m_{dd} \end{pmatrix} \qquad \text{(diagonal matrix)}$$

An *identity matrix* is a diagonal matrix with ones along the diagonal:

Definition P2.2:

$$\mathbf{I} = \begin{pmatrix} 1 & 0 & \cdots & 0 \\ 0 & 1 & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \cdots & 1 \end{pmatrix} \qquad \text{(identity matrix)}$$

An *upper triangular matrix* is a matrix whose elements below the diagonal are zero:

Definition P2.3:

$$\begin{pmatrix} m_{11} & m_{12} & \cdots & m_{1c} \\ 0 & m_{22} & \cdots & m_{2c} \\ \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \cdots & m_{rc} \end{pmatrix} \qquad \text{(upper triangular matrix)}$$

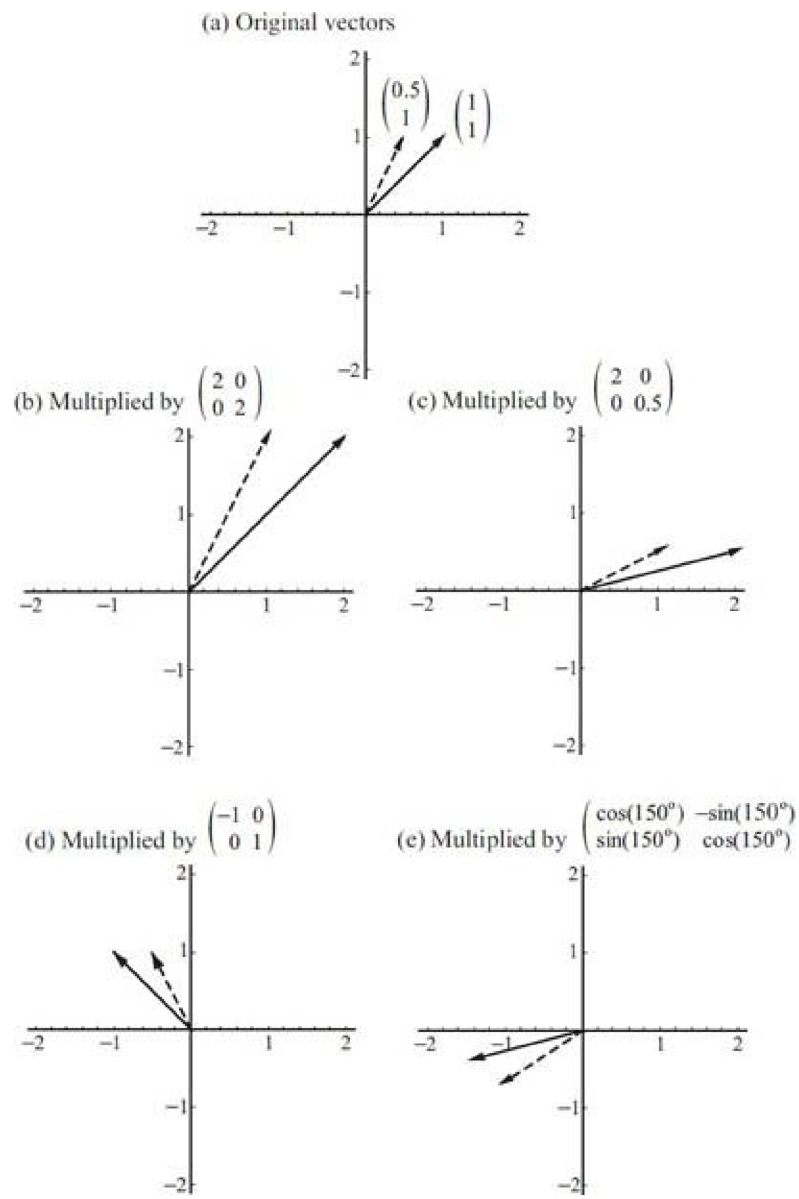


Figure P2.3: Matrices transform vectors into new vectors. When the original vectors in (a) are multiplied on the left by a matrix, the vectors are stretched and rotated. (b) Multiplication by $\begin{pmatrix} \gamma & 0 \\ 0 & \gamma \end{pmatrix}$ stretches the vectors by an amount γ(γ = 2). (c) Multiplication by $\begin{pmatrix} \gamma_x & 0 \\ 0 & \gamma_y \end{pmatrix}$ stretches the vectors by an amount γ_x long the x-axis and by γ_y along the y-axis (γ_x = 2, γ_y = 0.5). (d) Multiplication by $\begin{pmatrix} -1 & 0 \\ 0 & 1 \end{pmatrix}$ reflects the vectors across the y-axis. (Conversely, $\begin{pmatrix} 1 & 0 \\ 0 & -1 \end{pmatrix}$ reflects across the x-axis.) (e) Multiplication by the matrix $\begin{pmatrix} \cos(\theta) & -\sin(\theta) \\ \sin(\theta) & \cos(\theta) \end{pmatrix}$ rotates the vectors counterclockwise by an amount $\theta(\theta = 150°)$.

A *lower triangular matrix* is a matrix whose elements above the diagonal are zero:

Definition P2.4:

$$\begin{pmatrix} m_{11} & 0 & \cdots & 0 \\ m_{21} & m_{22} & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots \\ m_{r1} & m_{r2} & \cdots & m_{rc} \end{pmatrix} \qquad \text{(lower triangular matrix)}$$

It is sometimes useful to write a matrix in terms of submatrices, by blocking certain elements together. For example, the 4 × 4 matrix could be written in block form as

$$\begin{pmatrix} m_{11} & m_{12} & m_{13} & m_{14} \\ m_{21} & m_{22} & m_{23} & m_{24} \\ m_{31} & m_{32} & m_{33} & m_{34} \\ m_{41} & m_{42} & m_{43} & m_{44} \end{pmatrix}$$

could be written in block form as $\begin{pmatrix} \mathbf{A} & \mathbf{B} \\ \mathbf{C} & \mathbf{D} \end{pmatrix}$, where $\mathbf{A} = \begin{pmatrix} m_{11} & m_{12} \\ m_{21} & m_{22} \end{pmatrix}$, $\mathbf{B} = \begin{pmatrix} m_{13} & m_{14} \\ m_{23} & m_{24} \end{pmatrix}$, $\mathbf{C} = \begin{pmatrix} m_{31} & m_{32} \\ m_{41} & m_{42} \end{pmatrix}$, and $\mathbf{D} = \begin{pmatrix} m_{33} & m_{34} \\ m_{43} & m_{44} \end{pmatrix}$. But this is not the only possible block form. We could also write it as $\begin{pmatrix} \mathbf{E} & \mathbf{F} \\ \mathbf{G} & \mathbf{H} \end{pmatrix}$, where

$$\mathbf{E} = \begin{pmatrix} m_{11} & m_{12} & m_{13} \\ m_{21} & m_{22} & m_{23} \\ m_{31} & m_{32} & m_{33} \end{pmatrix}, \quad \mathbf{F} = \begin{pmatrix} m_{14} \\ m_{24} \\ m_{34} \end{pmatrix},$$

$\mathbf{G} = (m_{41}\ m_{42}\ m_{43})$, and $\mathbf{H} = (m_{44})$. For square matrices, we will confine our attention to block forms where the diagonal submatrices (**A** and **D** or **E** and **H**) are also square. Block form is particularly useful when one or both of the off-diagonal submatrices consist entirely of zeros. If matrix **B** *and* **C** consists of zeros, we say that the matrix has a “block diagonal form.” If matrix **B** *or* **C** consists of zeros, we say that the matrix has “block triangular form.”

Sometimes, it is useful to “transpose” a matrix, which makes the rows of the original matrix into the columns of a new matrix. The transpose is represented by a nonitalicized T superscript:

Rule P2.1:

$$\mathbf{M}^{\mathrm{T}} = \begin{pmatrix} m_{11} & m_{12} & \cdots & m_{1c} \\ m_{21} & m_{22} & \cdots & m_{2c} \\ \vdots & \vdots & \vdots & \vdots \\ m_{r1} & m_{r2} & \cdots & m_{rc} \end{pmatrix}^{\mathrm{T}} = \begin{pmatrix} m_{11} & m_{21} & \cdots & m_{r1} \\ m_{12} & m_{22} & \cdots & m_{r2} \\ \vdots & \vdots & \vdots & \vdots \\ m_{1c} & m_{2c} & \cdots & m_{rc} \end{pmatrix} \quad \text{(matrix transpose)}$$

For example, the transpose of $\begin{pmatrix} 1 & 2 \\ 3 & 4 \end{pmatrix}$ is and $\begin{pmatrix} 1 & 3 \\ 2 & 4 \end{pmatrix}$ the transpose of $\begin{pmatrix} a \\ b \end{pmatrix}$ is $(a,\ b)$. The transpose can be performed on matrices of any dimension. For example, the transpose of a column vector is a row vector, and vice versa.

Exercise P2.1: Determine the dimensionality of the following vectors and matrices and write down the transpose of each.

(a)
$$(2 \quad 4).$$

(b)
$$\begin{pmatrix} 1 \\ 2 \\ 3 \end{pmatrix}.$$

(c)
$$\begin{pmatrix} 6 & -4 \\ 2 & 0 \end{pmatrix}.$$

(d)
$$\begin{pmatrix} 1+x & 2+x & 3+x \\ 5 & 7 & 9 \end{pmatrix}.$$

(e)
$$\begin{pmatrix} a & b \\ c & d \\ e & f \end{pmatrix}.$$

[Answers to the exercises are provided at the end of the primer.]

P2.2 Vector and Matrix Addition

The real power and utility of linear algebra comes from the rules by which we add, subtract, and multiply vectors and matrices. These rules are simply things that we have to commit to memory, just as we committed the rules of addition, subtraction, and multiplication of numbers to memory in grade school. In sections P2.2–P2.6, we describe these basic matrix operations. We then turn our attention to important techniques that build upon these basic operations. When describing matrix operations, we will provide specific examples as well as general formulas using the following arbitrary vectors and matrices in d dimensions:

$$\vec{v}_1 = \begin{pmatrix} x_1 \\ x_2 \\ \vdots \\ x_d \end{pmatrix},\ \vec{v}_2 = \begin{pmatrix} y_1 \\ y_2 \\ \vdots \\ y_d \end{pmatrix},\ \mathbf{M} = \begin{pmatrix} m_{11} & m_{12} & \cdots & m_{1d} \\ m_{21} & m_{22} & \cdots & m_{2d} \\ \vdots & \vdots & \vdots & \vdots \\ m_{d1} & m_{d2} & \cdots & m_{dd} \end{pmatrix},\ \mathbf{N} = \begin{pmatrix} n_{11} & n_{12} & \cdots & n_{1d} \\ n_{21} & n_{22} & \cdots & n_{2d} \\ \vdots & \vdots & \vdots & \vdots \\ n_{d1} & n_{d2} & \cdots & n_{dd} \end{pmatrix}.$$

Vector *addition* involves adding each element of two vectors, one position at a time, and placing the answer in the same position of the resulting vector:

Rule P2.2:

$$\vec{v}_1 + \vec{v}_2 = \begin{pmatrix} x_1 \\ x_2 \\ \vdots \\ x_d \end{pmatrix} + \begin{pmatrix} y_1 \\ y_2 \\ \vdots \\ y_d \end{pmatrix} = \begin{pmatrix} x_1 + y_1 \\ x_2 + y_2 \\ \vdots \\ x_d + y_d \end{pmatrix} \qquad \text{(vector addition)}$$

For example, adding the row vectors (2, 3) and (8, 20) gives the row vector (10, 23). Vector *subtraction* is similarly straightforward:

Rule P2.3:

$$\vec{v}_1 - \vec{v}_2 = \begin{pmatrix} x_1 \\ x_2 \\ \vdots \\ x_d \end{pmatrix} - \begin{pmatrix} y_1 \\ y_2 \\ \vdots \\ y_d \end{pmatrix} = \begin{pmatrix} x_1 - y_1 \\ x_2 - y_2 \\ \vdots \\ x_d - y_d \end{pmatrix} \qquad \text{(vector subtraction)}$$

CAUTION: Vector addition and subtraction can be carried out only on vectors with the same dimensionality because corresponding positions must exist for each vector.

Graphically, adding two-dimensional vectors is akin to starting one vector at the end of the other vector, giving a new total vector that starts at the origin and ends at the tip of the second vector (Figure P2.4).

