Mathematical Techniques in Evolution and Ecology

Equilibria and stability analysis – Linear models with multiple variables

Based on Chapter 7 in Otto and Day (2007)

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Outline

Goals

- To construct dynamical models involving linear combinations of multiple variables
- To find equilibria of these models
- To analyse the stability of these equilibria

Concepts

- Multivariable equilibria
- Multivariable linear models
- Eigenvectors, eigenvalues
- Characteristic polynomial
- Leading eigenvalues in continuous- and discrete-time models

Models with more than one dynamic variable

Many questions in biology require multiple variables to be modeled jointly. For each variable, we write a dynamical equation, where a given variable may obviously occur in multiple equations. At a **multivariable equilibrium**, all variables must remain unchanged. Since, with multiple variables, there are many different directions in which the system can move, we need to develop an appropriate measure of whether a population is approaching or moving away from an equilibrium.

As a first, very simple example, consider the case of two bacterial species with two different exponential growth rates r_1 and r_2:

$$\begin{aligned} \frac{dn_1}{dt} &= r_1\, n_1, \\ \frac{dn_2}{dt} &= r_2\, n_2. \end{aligned} \tag{1}$$

Equation (1) represents two independent population-dynamic processes; the dynamics of n_1 to not depend on n_2 and vice versa. Each species grows or shrinks according to the exponential one-variable model.

Linear multivariate models of the form as in Eq. (1) have **only one joint equilibrium**, here $\hat{n}_1 = \hat{n}_2 = 0$. It is found by setting both equations in (1) to zero at the same time.

Exercise

- Use graphical arguments to determine when the equilibrium $\hat{n}_1 = \hat{n}_2 = 0$ is stable. Express your answer in terms of conditions on r_1 and r_2.
- Identify the two lines in a plane opened by the n_1 and n_2 axis from which the system never leaves. These lines are the **eigenvectors** of the system.

Definition: Eigenvector and eigenvalue

A system *grows or decays in the direction of its* **eigenvectors**. The *rate of change along an eigenvector* is given by the corresponding **eigenvalue**. Typically, linear models with *n* variables have *n* eigenvectors and *n* corresponding eigenvalues.

Remark: Keep in mind the difference between eigenvectors and null clines. In a phase-plane for a linear model with two variables:

- **Null clines** are lines along which *a particular variable does not change over time*. Each variable has one null cline. If the system is at a null cline, *the direction of change is perpendicular to the axis of the variable whose null cline it is, and parallel to the axis of the other variable*. The *equilibrium* is where the two null clines *intersect*, because this is where both variables do not change over time.
- **Eigenvectors** represent *combinations of the dynamic variables* for which the *relative values of the variables remain constant*. When a dynamical system is on an eigenvector, it never leaves the eigenvector. The movement along an eigenvector is either inward or outward.

Matrix form

A multivariate linear model can be written as a matrix of constants times a vector of variables:

$$\frac{d\vec{n}}{dt} = \mathbf{M}\,\vec{n}, \tag{2}$$

where

$$d\vec{n} = \begin{pmatrix} \frac{dn_1}{dt} \\ \frac{dn_2}{dt} \end{pmatrix}, \ \vec{n} = \begin{pmatrix} n_1 \\ n_2 \end{pmatrix}, \ \mathbf{M} = \begin{pmatrix} a & b \\ c & d \end{pmatrix}.$$

In our first example, $a = r_1$,

Affine models with multiple variables

As for models with one variable, there is also a second type of model for multivariable linear models: adding a constant term to the linear term produces an **affine multivariable linear model**:

$$\frac{d\vec{n}}{dt} = \mathbf{M}\,\vec{n} + \vec{c}, \tag{3}$$

where $\vec{c}$ is a vector of constants, each representing the rate of input or outflow to its corresponding variable. As in one-variable models, affine models can be transformed into non-affine models of the form in Eq. (2) by considering the dislocation from the equilibrium (details below).

Affine models also arise in discrete time and take the form

$$\vec{n}(t+1) = \mathbf{M}\,\vec{n}(t) + \vec{c}, \tag{4}$$

where again $\mathbf{M}$ is a matrix of constants and $\vec{c}$ a vector of constants.

Transforming affine to non-affine multivariable models

Starting from Eq. (2), we note that at equilibrium, each variable must not change. Hence, the equilibrium condition for a **continuous-time** affine model is

$$\vec{0} = \mathbf{M}\,\hat{\vec{n}} + \vec{c}, \tag{5}$$

where $\vec{0}$ is a vector of zeros. Moving $\vec{c}$ to the left side and multiplying both sides on the left by $\mathbf{M}^{-1}$, we can solve for the equilibrium:

$$\hat{\vec{n}} = -\mathbf{M}^{-1}\,\vec{c}. \tag{6}$$

If $\vec{c}$ is a vector of zeros, then the equilibrium is at the origin, i.e. $\hat{\vec{n}} = \vec{0}$, as expected for a non-affine linear model (Rule 7.1).

In **discrete time**, the equilibrium for Eq. (4) must satisfy the condition

$$\hat{\vec{n}} = \mathbf{M}\,\hat{\vec{n}} + \vec{c}. \tag{7}$$

Moving $\hat{\vec{n}}$ to the right and $\vec{c}$ to the left side gives $-\vec{c} = (\mathbf{M} - \mathbf{I})\,\hat{\vec{n}}$, and hence

$$\hat{\vec{n}} = -(\mathbf{M} - \mathbf{I})^{-1}\,\vec{c}. \tag{8}$$

As in the case of linear models with one variable, the behaviour of affine linear models with multiple variables can be understood using the techniques for non-affine models, provided that we make the appropriate **transformation**: We rewrite each variable *in terms of the deviation from its equilibrium*, so that the vector of these deviations takes the form of a non-affine linear model:

$$\vec{\delta} = \vec{n} - \hat{\vec{n}}. \tag{9}$$

Therefore, any result for linear non-affine models can be applied directly to affine models, once this transformation has been made.