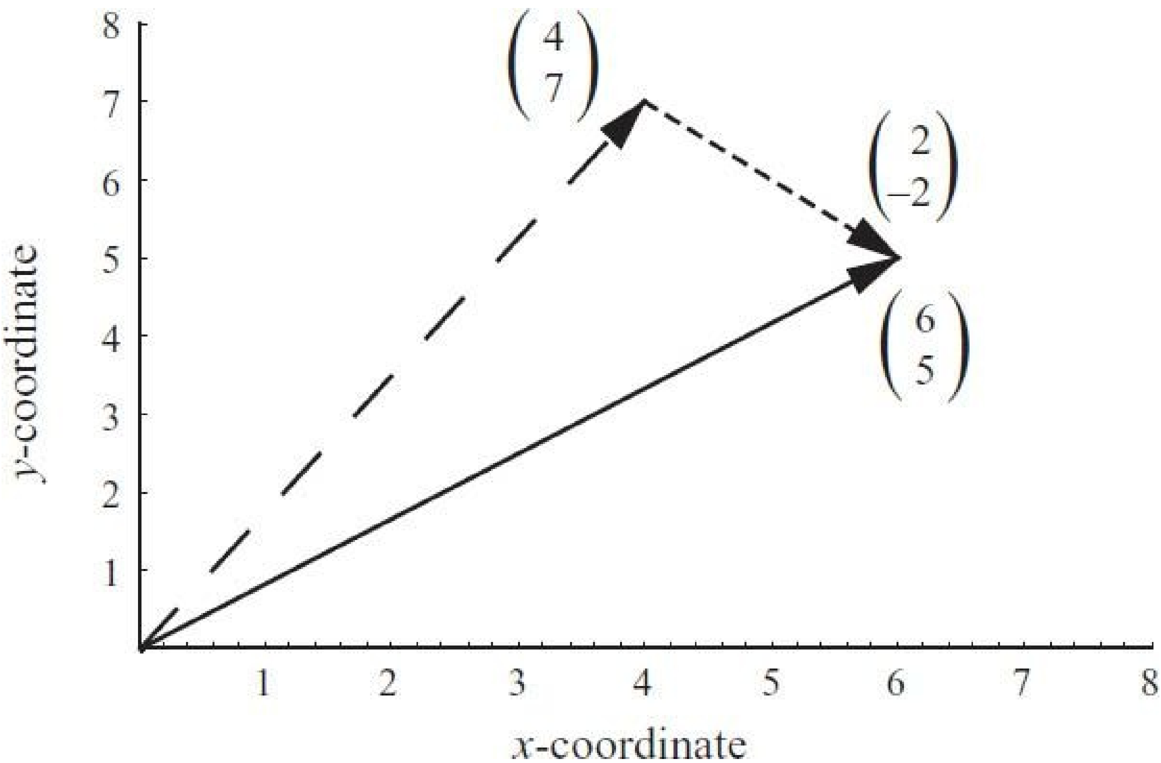


Figure P2.4: Vector addition. Vector addition represents the placement of one vector at the tip of another vector. Here, the short-dashed vector $\begin{pmatrix} 2 \\ -2 \end{pmatrix}$ is added to the long-dashed vector $\begin{pmatrix} 4 \\ 7 \end{pmatrix}$ to get the solid vector $\begin{pmatrix} 6 \\ 5 \end{pmatrix}$.

Exercise P2.2: Specify which of the following vector sums are valid and perform these summations.

(a) $$\begin{pmatrix} 5 \\ 7 \end{pmatrix} + (2 \quad 4).$$

(b) $$\begin{pmatrix} 5 \\ 7 \end{pmatrix} + \begin{pmatrix} 2 \\ 4 \end{pmatrix}.$$

(c) $$\begin{pmatrix} 1 \\ 2 \\ 3 \end{pmatrix} + \begin{pmatrix} 4 \\ 5 \\ 6 \end{pmatrix}.$$

(d) $$(1 \quad 2 \quad 3 \quad 4) + (5 \quad 6 \quad 7).$$

(e) $$(0.5 \quad 1.3 \quad 2) + (a \quad b \quad c).$$

Once you are comfortable with vector addition, matrix addition is straightforward. When adding two matrices (**M** + **N**), one makes a new matrix, with each position equal to the sum of the corresponding positions in the two original matrices:

Rule P2.4:

$$\mathbf{M} + \mathbf{N} = \begin{pmatrix} m_{11} + n_{11} & m_{12} + n_{12} & \cdots & m_{1d} + n_{1d} \\ m_{21} + n_{21} & m_{22} + n_{22} & \cdots & m_{2d} + n_{2d} \\ \vdots & \vdots & \vdots & \vdots \\ m_{d1} + n_{d1} & m_{d2} + n_{d2} & \cdots & m_{dd} + n_{dd} \end{pmatrix} \quad \text{(matrix addition)}$$

Rule P2.5:

$$\mathbf{M} - \mathbf{N} = \begin{pmatrix} m_{11} - n_{11} & m_{12} - n_{12} & \cdots & m_{1d} - n_{1d} \\ m_{21} - n_{21} & m_{22} - n_{22} & \cdots & m_{2d} - n_{2d} \\ \vdots & \vdots & \vdots & \vdots \\ m_{d1} - n_{d1} & m_{d2} - n_{d2} & \cdots & m_{dd} - n_{dd} \end{pmatrix} \quad \text{(matrix subtraction)}$$

As a concrete numerical example, $\begin{pmatrix} 12 & 10 \\ 8 & 6 \end{pmatrix}$ plus $\begin{pmatrix} 8 & 1 \\ 10 & -3 \end{pmatrix}$ equals $\begin{pmatrix} 20 & 11 \\ 18 & 3 \end{pmatrix}$.

CAUTION: Matrix addition and subtraction can only be carried out on matrices with the same dimensionality.

Exercise P2.3: Specify which of the following matrix sums are valid and perform these summations.

(a) $$\begin{pmatrix} 1 & 2 \\ 3 & 4 \end{pmatrix} + \begin{pmatrix} 6 & 4 \\ 2 & 0 \end{pmatrix}.$$

(b) $$\begin{pmatrix} 1 & 2 \\ 3 & 4 \end{pmatrix} + \begin{pmatrix} 1 & 2 & 3 \\ 5 & 7 & 9 \end{pmatrix}.$$

(c) $$\begin{pmatrix} a & b \\ c & d \end{pmatrix} - \begin{pmatrix} 1 & 2 \\ 3 & 4 \end{pmatrix}.$$

(d) $$\begin{pmatrix} a & b & c \\ d & e & f \end{pmatrix} + \begin{pmatrix} a & a & a \\ d & d & d \end{pmatrix}.$$

(e) $$\begin{pmatrix} 1 & 2 & 3 \\ 4 & 5 & 6 \\ 7 & 8 & 9 \end{pmatrix} - \begin{pmatrix} 1 & 2 & 3 \\ 4 & 5 & 6 \\ 7 & 8 & 9 \end{pmatrix}.$$

P2.3 Multiplication by a Scalar

Numbers, parameters, variables, and functions (basically anything that is not a vector or a matrix) are known as *scalars*. Multiplication of a vector by a scalar k is performed by multiplying each element in the vector by k:

A ***scalar*** is a single element.

Rule P2.6:

$$k\,\vec{v}_1 = \begin{pmatrix} k\,x_1 \\ k\,x_2 \\ \vdots \\ k\,x_d \end{pmatrix}. \qquad \text{(vector multiplication by a scalar)}$$

For example, if we were to multiply the column vector $\binom{1}{2}$ by the scalar x we would get $\binom{x}{2x}$. One can also undo this procedure and factor out a term from each element in a vector. For example, $\binom{x/W}{y/W}$ is the same as $\frac{1}{W}\binom{x}{y}$. Vector multiplication by a scalar has a very important graphical interpretation: it corresponds to stretching or compressing the vector by a factor k, without altering its direction (Figure P2.5).

Multiplying a vector by a scalar stretches the vector.

Matrix multiplication by a scalar proceeds in the same manner, multiplying every element in the matrix by the scalar:

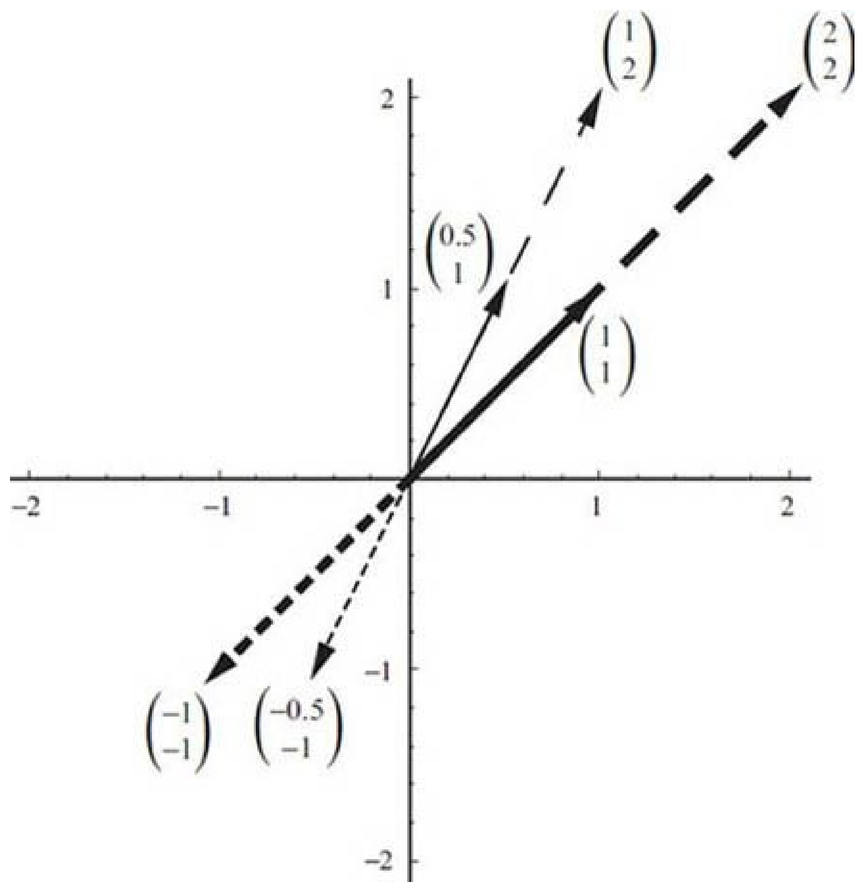


Figure P2.5: Multiplication of a vector by a scalar. A vector stretches or shrinks when multiplied by a scalar γ. The original thin-lined vector $\binom{0.5}{1}$ and thick-lined vector $\binom{1}{1}$ are multiplied by the scalar $\gamma = 2$ (long-dashed vectors) and by the scalar $\gamma = -1$ (short-dashed curves). A vector multiplied by a scalar always remains on the same line, although it can point in the opposite direction. Multiplication of two-dimensional vectors by a scalar, γ, is equivalent to multiplication by the matrix $\begin{pmatrix} \gamma & 0 \\ 0 & \gamma \end{pmatrix}$ (see Figure P2.3b).

Rule P2.7:

$$k\,\mathbf{M} = \begin{pmatrix} k\,m_{11} & k\,m_{12} & \cdots & k\,m_{1d} \\ k\,m_{21} & k\,m_{22} & \cdots & k\,m_{2d} \\ \vdots & \vdots & \vdots & \vdots \\ k\,m_{d1} & k\,m_{d2} & \cdots & k\,m_{dd} \end{pmatrix} \text{ (matrix multiplication by a scalar)}$$

When it comes to multiplication by a scalar, no warnings are needed. The multiplication can proceed regardless of the dimensionality of the vector or matrix.

Exercise P2.4: Specify which of the following scalar multiplications are valid and determine the result.

(a)
$$3\,(2 \quad 4).$$

(b)
$$(-1)\begin{pmatrix} 4 \\ 5 \\ 6 \end{pmatrix}.$$

(c)
$$2\begin{pmatrix} 1 & 2 \\ 3 & 4 \end{pmatrix}.$$

(d)
$$a\begin{pmatrix} 1 & 2 & 3 \\ 5 & 7 & 9 \end{pmatrix}.$$

(e)
$$(2 + a)\begin{pmatrix} 1 & 2 \\ 3 & 4 \end{pmatrix}.$$

P2.4 Multiplication of Vectors and Matrices

Vector and matrix *multiplication* is less straightforward and requires practice. The basic procedure is the multiplication of a row vector by a column vector of the same length:

Rule P2.8:

$$(x_1, x_2, \ldots, x_d)\begin{pmatrix} y_1 \\ y_2 \\ \vdots \\ y_d \end{pmatrix} = (x_1 y_1 + x_2 y_2 + \cdots + x_d y_d) \qquad \text{(vector multiplication)}$$

Multiplication of a $1 \times d$ row vector and a $d \times 1$ column vector results in a 1×1 element, which we can write compactly as $\sum_{i=1}^{d} x_i y_i$.

Here's a technique that can help you get used to vector multiplication. Put your left index finger on the first element of the left-hand vector and your right index finger on the first element of the right-hand vector. Multiply these together. Then move your left hand over to the right and your right hand down by one element. Multiply these together and add them to the previous result. Continue until your hands have moved all the way through the vectors. If the vectors have the same length, both hands will reach the last element at the same time. Try this technique using these examples: $(1, 1)\binom{x}{y} = (x + y)$, $(a, b)\binom{1}{2} = (a + 2b)$, and $(3, 5)\binom{1}{2} = (13)$.

To multiply a matrix and a vector together, this basic procedure is repeated, beginning with the first row of the matrix, proceeding to the second row of the matrix, etc. The resulting sums then go in the corresponding rows of a new vector:

Rule P2.9a:

$$\begin{pmatrix} m_{11} & m_{12} & \cdots & m_{1c} \\ m_{21} & m_{22} & \cdots & m_{2c} \\ \vdots & \vdots & \vdots & \vdots \\ m_{r1} & m_{r2} & \cdots & m_{rc} \end{pmatrix}\begin{pmatrix} y_1 \\ y_2 \\ \vdots \\ y_c \end{pmatrix} = \begin{pmatrix} \sum_{i=1}^{c} m_{1i} y_i \\ \sum_{i=1}^{c} m_{2i} y_i \\ \vdots \\ \sum_{i=1}^{c} m_{ri} y_i \end{pmatrix} \qquad \text{(matrix multiplication)}$$

For example, a two-dimensional matrix multiplied by a two-dimensional vector gives

Rule P2.9b:

$$\begin{pmatrix} a & b \\ c & d \end{pmatrix}\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} ax + by \\ cx + dy \end{pmatrix} \qquad \text{(2} \times \text{2 matrix multiplication)}$$

As illustrated in Figure P2.3, matrix multiplication of a vector *transforms* or moves the vector to a new position. Depending on the form of this matrix, this transformation might stretch, shrink, reflect, or rotate the vector (Figure P2.3). For example, the matrix $\begin{pmatrix} 2 & 0 \\ 0 & 2 \end{pmatrix}$ multiplied by the vector $\begin{pmatrix} 0.5 \\ 1 \end{pmatrix}$ stretches the solid arrow in Figure P2.3a to get the solid arrow in Figure P2.3b. Using Rule P2.9b, this matrix multiplication results in the vector $\begin{pmatrix} 2 \times 0.5 + 0 \times 1 \\ 0 \times 0.5 + 2 \times 1 \end{pmatrix} = \begin{pmatrix} 1 \\ 2 \end{pmatrix}$.

Multiplying a vector by a matrix stretches and rotates the vector.

We can extend this procedure to multiply together two matrices. Basically, we treat one column at a time in the second matrix and apply Rule P2.9, repeating the above procedure, beginning with the first column of the second matrix, then the second column, until the ends of the matrices are reached:

Rule P2.10:

$$\begin{pmatrix} m_{11} & m_{12} & \cdots & m_{1c} \\ m_{21} & m_{22} & \cdots & m_{2c} \\ \vdots & \vdots & \vdots & \vdots \\ m_{r1} & m_{r2} & \cdots & m_{rc} \end{pmatrix} \begin{pmatrix} n_{11} & n_{12} & \cdots & n_{1d} \\ n_{21} & n_{22} & \cdots & n_{2d} \\ \vdots & \vdots & \vdots & \vdots \\ n_{c1} & n_{c2} & \cdots & n_{cd} \end{pmatrix} = \begin{pmatrix} \sum_{l=1}^{c} m_{1l}\, n_{l1} & \sum_{l=1}^{c} m_{1l}\, n_{l2} & \cdots & \sum_{l=1}^{c} m_{1l}\, n_{ld} \\ \sum_{l=1}^{c} m_{2l}\, n_{l1} & \sum_{l=1}^{c} m_{2l}\, n_{l2} & \cdots & \sum_{l=1}^{c} m_{2l}\, n_{ld} \\ \vdots & \vdots & \vdots & \vdots \\ \sum_{l=1}^{c} m_{rl}\, n_{l1} & \sum_{l=1}^{c} m_{rl}\, n_{l2} & \cdots & \sum_{l=1}^{c} m_{rl}\, n_{ld} \end{pmatrix}$$

(general matrix multiplication)

This is where the trick of moving your hands can really help. To calculate the *ij*th element of the resulting matrix, place the index finger of your left hand at the start of the *i*th row of the first matrix and the index finger of your right hand at the start of the *j*th column of the second matrix. Multiply together these two terms, then move to the right with your left hand and down with your right hand. Multiply these two terms and add them to the previous result. Continue moving your hands, taking the product of the elements that you are pointing to and adding the product to the running total, until you reach the end of the *i*th row. The sum total of all of these products is then placed in the *i*th row and *j*th column of the new matrix.

CAUTION: Matrix multiplication requires that the left-hand matrix has the same number of columns as the right-hand matrix has rows. That is, an $r \times c$ matrix can only be multiplied on the right by $a c \times d$ matrix (c must be the same). The resulting matrix will have dimension $r \times d$.

Practicing matrix multiplication is critical for avoiding errors, so try these examples:

$$\begin{pmatrix} a & b \\ c & d \end{pmatrix}\begin{pmatrix} e & f \\ g & h \end{pmatrix} = \begin{pmatrix} ae + bg & af + bh \\ ce + dg & cf + dh \end{pmatrix} \quad (2 \times 2 \text{ multiplied by } 2 \times 2 \rightarrow 2 \times 2).$$

$$(a, b)\begin{pmatrix} x \\ y \end{pmatrix} = (ax + by) \quad (1 \times 2 \text{ multiplied by } 2 \times 1 \rightarrow 1 \times 1).$$

$$\begin{pmatrix} a \\ b \end{pmatrix}(x, y) = \begin{pmatrix} ax & ay \\ bx & by \end{pmatrix} \quad (2 \times 1 \text{ multiplied by } 1 \times 2 \rightarrow 2 \times 2).$$

$$\begin{pmatrix} a & b & c \\ d & e & f \end{pmatrix}\begin{pmatrix} x \\ y \\ z \end{pmatrix} = \begin{pmatrix} ax + by + cz \\ dx + ey + fz \end{pmatrix} \quad (2 \times 3 \text{ multiplied by } 3 \times 1 \rightarrow 2 \times 1).$$

$$\begin{pmatrix} a & b \\ c & d \end{pmatrix}(x, y) = \text{Cannot be done} \quad (2 \times 2 \text{ multiplied by } 1 \times 2 \text{ is not allowed}).$$

Now we arrive at the first main difference between linear algebra and regular algebra. We’re used to thinking that the order in which we multiply two things together does not matter; 2 times 3 is the same as 3 times 2. This is true of scalars, but it is not generally true of matrices and vectors! For example,

$$\begin{pmatrix} 1 & 2 \\ 3 & 4 \end{pmatrix}\begin{pmatrix} 5 & 6 \\ 7 & 8 \end{pmatrix} = \begin{pmatrix} 19 & 22 \\ 43 & 50 \end{pmatrix} \text{ does not equal } \begin{pmatrix} 5 & 6 \\ 7 & 8 \end{pmatrix}\begin{pmatrix} 1 & 2 \\ 3 & 4 \end{pmatrix} = \begin{pmatrix} 23 & 34 \\ 31 & 46 \end{pmatrix}.$$

In mathematical jargon, matrix multiplication is not *commutative* (**AB** ≠ **BA**). Matrix multiplication does, however, satisfy the following rules:

Rule P2.11:

$(\mathrm{AB})\mathrm{C} = \mathrm{A}(\mathrm{BC})$ (associative law)

Rule P2.12:

$(\mathrm{A} + \mathrm{B})\mathrm{C} = \mathrm{AC} + \mathrm{BC}$ (distributive law)

Rule P2.13:

$$\mathbf{A}(\mathbf{B} + \mathbf{C}) = \mathbf{AB} + \mathbf{AC} \qquad \text{(distributive law)}$$

Rule P2.14:

$$k(\mathbf{AB}) = (k\mathbf{A})\mathbf{B} = \mathbf{A}(k\mathbf{B}) = (\mathbf{AB})k \qquad \text{(commutative law for scalars)}$$

There is another important concept that is similar in linear algebra and regular algebra. In both, there is a special object that leaves other objects unchanged upon multiplication. In regular algebra, this is the number one; multiplying anything by one has no effect. In linear algebra, this special object is the identity matrix. Any square matrix (**M**) with dimensionality $d \times d$ can be multiplied by the $d \times d$ identity matrix on either the right or the left with no effect:

Rule P2.15:

$$\mathbf{MI} = \mathbf{IM} = \mathbf{M} \qquad \text{(multiplication by I)}$$

Demonstrate this to yourself using $\mathbf{I} = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}$ and any 2×2 matrix that pops to mind. Similarly, a vector remains unaltered when multiplied by an identity matrix; the vector retains its original length and direction.

Exercise P2.5: Using the matrices

$$\mathbf{A} = \begin{pmatrix} a & b \\ c & d \end{pmatrix}, \quad \mathbf{B} = \begin{pmatrix} e & f \\ g & h \end{pmatrix}, \quad \mathbf{C} = \begin{pmatrix} i & j \\ k & l \end{pmatrix}, \quad \mathbf{I} = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix},$$

(a) prove that **AB** does not equal **BA** (matrix multiplication is not commutative)

(b) prove that **A**(**B** + **C**) does equal **AB** + **AC** (matrix multiplication is distributive)

(c) prove that (**AB**)**C** does equal **A**(**BC**) (matrix multiplication is associative)

(d) prove that **AI** and **IA** equal **A** (multiplication by the identity matrix leaves the matrix unchanged)

There is one last fact about matrix multiplication that we will need. As long as the dimensions are appropriate, we are free to multiply any equation on both sides by a matrix *as long as we multiply both sides of the equation on the right or both sides of* *the equation on the left*. For example, if **A, B, C,** and **D** are square matrices of dimension d and if **AB** = **C**, then **ABD** = **CD**. To prove this, replace **AB** with **C** to get **CD** = **CD**, which is always true. Similarly, we could multiply on the left to get **DAB** = **DC**. But we will not generally preserve the validity of the equation if we multiply by **D** on the left on one side of the equation and on the right on the other side of the equation (that is, **ABD** ≠ **DC** and **DAB** ≠ **CD**). Try checking that **ABD** = **CD** and **DAB** = **DC** but that **ABD** ≠ **DC** using the 2 × 2 matrices

$$\mathbf{A} = \begin{pmatrix} 1 & 2 \\ 2 & 1 \end{pmatrix}, \quad \mathbf{B} = \begin{pmatrix} 1 & 1 \\ 3 & 1 \end{pmatrix}, \quad \mathbf{C} = \begin{pmatrix} 7 & 3 \\ 5 & 3 \end{pmatrix}, \quad \mathbf{D} = \begin{pmatrix} 2 & 1 \\ 2 & 5 \end{pmatrix}.$$

So far, we have focused on a type of matrix multiplication known as the "*dot product*" or "*inner product*" (Rules P2.8–P2.10). The dot product is the one most commonly encountered in mathematical biology, but a few other products make occasional appearances, and these are described in Sup. Mat. P2.1.

P2.5 The Trace and Determinant of a Square Matrix

The trace of a square matrix is simply the sum of its diagonal elements $(\mathrm{Tr}(\mathbf{M}) = \sum_{i=1}^{d} m_{ii})$. In two dimensions we have

Definition P2.5:

$$\mathrm{Tr}\begin{pmatrix} a & b \\ c & d \end{pmatrix} = a + d \qquad \text{(trace of a } 2 \times 2 \text{ matrix)}$$

The *trace* sums the diagonal elements of a matrix.

The trace of a matrix is a scalar. The trace has no obvious intuitive meaning, but it simplifies other matrix calculations that we will encounter later.

The determinant of a square matrix is another scalar. For a 2 × 2 matrix, the determinant is calculated as

Definition P2.6:

$$\text{Det}\begin{pmatrix} a & b \\ c & d \end{pmatrix} = \begin{vmatrix} a & b \\ c & d \end{vmatrix} = ad - bc \qquad \text{(determinant of a } 2 \times 2 \text{ matrix)}$$

The *determinant* measures whether the rows of a matrix are independent.

and is denoted either as Det(**M**) or simply as |**M**|. The determinant measures whether the rows of a matrix are *linearly independent* of one another. By linearly independent, we mean that we cannot write any row x as a linear function of the other rows (that is, there is no equation like $\text{row}_x = a_1 \text{ row}_1 + \ldots + a_{x-1} \text{ row}_{x-1} + a_{x+1} \text{ row}_{x+1} + \ldots + a_d \text{ row}_d$ that holds true no matter how we choose the constants a_i). If Det(**M**) = 0, then the rows are not independent, and a linear relationship does exist among the rows. For example,

$$\text{Det}\begin{pmatrix} 1 & 2 \\ 4 & 8 \end{pmatrix} = 8 - 8 = 0,$$

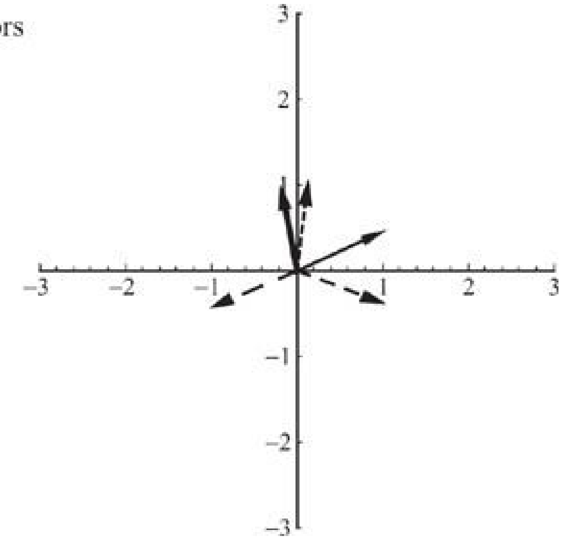
This reflects the fact that we can write the second row as four times the first row. But

$$\text{Det}\begin{pmatrix} 1 & 2 \\ 4 & 7 \end{pmatrix} = 7 - 8 = -1,$$

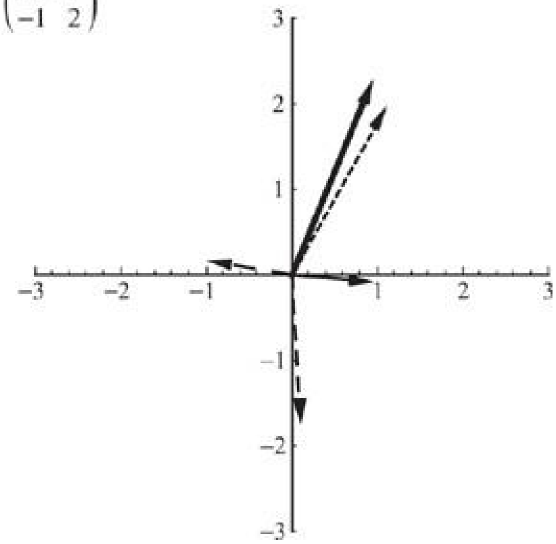
and there is no number by which we can multiply the first row to get the second row. If you are familiar with statistics, the determinant is closely related to the χ^2-statistic, which can be used to test independence between the rows and columns of a data table.

Graphically, when we use a 2 × 2 matrix whose determinant is zero to multiply a series of two-dimensional vectors, the resulting vectors always lie on the same line. For example, in Figure P2.6a, five vectors of length one were chosen to point in different directions. These vectors "span" the two-dimensional plane, meaning that we cannot draw a one-dimensional line that lies on top of all of the vectors. When we multiply these vectors by the matrix $\begin{pmatrix} 0.5 & 1 \\ -1 & 2 \end{pmatrix}$, whose determinant is 2, we get five new vectors, which again span the plane (Figure P2.6b). If, however, we multiply these vectors by $\begin{pmatrix} 0.5 & 1 \\ 1 & 2 \end{pmatrix}$, whose determinant is 0, we get five new vectors, which all fall along the same line (Figure P2.6c). In general, multiplying a vector by a matrix whose determinant is zero causes a loss of information about some dimensions of the vector. While we can undo multiplication by a matrix whose determinant is not zero to get back the original vectors (see section P2.6 on inverses), we cannot undo multiplication by a matrix whose determinant is zero, because we have lost some information about the original vector.

(a) Original vectors



(b) Multiplied by $\begin{pmatrix} 0.5 & 1 \\ -1 & 2 \end{pmatrix}$



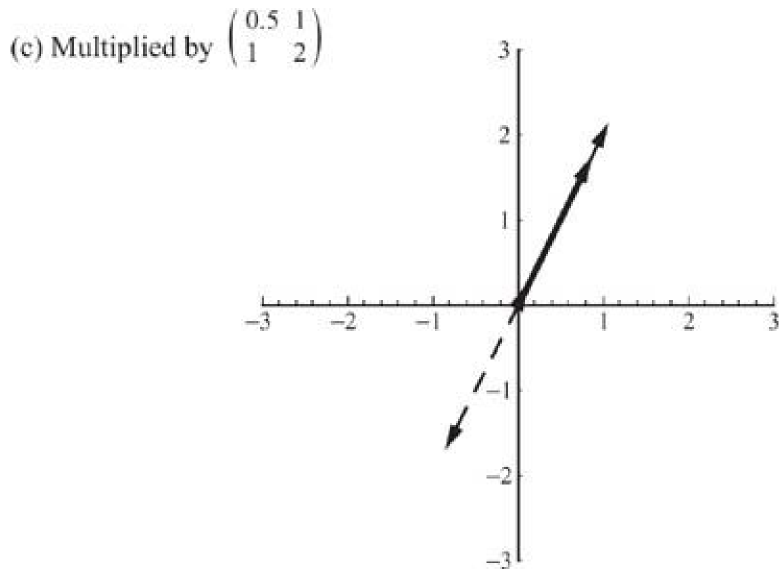


Figure P2.6: Comparing matrices with non-zero and zero determinants. (a) Five vectors of length one were chosen to point in different directions. (b) The five vectors were multiplied on the left by the matrix $\begin{pmatrix} 0.5 & 1 \\ -1 & 2 \end{pmatrix}$, whose determinant is non-zero. (c) The five vectors were multiplied on the left by the matrix $\begin{pmatrix} 0.5 & 1 \\ 1 & 2 \end{pmatrix}$, whose determinant is zero.

Conceptually, this fact has an analogy in regular (nonmatrix) algebra. Any number x can be multiplied by a number a to get a new number b. We can undo this process by dividing b by a to get back $x = b/a$. This does not work, however, if a equals zero because all information about the original number x is lost once we multiply it by zero.

Exercise P2.6: Calculate the trace and determinant of the following matrices:

$$\mathbf{A} = \begin{pmatrix} 1 & 2 \\ 3 & 4 \end{pmatrix}, \quad \mathbf{B} = \begin{pmatrix} 1 & 3 \\ 2 & 4 \end{pmatrix}, \quad \mathbf{C} = \begin{pmatrix} -1 & -2 \\ -3 & -4 \end{pmatrix}.$$

Exercise P2.7: In which of the following matrices are the rows independent of one another? When the rows are not independent, specify how they are related.

$$\mathbf{D} = \begin{pmatrix} 1 & 2 \\ -3 & -6 \end{pmatrix}, \quad \mathbf{E} = \begin{pmatrix} 1 & 3 \\ 3 & 3 \end{pmatrix}, \quad \mathbf{F} = \begin{pmatrix} 1 & 3 \\ x & 3x \end{pmatrix}.$$

For a 2×2 matrix, it is pretty straightforward to eyeball the matrix to see whether the rows are independent, even without calculating the determinant. But for larger matrices, it can be very hard to see whether any relationship exists among the rows.

The determinant is straightforward (if tedious) to calculate for any square matrix, however, and is nonzero if and only if all rows are linearly independent of each other. Again, multiplication of a vector by a $d \times d$ matrix whose determinant is zero causes a loss of information about some of the dimensions of the original vector.

For a 3×3 matrix, the determinant is

Rule P2.16:

(determinant of a 3×3 matrix)

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

That is, one calculates the determinant by moving across the first row, taking each term m_{1j}, and multiplying it by the determinant of the smaller matrix obtained by deleting the first row and the jth column, alternately adding or subtracting this product to the running total. As an example,

$$\begin{vmatrix} 1 & 2 & 3 \\ 7 & 3 & 5 \\ 11 & 0 & 1 \end{vmatrix} = 1\begin{vmatrix} 3 & 5 \\ 0 & 1 \end{vmatrix} - 2\begin{vmatrix} 7 & 5 \\ 11 & 1 \end{vmatrix} + 3\begin{vmatrix} 7 & 3 \\ 11 & 0 \end{vmatrix} = 3 + 96 - 99 = 0.$$

In this example, it is hard to tell that the rows are related, but the third row is just twice the second row minus three times the first row: $(11 \;\; 0 \;\; 1) = 2(7 \;\; 3 \;\; 5) - 3(1 \;\; 2 \;\; 3)$. The fact that the determinant is zero tells us that some such relationship exists.

For a larger square matrix, the procedure for calculating the determinant is just a generalization of the three-dimensional case:

Rule P2.17:

$$|\mathbf{M}| = \sum_{j=1}^{d}(-1)^{j+1}\, m_{1j}\, |\mathbf{M_{1j}}| \qquad \text{(determinant of a } d \times d \text{ matrix)}$$

Again, the determinant is calculated by rewriting it in terms of the elements of the first row m_{1j} times determinants of smaller matrices $\mathbf{M_{1j}}$, each of which is obtained by eliminating the first row and jth column. This procedure seems straightforward until you realize that the determinant of a 10×10 matrix is a function of the determinants of ten 9 × 9 matrices, which are each in turn functions of determinants of nine 8 × 8 matrices, etc. In practice, what this means is that we would almost always use a computer to calculate the determinant of a large matrix.

If a matrix contains a row or a column with several zeros in it, it is easier to calculate the determinant by moving across the row with the most zeros (or moving down the column with the most zeros). The only caveat is that we must multiply the determinant by −1 if we use an even-numbered row or an even-numbered column. Thus, we can generalize Rule P2.17 to allow us to use the kth row to find the determinant:

Rule P2.18a:

$$|\mathbf{M}| = (-1)^{k+1} \sum_{j=1}^{d} (-1)^{j+1}\, m_{kj}\, |\mathbf{M_{kj}}| \qquad \text{(determinant of a } d \times d \text{ matrix)}$$

or the kth column to find the determinant:

Rule P2.18b:

$$|\mathbf{M}| = (-1)^{k+1} \sum_{j=1}^{d} (-1)^{j+1}\, m_{jk}\, |\mathbf{M_{jk}}| \qquad \text{(determinant of a } d \times d \text{ matrix)}$$

These rules can be used to prove the following other handy rules:

Rule P2.19:
The determinant of a matrix is the same as the determinant of its transpose.

Rule P2.20:
The determinant of a diagonal, upper triangular, or lower triangular matrix is the product of the elements along the diagonal $(|\boldsymbol{M}| = \prod_{i=1}^{d} m_{ii})$.

Rule P2.21:
The determinant of a block-diagonal matrix or a block-triangular matrix is the product of the determinants of the diagonal submatrices.

Rule P2.22:
If a d × d matrix **M** contains a row (or a column) that is all zeros except for

the element along the diagonal (m_{ii}), then the determinant of **M** equals m_{ii} times the determinant of a smaller matrix obtained by deleting the ith row and ith column of **M**.

One way to calculate the determinant of a large matrix is to turn the original matrix into a triangular matrix by combining rows together (or columns together) as described in Sup. Mat. P2.2. Because the determinant of a triangular matrix is easy to calculate (Rule P2.20), these operations can simplify matters substantially, especially if the original matrix is "sparse" (meaning that it already contains several zeros).

Exercise P2.8: Using the definitions for the determinant of a 2 × 2 and a 3 × 3 matrix, demonstrate to yourself that Rule P2.20 holds for the following matrices:

$$\mathbf{A} = \begin{pmatrix} 2 & 4 \\ 0 & 3 \end{pmatrix}, \qquad \mathbf{B} = \begin{pmatrix} 2 & 4 & 7 \\ 0 & 3 & 8 \\ 0 & 0 & 1 \end{pmatrix}.$$

P2.6 The Inverse

While we have discussed matrix addition, subtraction, and multiplication, we have not mentioned one fundamental algebraic operation: division. Interestingly, the standard division operator is absent in linear algebra. We cannot just take **AB** = **C** and rewrite it as **B** = **C**/**A**. If standard division were possible, we could undo it by multiplying both sides by the denominator to get **BA** = **C**, but this equation is not the same as **AB** = **C** because matrix multiplication is not commutative. There is, however, a matrix operation on square matrices whose role is analogous to division, which involves the *inverse* of a matrix. By definition, a matrix **M** times its inverse, which we write as $\mathbf{M}^{-1}$, equals the identity matrix **I**:

The *inverse* matrix, $\mathbf{M}^{-1}$, reverses the stretching and rotating accomplished by the matrix, **M**.

Rule P2.23a:

$$\mathbf{M}\,\mathbf{M}^{-1} = \mathbf{I} \quad \text{and} \quad \mathbf{M}^{-1}\,\mathbf{M} = \mathbf{I}. \qquad \text{(inverse matrix)}$$

In essence, multiplication by $\mathbf{M}^{-1}$ "reverses" the stretching and rotating accomplished by **M** itself. Thus, a vector multiplied by **M** and then $\mathbf{M}^{-1}$ has the exact same length and direction as the original vector, $\mathbf{M}^{-1}\mathbf{M}\vec{v} = \vec{v}$. The notation used to denote inverses (i.e., $\mathbf{M}^{-1}$) hints at this interpretation. In a sense the inverse is like "one over **M**" in that it reverses the effect of multiplication by the matrix.

If we write a 2 × 2 matrix in the general form $\mathbf{M} = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$, its inverse is

Rule P2.23b:

$$\mathbf{M}^{-1} = \begin{pmatrix} a & b \\ c & d \end{pmatrix}^{-1} = \begin{pmatrix} \frac{d}{ad - bc} & \frac{-b}{ad - bc} \\ \frac{-c}{ad - bc} & \frac{a}{ad - bc} \end{pmatrix} \quad \text{(inverse of a 2×2 matrix)}$$

It is worth memorizing the inverse of a 2 × 2 matrix. This is made easier by noticing that the inverse involves reversing the elements on the main diagonal (a and d), changing the signs of the off-diagonal elements (b and c), and then dividing everything by the determinant Det(**M**) = $ad - bc$. The inverse of a 2 × 2 matrix should always be a 2 × 2 matrix, and you should always get the identity matrix if you multiply a matrix by its inverse. We run into problems, however, if the determinant of a matrix is zero, because the inverse involves division by zero and becomes undefined. In general, inverse matrices exist only for square matrices with nonzero determinants. Such matrices are called "nonsingular" or "invertible." In contrast, matrices whose determinant is zero are known as "singular" or "noninvertible."

Exercise P2.9: Determine the inverse of the following matrices (if in doubt, check your answer by multiplying the matrix by its inverse, which should return the identity matrix):

(a) $$\begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}.$$

(b) $$\begin{pmatrix} 1 & 0 \\ 0 & 3 \end{pmatrix}.$$

(c)
$$\begin{pmatrix} 1 & 3 \\ 1 & 3 \end{pmatrix}.$$

(d)
$$\begin{pmatrix} 1 & 2 \\ 1 & 4 \end{pmatrix}.$$

(e)
$$\begin{pmatrix} 1 & 2 \\ 3 & 4 \end{pmatrix}.$$

Exercise P2.10: Multiply the general 2 × 2 matrix $\begin{pmatrix} a & b \\ c & d \end{pmatrix}$ by its inverse

$$\begin{pmatrix} \dfrac{d}{ad - bc} & \dfrac{-b}{ad - bc} \\ \dfrac{-c}{ad - bc} & \dfrac{a}{ad - bc} \end{pmatrix},$$

either on the left or the right. Show that you can simplify the result to get the identity matrix $\begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}$.

The inverse of larger matrices can be found using the method of row reduction (see Sup. Mat. P2.3), although a much less tedious method is to use a mathematical software package, such as *Mathematica* or Maple. If the matrix happens to be diagonal (see Definition P2.1), however, its inverse is found simply by inverting each diagonal element:

Rule P2.24:

$$\mathbf{D}^{-1} = \begin{pmatrix} 1/m_{11} & 0 & \cdots & 0 \\ 0 & 1/m_{22} & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \cdots & 1/m_{dd} \end{pmatrix} \quad \text{(inverse of a diagonal matrix)}$$

P2.7 Solving Systems of Equations

Knowing the inverse of a matrix is very handy for solving problems involving multiple variables. Consider first a nonmatrix linear equation $m\, n = v$, which we want to solve for n. To find n, we divide both sides by m. This is equivalent to multiplying both sides by m^{-1}, giving the solution $n = m^{-1}v$. This is also the way we will solve matrix equations using inverse matrices.

Suppose you wanted to solve the system of linear equations

$$\begin{aligned} an_1 + bn_2 &= v_1, \\ cn_1 + dn_2 &= v_2 \end{aligned} \tag{P2.1}$$

for the two unknown variables n_1 and n_2. For example, equation Equations (P2.1) might represent the conditions for a model to be at equilibrium (see Chapter 7). First, let us solve (P2.1) by hand using Recipe P2.1.

Recipe P2.1

Solving a system of *d* linear equations for the *d* unknowns $n_1, \ldots, n_d$.

Step 1: Choose the simplest of the equations, and solve for one of the unknowns (say, n_j) in terms of the other unknowns. Record this solution.

Step 2: Eliminate the equation chosen in Step 1 and replace n_j in all remaining equations with the solution found in Step 1. Simplify the remaining equations where possible.

Step 3: Return to Step 1 until one equation remains. Solve this one remaining equation for the one remaining unknown.

Step 4: Work backward through the solutions that you have recorded, at each step updating the solution by replacing all other unknowns by their solutions. When you have finished, you should have d solutions for the d unknowns.

Equations (P2.1) are equally complex, so let us solve the first equation for n_1 (Step 1), giving $n_1 = (v_1 - b\, n_2)/a$, which we record. We then toss out the first equation and plug this solution for n_1 into the second equation (Step 2), giving $c\,(v_1 - b\, n_2)/a + d\, n_2 = v_2$. We can simplify this equation by bringing all terms involving the unknown variable n_2 to one side, $n_2\,(-c\, b/a + d) = v_2 - cv_1/a$. As this is our last equation, we solve it for the one remaining unknown variable n_2, and then multiply the numerator and denominator by a to avoid fractions over fractions, giving us $n_2 = (a\, v_2 - c\, v_1)/(a\, d - b\, c)$ (Step 3). This provides a solution for the unknown n_2 in terms of the parameters. Finally, we plug this solution for n_2 into the recorded equation from Step 1, $n_1 = (v_1 - b\, n_2)/a$, which can be factored to give the solution $n_1 = (d\, v_1 - b\, v_2)/(a\, d - b\, c)$ (Step 4).

Alternatively, we can write equations (P2.1) using matrix notation as

$$\mathbf{M}\,\vec{n} = \vec{v} \tag{P2.2}$$

where $\mathbf{M} = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$, $\vec{n} = \begin{pmatrix} n_1 \\ n_2 \end{pmatrix}$, and $\vec{v} = \begin{pmatrix} v_1 \\ v_2 \end{pmatrix}$. Using the definition of an inverse matrix, equation (P2.2) can by solved immediately by multiplying both sides on the left by $\mathbf{M}^{-1}$, giving the solution

$$\vec{n} = \mathbf{M}^{-1}\,\vec{v}. \tag{P2.3}$$

(We multiply on the left by $\mathbf{M}^{-1}$ so that $\mathbf{M}\,\vec{n}$ becomes $\mathbf{M}^{-1}\,\mathbf{M}\,\vec{n} = \mathbf{I}\,\vec{n}$, which equals $\vec{n}$. Multiplying on the right would give us $\mathbf{M}\,\vec{n}\,\mathbf{M}^{-1}$, which does not equal $\vec{n}$.) You should calculate $\mathbf{M}^{-1}\,\vec{v}$ using Rule P2.23b and show that it generates the same solutions as in the last paragraph. There is even a third method for solving linear equations, known as the *method of row reduction*, which is particularly useful for numerical solutions to larger matrix equations (it is described in Supplementary Material P2.3). All three methods are mathematically equivalent, however, so you are free to choose the one that is easiest for any particular application.

Exercise P2.11: tRNA molecules are key to the translation of mRNA into proteins. tRNAs can exist in one of two states, unbound or bound to an amino acid. Let the number of unbound tRNA molecules within a cell equal n_1, and let the number that are bound equal n_2. If α is the rate of tRNA production by transcription, β is the rate of amino acid binding, γ is the rate of amino acid loss (e.g., by translating an mRNA into a protein), and δ is the rate of tRNA degradation, a reasonable model for the change in the number of tRNA molecules over time might be

$$\frac{\mathrm{d}n_1}{\mathrm{d}t} = \alpha - \beta n_1 + \gamma n_2 - \delta n_1,$$

$$\frac{\mathrm{d}n_2}{\mathrm{d}t} = \beta n_1 - \gamma n_2 - \delta n_2.$$

These equations can be written in matrix form as $\mathrm{d}\vec{n}/\mathrm{d}t = \mathbf{M}\,\vec{n} - \vec{v}$. Determine the matrix $\mathbf{M}$ and the constant vector $\vec{v}$. Any equilibrium to the model must satisfy $\mathbf{M}\,\vec{n} = \vec{v}$. Find the inverse matrix $\mathbf{M}^{-1}$, and use it to obtain the equilibrium number of unbound and bound tRNAs from $\vec{n} = \mathbf{M}^{-1}\vec{v}$.

P2.8 The Eigenvalues of a Matrix

In biological models, arguably the most important attributes of a matrix are its eigenvalues, which can be used to predict whether variables grow or shrink over time (Chapters 7–9). By definition, an eigenvalue λ of an invertible square matrix $\mathbf{M}$ satisfies the equation

Eigenvalues can be used to determine whether a matrix stretches or shrinks a system.

$$\mathbf{M}\,\vec{u} = \lambda\,\vec{u} \tag{P2.4a}$$

for some nonzero vector $\vec{u}$. ($\vec{u}$ must point in some direction; it cannot be a vector of all zeros.)

But how do we find the eigenvalues λ of a matrix? First, let us try to find $\vec{u}$ by bringing all terms involving $\vec{u}$ to one side: $\mathbf{M}\,\vec{u} - \lambda\vec{u} = \vec{0}$, where $\vec{0}$ is a vector of zeros. At this point, we cannot just factor out $\vec{u}$ to get $(\mathbf{M} - \lambda)\vec{u} = \vec{0}$, because this involves an invalid subtraction (the scalar λ does not have the same number of dimensions as the matrix $\mathbf{M}$). A trick that we will use repeatedly in such cases is to multiply terms that are not multiplied by a matrix by the identity matrix $\mathbf{I}$. Here, we rewrite $\mathbf{M}\,\vec{u} - \lambda\vec{u} = \vec{0}$ as $\mathbf{M}\,\vec{u} - \lambda\,\mathbf{I}\,\vec{u} = \vec{0}$. In accordance with the distributive law (Rule P2.12), this equation can now be factored to give

$$(\mathbf{M} - \lambda\mathbf{I})\vec{u} = \vec{0} \tag{P2.4b}$$

If the matrix $(\mathbf{M} - \lambda\mathbf{I})$ were invertible, then the vector $\vec{u}$ would be given by $\vec{u} = (\mathbf{M} - \lambda\mathbf{I})^{-1}\vec{0}$. Any time a matrix is multiplied by a vector of zeros, the result is a vector of zeros, $\vec{0}$, indicating that $\vec{u}$ would be a vector of zeros. But we said earlier that $\vec{u}$ must point in some direction and that it cannot be a vector of zeros. The only way out of this apparent contradiction is to conclude that $(\mathbf{M} - \lambda\mathbf{I})$ must not be invertible, which requires that the determinant of $(\mathbf{M} - \lambda\mathbf{I})$ be zero. Indeed, this conclusion allows us to determine the eigenvalues of a matrix without having to calculate the vector $\vec{u}$:

Definition P2.7:

The *characteristic polynomial* of an invertible $d \times d$ matrix $\mathbf{M}$ is defined as $\mathrm{Det}(\mathbf{M} - \lambda\mathbf{I}) = 0$, which is a dth-order polynomial in λ. The d eigenvalues of the matrix $\mathbf{M}$ are the d roots of this characteristic polynomial: $\lambda_1, \lambda_2, \ldots, \lambda_d$.

Eigenvalues are found by determining the roots of a *characteristic polynomial*.

For example, in the $d = 2$ case with $\mathbf{M} = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$,

$$(\mathbf{M} - \lambda\mathbf{I}) = \begin{pmatrix} a - \lambda & b \\ c & d - \lambda \end{pmatrix}, \tag{P2.5}$$

so that

$$\begin{aligned} \mathrm{Det}(\mathbf{M} - \lambda\mathbf{I}) &= (a - \lambda)(d - \lambda) - bc \\ &= \lambda^2 - \lambda(a + d) + (ad - bc) = 0. \end{aligned} \tag{P2.6}$$

Equation (P2.6) is the characteristic polynomial of **M**. For a 2 × 2 matrix, the characteristic polynomial is a quadratic equation. The two roots of this equation are the two eigenvalues of **M**. Using the quadratic formula (Rule A1.10), these eigenvalues are

$$\lambda_1 = \frac{(a + d) + \sqrt{(a + d)^2 - 4(ad - bc)}}{2}, \tag{P2.7a}$$

$$\lambda_2 = \frac{(a + d) - \sqrt{(a + d)^2 - 4(ad - bc)}}{2}. \tag{P2.7a}$$

Alternatively, we can write the eigenvalues for a 2 × 2 matrix in terms of its trace and determinant:

$$\lambda_1 = \frac{\mathrm{Tr}(\mathbf{M}) + \sqrt{(\mathrm{Tr}(\mathbf{M}))^2 - 4\,\mathrm{Det}(\mathbf{M})}}{2} \tag{P2.8a}$$

$$\lambda_2 = \frac{\mathrm{Tr}(\mathbf{M}) - \sqrt{(\mathrm{Tr}(\mathbf{M}))^2 - 4\,\mathrm{Det}(\mathbf{M})}}{2}. \tag{P2.8b}$$

A good check that you've done your algebra correctly is that the eigenvalues of a 2 × 2 matrix **M** should sum to Tr(**M**) (i.e., to the sum of the diagonal elements of **M**). Another good check is that the product of the eigenvalues should equal Det(**M**). (You can demonstrate these facts using equation (P2.8).) These relationships remain true for larger matrices and can be extremely handy. For example

Rule P2.25:

The two eigenvalues of a 2×2 matrix must have the same sign if their product Det(**M**) is positive. When Det(**M**) > 0, the real parts of both eigenvalues will be positive if their sum Tr(**M**) is positive and will be negative if Tr(**M**) is negative. When Det(**M**) < 0, one eigenvalue will be positive and one negative.

To get some practice finding eigenvalues, let us consider some numerical examples:

$$\mathbf{A} = \begin{pmatrix} 2 & 4 \\ 0 & 3 \end{pmatrix}, \qquad \mathbf{B} = \begin{pmatrix} 2 & 4 & 7 \\ 0 & 3 & 5 \\ 0 & 0 & 1 \end{pmatrix}, \qquad \mathbf{C} = \begin{pmatrix} 1 & 0 & 0 \\ 3 & 4 & -3 \\ 2 & 2 & -1 \end{pmatrix}. \qquad \text{(P2.9)}$$

Following Definition P2.7, the two eigenvalues of **A** are the two roots of Det $(\mathbf{A} - \lambda I) = 0$. Taking the determinant of

$$\begin{pmatrix} 2 - \lambda & 4 \\ 0 & 3 - \lambda \end{pmatrix},$$

we get the characteristic polynomial of **A**: $(2 - \lambda)(3 - \lambda) = 0$. This equation has two solutions $\lambda = 2$ and 3, which are the two eigenvalues of **A**. Alternatively, because **A** is a 2×2 matrix, we can use equation (P2.8) to write the eigenvalues in terms of the trace and determinant, Tr(**A**) = 5 and Det(**A**) = 6:

$$\lambda_1 = \frac{5 + \sqrt{(5)^2 - 4(6)}}{2} = 3,$$

$$\lambda_2 = \frac{5 - \sqrt{(5)^2 - 4(6)}}{2} = 2.$$

Similarly, we can use Definition P2.7 to find the eigenvalues of **B**, by first finding the determinant,

$$\text{Det}(\mathbf{B} - \lambda \mathbf{I}) = \begin{vmatrix} 2 - \lambda & 4 & 7 \\ 0 & 3 - \lambda & 5 \\ 0 & 0 & 1 - \lambda \end{vmatrix}.$$

Because this is an upper triangular matrix, we can use Rule P2.20 to identify the determinant quickly as the product of the diagonal elements: $(2 - \lambda)(3 - \lambda)(1 - \lambda)$. Setting this to zero gives a characteristic polynomial whose three roots (the three eigenvalues of **B**) are easy to find: $\lambda = 2$, $\lambda = 3$, and $\lambda = 1$.

These examples suggest a more general rule. Because the determinant of any diagonal, upper triangular, or lower triangular matrix is the product of the diagonal elements (Rule P2.20), the characteristic polynomial of such a matrix **M** always factors into a product of terms $(m_{ii} - \lambda)$ involving only the diagonal elements m_{ii}. As a consequence,

Rule P2.26:

The eigenvalues of a diagonal or triangular matrix are the elements along the diagonal ($\lambda_1 = m_{11}, \lambda_2 = m_{22}, \ldots, \lambda_d = m_{dd}$).

For a broader class of matrices, the following rules can help to identify eigenvalues:

Rule P2.27:

The eigenvalues of a block-diagonal matrix or a block-triangular matrix are the eigenvalues of the submatrices along the diagonal.

Rule P2.28:

If a matrix **M** contains a row (or a column) that is all zeros except for the element along the diagonal (m_{ii}), one of the eigenvalues of the matrix is m_{ii} and the remainder are the eigenvalues of a smaller matrix obtained by deleting the ith row and ith column of **M**.

As a final example, let us determine the eigenvalues of matrix **C**. The characteristic polynomial of **C** is found by calculating the determinant:

$$\mathrm{Det}(\mathbf{C} - \lambda\mathbf{I}) = \begin{vmatrix} 1-\lambda & 0 & 0 \\ 3 & 4-\lambda & -3 \\ 2 & 2 & -1-\lambda \end{vmatrix} = 0.$$

Using Rule P2.16, this determinant is

$$\mathrm{Det}(\mathbf{C} - \lambda\mathbf{I}) = (1 - \lambda)\begin{vmatrix} 4 - \lambda & -3 \\ 2 & -1 - \lambda \end{vmatrix}$$
$$- (0)\begin{vmatrix} 3 & -3 \\ 2 & -1 - \lambda \end{vmatrix} + (0)\begin{vmatrix} 3 & 4 - \lambda \\ 2 & 2 \end{vmatrix} = 0.$$

The last two terms are zero, which leaves us with

$$\begin{aligned} \mathrm{Det}(\mathbf{C} - \lambda\mathbf{I}) &= (1 - \lambda)\begin{vmatrix} 4 - \lambda & -3 \\ 2 & -1 - \lambda \end{vmatrix} \\ &= (1 - \lambda)((4 - \lambda)(-1 - \lambda) + 6) \\ &= (1 - \lambda)(2 - 3\lambda + \lambda^2) \\ &= (1 - \lambda)(2 - \lambda)(1 - \lambda). \end{aligned}$$

This characteristic polynomial also factors nicely (we chose **C** so that it would), allowing us to identify the three roots of the characteristic polynomial: $\lambda = 1$, $\lambda = 2$, and $\lambda = 1$. Because $\lambda = 1$ appears twice in this list, we say that matrix **C** has a *repeated* eigenvalue.

In this example, we can find the eigenvalues of **C** faster by recognizing that it is a block-triangular matrix and applying Rule P2.27. Matrix **C** can be written in block form as $\begin{pmatrix} \mathbf{E} & \mathbf{F} \\ \mathbf{G} & \mathbf{H} \end{pmatrix}$, where $\mathbf{E} = (1)$, $\mathbf{F} = (0\ 0)$, $\mathbf{G} = \begin{pmatrix} 3 \\ 2 \end{pmatrix}$, and $\mathbf{H} = \begin{pmatrix} 4 & -3 \\ 2 & -1 \end{pmatrix}$. Then according to Rule P2.27, the eigenvalues of **C** are the eigenvalues of the diagonal submatrices **E** and **H**. A 1×1 matrix, like **E**, is the simplest example of a diagonal matrix, and the one element in the matrix is its eigenvalue (Rule P2.26). Here, $\lambda = 1$. That leaves us to find the eigenvalues of **H**. Taking the determinant $\mathrm{Det}(\mathbf{H} - \lambda\mathbf{I})$, we get the characteristic polynomial of **H**, $(4 - \lambda)(-1 - \lambda) + 6 = 0$, which can be factored into $(2 - \lambda)(1 - \lambda) = 0$, indicating that the second and third eigenvalues are $\lambda = 2$ and $\lambda = 1$.

This example illustrates why writing matrices in block-diagonal form or block-triangular form can be so helpful: doing so allows you to determine the eigenvalues of a large matrix from the eigenvalues of smaller matrices. Furthermore, there are elementary matrix operations that can be applied to the matrix $(\mathbf{M} - \lambda\mathbf{I})$ without altering its eigenvalues (see Sup. Mat. P2.2). These operations can be used to massage $(\mathbf{M} - \lambda\mathbf{I})$ into block-triangular form so that Rule P2.27 can be applied. Alternatively, these operations can be used to create a row (or a column) whose entries are all zero except on the diagonal, so that Rule P2.28 can be applied. These techniques allow you to reduce the size of a matrix until it becomes manageable.

In the above examples, the eigenvalues have been real numbers. Even when a matrix contains only real elements, its eigenvalues can be complex numbers. We can see this clearly for 2 × 2 matrices from expression (P2.7), which will yield complex values whenever $(a + d)^2 - 4(ad - bc) < 0$. The matrix $\begin{pmatrix} 1 & -1 \\ 1 & 1 \end{pmatrix}$ is a numerical example, having complex eigenvalues $\lambda = 1 + \sqrt{-1}$ and $\lambda = 1 - \sqrt{-1}$. As we shall see, complex eigenvalues are typical of models in which the variables cycle over time (see Chapters 7–9). For certain matrices, it is possible to tell whether or not the eigenvalues will be real. For example,

Eigenvalues that are complex numbers indicate cycling.

Rule P2.29:
If a matrix **M** is symmetric above and below the diagonal (i.e., $m_{ij} = m_{ji}$ for all i and j), all of its eigenvalues are real.

In Appendix 3, we describe the Perron-Frobenius theorem, which can be used to determine the type of eigenvalues for a broader class of matrices. As this material is more advanced, we recommend that it be read later, along with Chapter 10, where it is more extensively used.

In section P2.6, we said that the determinant must not be zero for a matrix to have an inverse. Yet we can still calculate the eigenvalues of a matrix whose determinant is zero. Interestingly, when the determinant is zero, one eigenvalue always equals zero. That is, when Det(**M**) = 0, λ factors out of the characteristic polynomial, because the constant terms in the characteristic polynomial (i.e., the terms not involving λ) are given by Det(**M**). As mentioned earlier, multiplication by a matrix whose determinant is zero causes a loss of information along some axis (see Figure P2.6). Regardless of where the system starts, it reaches zero along this axis in the next time step. The eigenvalue of zero reflects this loss of information, indicating that there is some direction in which the system immediately shrinks to zero. Eigenvalues of zero commonly arise whenever the variables of a model are constrained to satisfy a particular relationship (for example, when genotype frequencies are constrained to be at Hardy-Weinberg equilibrium).

The *leading eigenvalue* dominates the long-term dynamics of a system.

Finally, as mentioned earlier, eigenvalues are useful for determining when multiplication by a matrix expands or shrinks the variables of a system. For example, we will use eigenvalues to predict things such as whether a mutation is likely to spread (a variable is expanding) or a population is likely to go extinct (a variable is shrinking). As we will see, the long-term fate of a system does not actually depend equally on all of its eigenvalues. By definition, the *leading eigenvalue* is the eigenvalue that dominates a system's long-term behavior. In discrete-time models, the leading eigenvalue is the eigenvalue with the largest magnitude. In continuous-time models, it is the eigenvalue with the largest real part. (We shall see why these eigenvalues dominate the long-term behaviour in Chapter 9.) For example, the leading eigenvalues of matrices **A**, **B**, and **C** are 3, 3, and 2, respectively. We will delve more deeply into the topic of leading eigenvalues in Chapters 7–9.

Exercise P2.12: Determine the eigenvalues of the following matrices using Rules P2.26–P2.28 as appropriate.

(a)
$$\begin{pmatrix} \alpha & 0 \\ \beta & 3\delta \end{pmatrix}.$$

(b)
$$\begin{pmatrix} 1 & 2 \\ 3 & 2 \end{pmatrix}.$$

(c)
$$\begin{pmatrix} 2 & 7 & 5 \\ 0 & 19 & 0 \\ 4 & 3 & 1 \end{pmatrix}.$$

(d)
$$\begin{pmatrix} 1 & 2 & 0 \\ 3 & 2 & 0 \\ x & y & z \end{pmatrix}.$$

(e)
$$\begin{pmatrix} \alpha & \beta & \alpha\delta & \beta(\delta-\gamma) \\ \beta & \alpha & \beta(\delta-\gamma) & \alpha\delta \\ 0 & 0 & \delta & \delta-\gamma \\ 0 & 0 & \delta-\gamma & \delta \end{pmatrix}.$$

Exercise P2.13: A simple model of ecological succession in a forest assumes that early successional forests (E) give rise at some rate to mid-successional forests (M), which in turn give rise to late successional forests (L), where E, M, and L

represent the fraction of all forests in each state. If late successional forests undergo disturbance (e.g., fire) at some rate to regenerate early successional forests, ecological succession can be described by a system of differential equations:

$$\begin{pmatrix} dE/dt \\ dM/dt \\ dL/dt \end{pmatrix} = \begin{pmatrix} -a & 0 & c \\ a & -b & 0 \\ 0 & b & -c \end{pmatrix} \begin{pmatrix} E \\ M \\ L \end{pmatrix}.$$

Using Definition P2.7 and Rule P2.16, what is the characteristic polynomial for the above rate matrix? What are its three eigenvalues?

P2.9 The Eigenvectors of a Matrix

We began the last section by saying that an eigenvalue λ of a matrix **M** satisfies the equation $\mathbf{M}\vec{u} = \lambda\vec{u}$ for some nonzero vector $\vec{u}$. But we were able to solve for the eigenvalues using Definition P2.7 without ever specifying what this vector was. The vector $\vec{u}$ is known as an *eigenvector* of matrix **M**. Eigenvectors play an important role in dynamical models too, as they specify the directions along which a system tends to expand or shrink without being rotated. Each eigenvalue of a matrix, λ_i, has an associated eigenvector, $\vec{u}_i$. Once an eigenvalue is identified, its associated eigenvector can be found by solving

Eigenvectors specify directions in which a system expands or shrinks.

$$\mathbf{M}\vec{u}_i = \lambda_i \vec{u}_i. \tag{P2.10}$$

Equation (P2.10) tells us something interesting and special about an eigenvector: when multiplied by the matrix **M**, an eigenvector is stretched or shrunk by a factor equal to its associated eigenvalue λ_i, but the direction of the eigenvector remains unchanged (Figure P2.7). This is the defining feature of all eigenvectors.

Equation (P2.10) describes d equations in d unknowns (the elements of the column vector $\vec{u}_i$). These equations can be solved using either Recipe P2.1 or the method of row reduction described in Supplementary Material P2.3. You might be tempted to solve equation (P2.10) by matrix manipulation, but the answer, $\vec{u}_i = (\mathbf{M} - \lambda_i\mathbf{I})^{-1}\vec{0}$, involves an inverse that is undefined because Det($\mathbf{M} - \lambda_i\mathbf{I}$) is zero by the definition of an eigenvalue. Therefore, to illustrate how (P2.10) can be solved, let us work through a few examples.

First, we calculate the eigenvectors of $\mathbf{A} = \begin{pmatrix} 2 & 4 \\ 0 & 3 \end{pmatrix}$. We already identified the two eigenvalues as 2 and 3. To begin, we must choose one eigenvalue, say $\lambda = 2$, and find the eigenvector that satisfies equation (P2.10) with $\lambda = 2$:

$$\begin{pmatrix} 2 & 4 \\ 0 & 3 \end{pmatrix}\begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = 2\begin{pmatrix} u_1 \\ u_2 \end{pmatrix}.$$

This provides us with two equations that both must be satisfied by the eigenvector $\begin{pmatrix} u_1 \\ u_2 \end{pmatrix}$:

$$\begin{aligned} 2u_1 + 4u_2 &= 2u_1, \\ 3u_2 &= 2u_2. \end{aligned}$$

The second equation can only be satisfied if $u_2 = 0$, in which case the first equation becomes $u_1 = u_1$, which is always true. Thus, any value of u_1 will satisfy the first equation when $u_2 = 0$. When finding eigenvectors, it will always be the case that the value of one of the elements is arbitrary, because eigenvectors describe a direction, but their length does not matter. Therefore, we arbitrarily choose $u_1 = 1$, giving us the eigenvector $\vec{u} = \begin{pmatrix} 1 \\ 0 \end{pmatrix}$ associated with the eigenvalue $\lambda = 2$. If you choose a larger number for u_1, you will get a longer eigenvector, but it will still point in the same direction. In general,

Rule P2.30:

An eigenvector can be multiplied by any nonzero number, and it will still represent an eigenvector of the same eigenvalue.

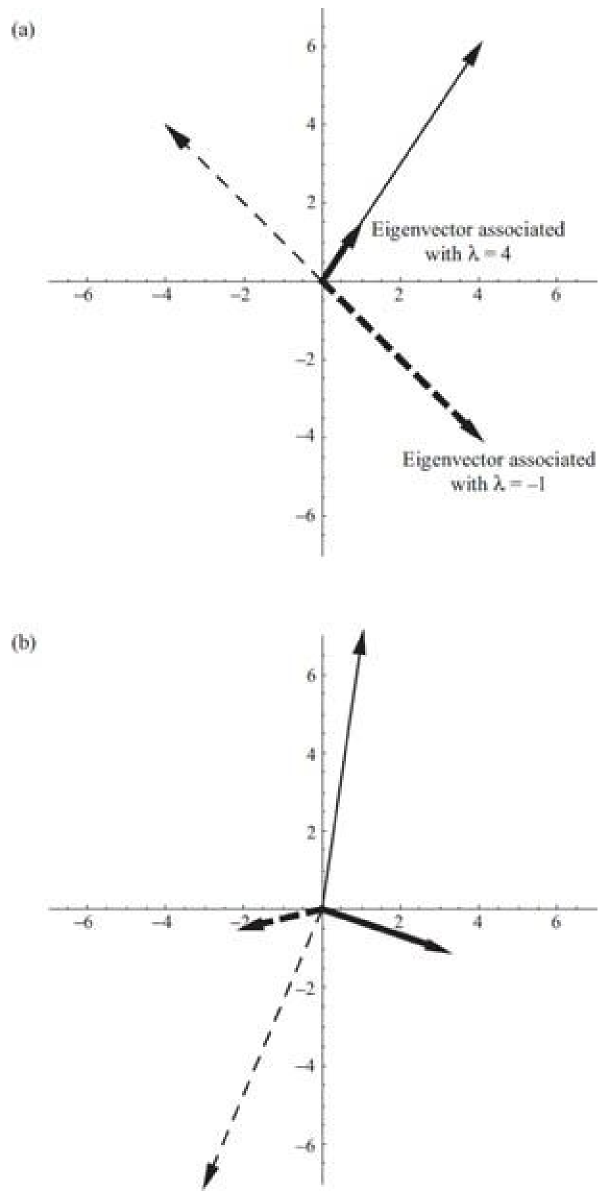


Figure P2.7: A matrix stretches or shrinks but does not rotate eigenvectors. Here, we use the matrix $\begin{pmatrix} 1 & 2 \\ 3 & 2 \end{pmatrix}$ to multiply original vectors (thick lines) to get new vectors (thin lines). (a) The two original vectors, $\begin{pmatrix} 1 \\ 3/2 \end{pmatrix}$ and $\begin{pmatrix} 4 \\ -4 \end{pmatrix}$, represent two eigenvectors of this matrix. The solid eigenvector is associated with the eigenvalue 4 and becomes stretched by a factor of 4 when multiplied on the left by the matrix. The dashed eigenvector is associated with the eigenvalue −1 and changes sign when multiplied by the matrix. (b) The two original vectors, $\begin{pmatrix} 3 \\ -1 \end{pmatrix}$ and $\begin{pmatrix} -2 \\ -0.5 \end{pmatrix}$, do not point in the direction of the eigenvectors. These vectors are rotated as well as stretched when multiplied by the matrix.

Next, we turn to the second eigenvalue, $\lambda = 3$, and find the eigenvector that satisfies equation (P2.10) with $\lambda = 3$:

$$\begin{pmatrix} 2 & 4 \\ 0 & 3 \end{pmatrix}\begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = 3\begin{pmatrix} u_1 \\ u_2 \end{pmatrix},$$

which can be written out as

$$\begin{aligned} 2u_1 + 4u_2 &= 3u_1, \\ 3u_2 &= 3u_2. \end{aligned}$$

Again, it is easier to start with the second equation, which is always true, so we arbitrarily choose $u_2 = 1$. Plugging this into the first equation indicates that $u_1 = 4$, so the eigenvector associated with $\lambda = 3$ is $\vec{u} = \binom{4}{1}$.

In the general case of a 2 × 2 matrix $\mathbf{M} = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$, the eigenvectors must satisfy

$$\begin{pmatrix} a & b \\ c & d \end{pmatrix}\begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = \lambda_i\begin{pmatrix} u_1 \\ u_2 \end{pmatrix},$$

which can be written out as

$$\begin{aligned} a\,u_1 + b\,u_2 &= \lambda_i\,u_1, \\ c\,u_1 + d\,u_2 &= \lambda_i\,u_2. \end{aligned}$$

Using the first equation and arbitrarily setting $u_1 = 1$, u_2 must equal $(\lambda_i - a)/b$. Multiplying this eigenvector by b to avoid fractions, we get a general equation for the two eigenvectors of a 2 × 2 matrix:

$$\vec{u} = \begin{pmatrix} b \\ \lambda_i - a \end{pmatrix}, \tag{P2.11}$$

one for each eigenvalue λ_i given by (P2.7). Alternatively, we could use the second equation to write the eigenvector as $\vec{u}_i = \binom{\lambda_i - d}{c}$, but this points in the same direction as (P2.11) if the correct eigenvalues are used (check this claim for the matrix **A** examined in the previous paragraph).

Let us next calculate the eigenvectors of a 3 × 3 matrix

$$\mathbf{C} = \begin{pmatrix} 1 & 0 & 0 \\ 3 & 4 & -3 \\ 2 & 2 & -1 \end{pmatrix}.$$

In the last section, we identified the three eigenvalues of this matrix as $\lambda = 1$, $\lambda = 2$, and $\lambda = 1$. We start with the eigenvalue that is not repeated, $\lambda = 2$, and find the eigenvector that satisfies equation (P2.10):

$$\begin{pmatrix} 1 & 0 & 0 \\ 3 & 4 & -3 \\ 2 & 2 & -1 \end{pmatrix}\begin{pmatrix} u_1 \\ u_2 \\ u_3 \end{pmatrix} = 2\begin{pmatrix} u_1 \\ u_2 \\ u_3 \end{pmatrix}.$$

This provides us with three equations:

$$\begin{aligned} u_1 &= 2u_1, \\ 3u_1 + 4u_2 - 3u_3 &= 2u_2, \\ 2u_1 + 2u_2 - u_3 &= 2u_3. \end{aligned}$$

The first equation can only be satisfied if $u_1 = 0$, in which case the second and third equations can both be rewritten as $\mathbf{2}u_2 - 3u_3 = 0$. Therefore, we arbitrarily choose $u_2 = 1$ so that u_3 must equal 2/3, giving us the eigenvector

$$\vec{u} = \begin{pmatrix} 0 \\ 1 \\ 2/3 \end{pmatrix}$$

associated with the eigenvalue $\lambda = 2$. Next, we turn to the repeated eigenvalue $\lambda = 1$. Our goal is to find two eigenvectors that satisfy equation (P2.10) with $\lambda = 1$:

$$\begin{pmatrix} 1 & 0 & 0 \\ 3 & 4 & -3 \\ 2 & 2 & -1 \end{pmatrix}\begin{pmatrix} u_1 \\ u_2 \\ u_3 \end{pmatrix} = \begin{pmatrix} u_1 \\ u_2 \\ u_3 \end{pmatrix},$$

which can be written out as

$$\begin{aligned} u_1 &= u_1, \\ 3u_1 + 4u_2 - 3u_3 &= u_2, \\ 2u_1 + 2u_2 - u_3 &= u_3. \end{aligned}$$

The first equation is always true, so let us arbitrarily choose $u_1 = 1$. Plugging this into the second and third equations and bringing all the terms to the left-hand side gives us

$$\begin{aligned} 3 + 3u_2 - 3u_3 &= 0, \\ 2 + 2u_2 - 2u_3 &= 0. \end{aligned}$$

These equations are both multiples of $1 + u_2 - u_3 = 0$, so any eigenvector that satisfies this equation will work. For example, we can let $u_2 = 1$ and then $u_3 = 2$, giving us one eigenvector,

$$\vec{u} = \begin{pmatrix} 1 \\ 1 \\ 2 \end{pmatrix}$$

associated with $\lambda = 1$. But can we find a second eigenvector for the second eigenvalue of 1? Let us try another value for u_2, say $u_2 = 0$, in which case $u_3 = 1$ satisfies the equations, giving us a second eigenvector associated with $\lambda = 1$:

$$\vec{u} = \begin{pmatrix} 1 \\ 0 \\ 1 \end{pmatrix}.$$

At this point, however, we must make sure that the eigenvectors that we have chosen are not just multiples of one another. They don't appear to be, but one way to check is to place all the eigenvectors as columns in a new matrix

$$\begin{pmatrix} 0 & 1 & 1 \\ 1 & 1 & 0 \\ 2/3 & 2 & 1 \end{pmatrix}.$$

As long as the determinant of this matrix is not zero, the rows will be linearly independent, and we have made an appropriate choice of eigenvectors that point in different directions. The determinant of this matrix is 1/3, so we are fine.

We could have made many other choices along the way. We will have succeeded in finding an appropriate set of eigenvectors as long as they satisfy equation (P2.10) and are linearly independent. If you are ever unsure of your choices and your algebra, however, remember that you can always plug each eigenvalue and its eigenvector back into equation (P2.10) to make sure that they work. This is a fast check that is worth doing. It is also important to emphasize that each eigenvalue has its own associated eigenvector and that one must keep track of which belong together. If you mix up the eigenvalues and eigenvectors, they will not, in general, satisfy (P2.10).

For most $d \times d$ matrices with repeated eigenvalues, it will be possible to find d eigenvectors that point in different directions. That is, the eigenvectors will be linearly independent (i.e., if placed together in a matrix, they yield a matrix whose determinant is not zero). Sometimes, however, it will prove impossible to choose eigenvectors that point in different directions every time an eigenvalue is repeated (e.g., Exercise P2.15).

A $d \times d$ matrix that does not have d linearly independent eigenvectors is called "defective" (only matrices with repeated eigenvalues can be defective). The general solutions described in Chapter 9 are not valid for defective matrices, but fortunately defective matrices do not arise too often in biological models. When they do, other methods can be applied to obtain general solutions (see Further Readings).

The above results illustrate how we can go about calculating the eigenvectors associated with all the eigenvalues of a matrix, but why are these special vectors useful? Once again, graphs can provide us with a better intuitive feel. Consider the vectors in Figure P2.6a. Looking at these vectors, it is hard to "see" how they change when multiplied by the matrix $\begin{pmatrix} 0.5 & 1 \\ -1 & 2 \end{pmatrix}$ to give the vectors in Figure P2.6b. In fact, the changes in the vectors are particularly hard to see because we use the standard horizontal and vertical axes to measure the vectors. But there is no reason why we have to use this standard coordinate system as our yardstick. In fact, if we choose the eigenvectors as our axes, then matrix multiplication results in very simple changes to a vector. In the direction of each eigenvector, a vector is stretched or shrunk by a factor equal to the eigenvalue associated with that eigenvector (Figure P2.8). Eigenvectors are therefore a more natural coordinate system in which to measure changes caused by matrix multiplication, a fact that we will use in Chapter 9 to analyze models. Also notice that the eigenvectors need not be perpendicular to one another (Figure P2.8), although they will be if the matrix is symmetric ($m_{ij} = m_{ji}$).

Before ending our introduction of eigenvectors, we note that the eigenvector defined by equation (P2.10) is more specifically called the *right eigenvector* of the matrix **M**, because the matrix is multiplied on the *right* by the eigenvector. Although the right eigenvector is more commonly encountered (e.g., in Chapters 7–9), the left eigenvector also appears in various applications (e.g., in Chapters 10 and 14). As you might have guessed, the *left eigenvector* of **M** is defined by

$$\vec{v}_i^{\mathrm{T}} \mathbf{M} = \lambda_i \vec{v}_i^{\mathrm{T}}, \tag{P2.12}$$

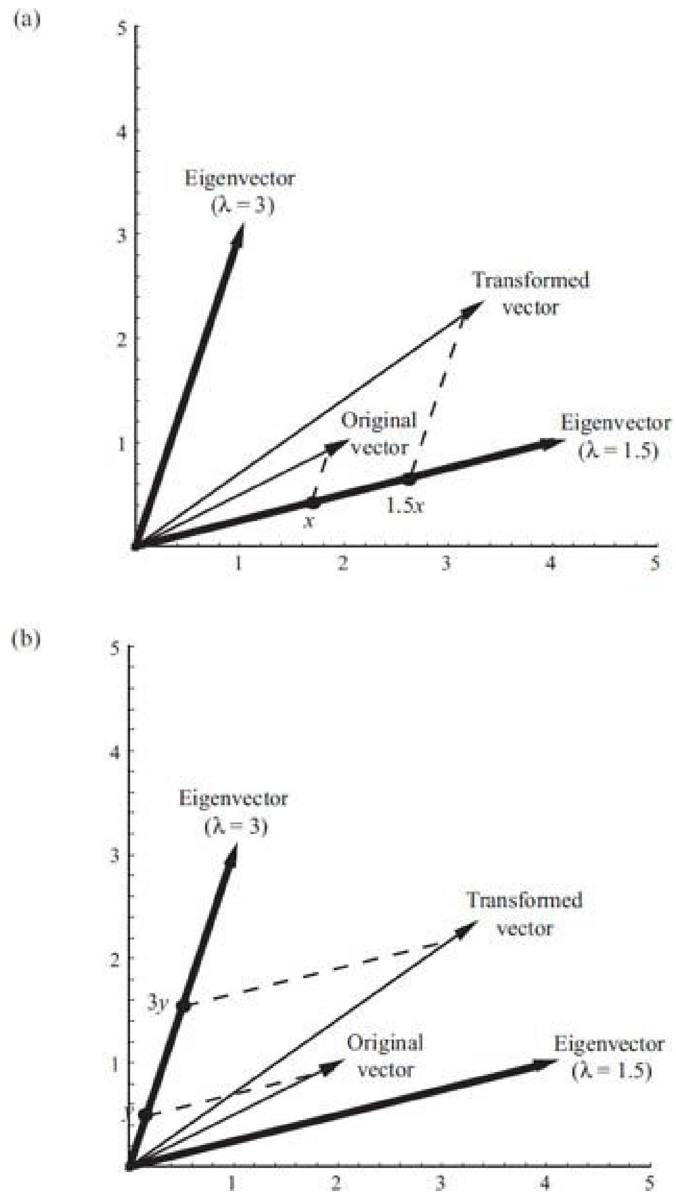


Figure P2.8: Matrix multiplication visualized using eigenvectors as axes. The matrix $\mathbf{M} = \begin{pmatrix} 15/11 & 6/11 \\ -9/22 & 69/22 \end{pmatrix}$ has one eigenvector of $\begin{pmatrix} 4 \\ 1 \end{pmatrix}$ associated with an eigenvalue of 1.5 and a second eigenvector of $\begin{pmatrix} 1 \\ 3 \end{pmatrix}$ associated with an eigenvalue of 3. These eigenvectors are drawn using thick lines. An original vector $\begin{pmatrix} 2 \\ 1 \end{pmatrix}$ is multiplied on the left by $\mathbf{M}$ to get the transformed vector $\begin{pmatrix} 36/11 \\ 51/22 \end{pmatrix}$. This transformation does not appear to follow a pattern. (a) If we project the original and transformed vectors onto the first eigenvector by following the dashed lines, we see, however, that the transformed vector has a length that is $\lambda = 1.5$ times the length of the original vector (x). (b) Similarly, if we project the vectors onto the second eigenvector, we see that the transformed vector has a length that is $\lambda = 3$ times the length of the original vector (y). Thus, multiplication by $\mathbf{M}$ stretches a vector along each eigenvector by an amount proportional to the associated eigenvalue. The dashed lines that allow us to project a vector onto an eigenvector are parallel to the other eigenvector.

where now the matrix is multiplied on the *left* by the eigenvector $\vec{v}_i$, transposed to become a row vector. When it is not specified whether an eigenvector is "right" (P2.10) or "left" (P2.12), then we will take it for granted that we are referring to the right eigenvector.

The right and left eigenvectors of a matrix are not generally the same. To demonstrate this point, we now find the left eigenvectors of $\mathbf{A} = \begin{pmatrix} 2 & 4 \\ 0 & 3 \end{pmatrix}$. Beginning again with the eigenvalue $\lambda = 2$, the left eigenvector must satisfy equation (P2.12) with $\lambda = 2$:

$$(v_1 \quad v_2)\begin{pmatrix} 2 & 4 \\ 0 & 3 \end{pmatrix} = 2(v_1 \quad v_2).$$

This provides us with two equations that both must be satisfied by the left eigenvector (v_1,v_2):

$$\begin{aligned} 2v_1 &= 2v_1, \\ 4v_1 + 3v_2 &= 2v_2. \end{aligned}$$

These equations are not satisfied by the right eigenvector $\begin{pmatrix} 1 \\ 0 \end{pmatrix}$. To find the left eigenvector, we set v_1 to 1. This solves the first equation and causes the second equation to become $4 + 3v_2 = 2v_2$, which is true if $v_2 = -4$. Thus, we have a left eigenvector of $\vec{v}^{\mathrm{T}} = (1, -4)$ associated with the eigenvalue $\lambda = 2$. Next, we find the left eigenvector that satisfies equation (P2.10) with $\lambda = 3$:

$$(v_1 \quad v_2)\begin{pmatrix} 2 & 4 \\ 0 & 3 \end{pmatrix} = 3(v_1 \quad v_2),$$

which can be written out as

$$\begin{aligned} 2v_1 &= 3v_1, \\ 4v_1 + 3v_2 &= 3v_2. \end{aligned}$$

The first equation will never be true unless we choose $v_1 = 0$. Plugging this into the second equation leaves $3v_2 = 3v_2$, which is true for all values of v_2. We can arbitrarily choose $v_2 = 1$ giving the left eigenvector $\vec{v}^{\mathrm{T}} = (0, 1)$ associated with $\lambda = 3$ (the only bad choice for v_2 would be 0 because then all elements of the eigenvector would be zero).

Exercise P2.14: For the following matrices, find right eigenvectors associated with the eigenvalues found in Exercise P2.12:

(a)
$$\begin{pmatrix} \alpha & 0 \\ \beta & 3\delta \end{pmatrix}.$$

(b)
$$\begin{pmatrix} 1 & 2 \\ 3 & 2 \end{pmatrix}.$$

(c)
$$\begin{pmatrix} 2 & 7 & 5 \\ 0 & 19 & 0 \\ 4 & 3 & 1 \end{pmatrix}.$$

Exercise P2.15: Find the eigenvalues, right eigenvectors, and left eigenvectors of the following matrices. Specify which matrices are defective.

(a)
$$\begin{pmatrix} 7 & -10 \\ 5 & -8 \end{pmatrix},$$

(b)
$$\begin{pmatrix} 3 & 5 \\ 3 & 1 \end{pmatrix},$$

(c)
$$\begin{pmatrix} 1 & 1 \\ -1 & 3 \end{pmatrix}.$$

(d)
$$\begin{pmatrix} 3 & -2 \\ 2 & -1 \end{pmatrix}.$$

Further Readings

The following books offer more information on linear algebra at an introductory level with many exercises:

• Lay, D. C. 2003. *Linear Algebra and Its Applications*, 3rd ed. Addison-Wesley-Longman, New York.
• Lay, D. C. 2003. *Student's Study Guide*, 3rd ed. Addison-Wesley-Longman, New York.
• Lipschutz, S., and M. Lipson. 2000. *Schaum's Outline of Linear Algebra*, 3rd ed. Schaum's Outline Series.

The following books offer information on linear algebra at an advanced level, describing powerful methods and proofs in linear algebra:

• Gantmacher, F. R. 1990. *Matrix Theory*, Vol. 1, 2nd ed., Chelsea Publications, London.
• Gantmacher, F. R. 2000. *Theory of Matrices*, Vol. 2, 2nd ed., Chelsea Publications, London.

Answers to Exercises

Exercise P2.1

(a) Two-dimensional row vector (or a 1 × 2 matrix) whose transpose is $\begin{pmatrix} 2 \\ 4 \end{pmatrix}$.

(b) Three-dimensional column vector (or a 3 × 1 matrix) whose transpose is (1 2 3). (c) A 2 × 2 matrix whose transpose is $\begin{pmatrix} 6 & 2 \\ -4 & 0 \end{pmatrix}$. (d) A 2 × 3 matrix whose transpose is $\begin{pmatrix} 1+x & 5 \\ 2+x & 7 \\ 3+x & 9 \end{pmatrix}$. (e) A 3 × 2 matrix whose transpose is $\begin{pmatrix} a & c & e \\ b & d & f \end{pmatrix}$.

Exercise P2.2

Only (b), (c), and (e) are valid. (b) $\begin{pmatrix} 7 \\ 11 \end{pmatrix}$. (c) $\begin{pmatrix} 5 \\ 7 \\ 9 \end{pmatrix}$. (e) $(0.5 + a \quad 1.3 + b \quad 2 + c)$.

Exercise P2.3

(a), (c), (d), and (e) are valid. (a) $\begin{pmatrix} 7 & 6 \\ 5 & 4 \end{pmatrix}$. (c) $\begin{pmatrix} a-1 & b-2 \\ c-3 & d-4 \end{pmatrix}$. (d) $\begin{pmatrix} 2a & b+a & c+a \\ 2d & e+d & f+d \end{pmatrix}$.
(e) $\begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$.

Exercise P2.4

Scalar multiplication is always valid. (a) (6 12). (b) $\begin{pmatrix} -4 \\ -5 \\ -6 \end{pmatrix}$. (c) $\begin{pmatrix} 2 & 4 \\ 6 & 8 \end{pmatrix}$. (d) $\begin{pmatrix} a & 2a & 3a \\ 5a & 7a & 9a \end{pmatrix}$.
(e) $\begin{pmatrix} 2+a & 4+2a \\ 6+3a & 8+4a \end{pmatrix}$.

Exercise P2.5

(a) $\mathbf{AB} = \begin{pmatrix} ae+bg & af+bh \\ ce+dg & cf+dh \end{pmatrix}$, which does not equal $\mathbf{BA} = \begin{pmatrix} ea+fc & eb+fd \\ ga+hc & gb+hd \end{pmatrix}$.

Exercise P2.6

The trace of matrices **A** and **B** is 5. The trace of matrix **C** is −5. All of these matrices have the same determinant, namely, −2.

Exercise P2.7

Because the determinant of matrices **D** and **F** is zero, their rows are not independent. For matrix **D**, the second row is −3 times the first row. For matrix **F**, the second row is x times the first row. Only matrix **E** has linearly independent rows, because its determinant is not zero but −6.

Exercise P2.8

Using Definition P2.6, the determinant of **A** is 6, which equals the product of the diagonal elements (2 × 3) because this is an upper triangular matrix. Using Rule P2.16, the determinant of **B** is also 6, which equals the product of the diagonal elements (2 × 3 × 1) because this is an upper triangular matrix.

Exercise P2.9

(a) $\begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}$. (b) $\begin{pmatrix} 1 & 0 \\ 0 & 1/3 \end{pmatrix}$. (c) This matrix is noninvertible because its determinant is zero. (d) $\begin{pmatrix} 2 & -1 \\ -1/2 & 1/2 \end{pmatrix}$. (e) $\begin{pmatrix} -2 & 1 \\ 3/2 & -1/2 \end{pmatrix}$.

Exercise P2.11

$\mathbf{M} = \begin{pmatrix} -\beta-\delta & \gamma \\ \beta & -\gamma-\delta \end{pmatrix}$, $\vec{v} = \begin{pmatrix} -\alpha \\ 0 \end{pmatrix}$, and

$$\mathbf{M}^{-1} = \begin{pmatrix} \dfrac{-\gamma - \delta}{\delta(\beta + \gamma + \delta)} & \dfrac{-\gamma}{\delta(\beta + \gamma + \delta)} \\ \dfrac{-\beta}{\delta(\beta + \gamma + \delta)} & \dfrac{-\beta - \delta}{\delta(\beta + \gamma + \delta)} \end{pmatrix}.$$

Thus,

$$\vec{n} = \begin{pmatrix} \dfrac{\gamma\alpha + \delta\alpha}{\delta(\beta + \gamma + \delta)} \\ \dfrac{\beta\alpha}{\delta(\beta + \gamma + \delta)} \end{pmatrix}$$

is the equilibrium number of unbound (top row) and bound (bottom row) tRNAs.

Exercise P2.12

(a) $\lambda_1 = \alpha$ and $\lambda_2 = 3\delta$ using Rule P2.26. (b) $\lambda_1 = 4$ and $\lambda_2 = -1$ using Definition P2.7. (c) $\lambda_1 = 6$, $\lambda_2 = -3$, and $\lambda_3 = 19$ using Rule P2.28 and Definition P2.7. (d) $\lambda_1 = 4$, $\lambda_2 = -1$, and $\lambda_3 = z$ using Rule P2.27 or P2.28 and the answer to (b). (e) $\lambda_1 = \alpha + \beta$, $\lambda_2 = \alpha - \beta$, $\lambda_3 = \gamma$, and $\lambda_4 = 2\delta - \gamma$ using Rule P2.27 and Definition P2.7.

Exercise P2.13

(a) The characteristic polynomial is $-\lambda\,(a\,b + a\,c + b\,c + (a + b + c)\,\lambda + \lambda^2) = 0$. (b) $\lambda_1 = 0$, $\lambda_2 = (-(a+b+c) + \sqrt{(a+b+c)^2 - 4(ab+ac+bc)})/2$ and $\lambda_3 = (-(a+b+c) - \sqrt{(a+b+c)^2 - 4(ab+ac+bc)})/2$. Note that λ_2 and λ_3 can be complex numbers. For example, if all the transition rates equal a, these eigenvalues become $-3/2\,a \pm \sqrt{3}ai/2$, where $i = \sqrt{-1}$. As described in Chapter 8, complex eigenvalues are typical of models with cyclic dynamics.

Exercise P2.14

The eigenvector that you choose is correct if it is a constant multiple of the following choices (i.e., if it points along the same line). (a) $\vec{u} = \begin{pmatrix} 0 \\ 1 \end{pmatrix}$ associated with $\lambda_1 = 3\delta$ and $\vec{u} = \begin{pmatrix} 1 \\ \beta/(\alpha - 3\delta) \end{pmatrix}$ associated with $\lambda_2 = \alpha$. (b) $\vec{u} = \begin{pmatrix} 2 \\ 3 \end{pmatrix}$ associated with $\lambda_1 = 4$ and $\vec{u} = \begin{pmatrix} 1 \\ -1 \end{pmatrix}$ associated with $\lambda_2 = -1$. (c) $\vec{u} = \begin{pmatrix} 1 \\ 0 \\ 4/5 \end{pmatrix}$ associated with $\lambda_1 = 6$, $\vec{u} = \begin{pmatrix} 1 \\ 0 \\ -1 \end{pmatrix}$ associated with $\lambda_2 = -3$, and $\vec{u} = \begin{pmatrix} 141 \\ 286 \\ 79 \end{pmatrix}$ associated with $\lambda_3 = 19$.

Exercise P2.15

The eigenvector that you choose is correct if it is a constant multiple of the following choices (i.e., if it points along the same line). (a) Left $\vec{v}^T = (1, -2)$ and right $\vec{u} = \begin{pmatrix} 1 \\ 1 \end{pmatrix}$ associated with $\lambda_1 = -3$; left $\vec{v}^T = (1, -1)$ and right $\vec{u} = \begin{pmatrix} 2 \\ 1 \end{pmatrix}$ associated with $\lambda_2 = 2$. (b) Left $\vec{v}^T = (1, 1)$ and right $\vec{u} = \begin{pmatrix} 5 \\ 3 \end{pmatrix}$ associated with $\lambda_1 = 6$; left $\vec{v}^T = (3, -5)$ and right $\vec{u} = \begin{pmatrix} 1 \\ -1 \end{pmatrix}$ associated with $\lambda_2 = -2$. (c) Left $\vec{v}^T = (1, -1)$ and right $\vec{u} = \begin{pmatrix} 1 \\ 1 \end{pmatrix}$ assosiatd with $\lambda_1 = 2$, and there are no other independent choices for $\lambda_2 = 2$ (the matrix is defective). (d) Left $\vec{v}^T = (1, -1)$ and right $\vec{u} = \begin{pmatrix} 1 \\ 1 \end{pmatrix}$ associated with $\lambda_1 = 1$ and there are no other independent choices for $\lambda_2 = 1$ (the matrix is defective).