Linear multivariable models in continuous time

We first summarise the steps to identify the equilibrium of a linear model with multiple variables in continuous time. Then, we learn how to assess the stability of the equilibrium. We will treat the case of discrete time separately later.

We find the equilibria by solving the equilibrium condition,

$$\vec{0} = \mathbf{M}\,\hat{\vec{n}}, \tag{10}$$

for $\hat{\vec{n}}$. We can already anticipate that the only solution is $\hat{\vec{n}} = \vec{0}$. However, let us take another route here.

Writing the model in non-matrix form, we have

$$\begin{aligned} 0 &= a\, n_1 + b\, n_2, \\ 0 &= c\, n_1 + d\, n_2. \end{aligned} \tag{11}$$

Solving both equations in (11) for the same variable, e.g. n_2, we find $n_2 = (-a/b)\, n_1$ and $n_2 = (-c/d)\, n_1$. Of course, these two equations define the null clines. The equilibrium conditions for Eq. (11) are satisfied by the same value of n_2 only if $(-a/b)\, \hat{n}_1 = (-c/d)\, \hat{n}_1$. In general, this will only hold true if $\hat{n}_1 = 0$. This further implies that $\hat{n}_2 = 0$. We have just confirmed that the equilibrium occurs where the two null clines intersect, and that this happens at the origin $\vec{0}$.

In the **special case where the two null clines coincide**, there are multiple equilibria. In fact, the whole common null cline is one equilibrium. In this case, we must have $-a/b = -c/d$. Interestingly, this is also the condition for *the determinant of* **M** *to be zero*, i.e. for **M** to be non-invertible. Having a determinant of 0 is *a special case of the parameters*, analogous to $r = 0$ in the case of one-variable models.

Rule 7.1: Equilibrium of a linear multivariable model in continuous time

A linear model in continuous time has **only one equilibrium** regardless of tthe number of variables, *provided that the determinant of* **M** *is not zero*.

- For a linear model of the form $d\vec{n}/dt = \mathbf{M}\,\vec{n}$, the equilibrium point is the origin, $\hat{\vec{n}} = \vec{0}$.
- For an affine model of the form $d\vec{n}/dt = \mathbf{M}\,\vec{n} + \vec{c}$, the equilibrium point is $\hat{\vec{n}} = -\mathbf{M}^{-1}\,\vec{c}$

If the *determinant of* **M** *is zero*, there are an *infinite number of equilibria*.

Determining the stability of the equilibrium

As we have seen, a linear system eventually grows or shrinks along the eigenvectors as time progresses. If we choose a starting position that lies on an eigenvector, then by definition the system will grow or decay exponentially along the eigenvector and never leave it. While the absolute values of the variables may change, their relative values with respect to each other will remain constant.

To determine if an equilibrium is stable, we are therefore interested in the rate at which the variables shrink or grow along the eigenvector. If the variables all shrink along the eigenvectors, we know that the system will eventually approach the origin, in which case the single equilibrium there is stable. If at least one variable grows along an eigenvector, the equilibrium cannot be stable.

The rate at which a system grows or shrinks in the direction of an eigenvector is given by the corresponding **eigenvalue**. Therefore, if we start the system along an eigenvector $\vec{v}$, all the components of $\vec{v}$ must grow or shrink at the same rate r, the eigenvalue:

$$\frac{d\vec{v}}{dt} = r\,\vec{v}. \tag{12}$$

But we also know that the dynamics must satisfy the original equation,

$$\frac{d\vec{v}}{dt} = \mathbf{M}\,\vec{v}. \tag{13}$$

Combining Eqs. (12) and (13), the eigenvector and its associated eigenvalue must satisfy

$$\mathbf{M}\,\vec{v} = r\,\vec{v}. \tag{14}$$

Mathematically, equation (14) the eigenvalues and eigenvectors of the matrix **M**.

For our purpose, we are only interested in the eigenvalue r. As shown in Primer 2 of OD2007, the *eigenvalues* of a matrix **M** *satisfy the* **characteristic polynomial**.

Definition: Characteristic polynomial

The characteristic polynomial of a matrix M is given by the equation

$$\text{Det}(\mathbf{M} - \mathbf{I}\, r) = 0, \tag{15}$$

where $\text{Det}(\mathbf{M} - \mathbf{I}\, r)$ is the determinant of the matrix $\mathbf{M} - \mathbf{I}\, r$. The number of variables in the model determines the degree of the characteristic polynomial.

The eigenvalues of the system are found by determining the roots of the characteristic polynomial in Eq. (15). Assuming that the eigenvalues are real, **the origin is a stable equilibrium if and only if all eigenvalues are negative**, i.e. that the system shrinks along all eigenvectors.

In general, solving the characteristic polynomial can be tricky, and is a task for which we would usually use a software like *Maple* or *Mathematica*.

However, for a model with only two variables, the calculations are easy. At this point, it is worth recalling that the determinant of a $2 x 2$ matrix $\mathbf{L} = \begin{pmatrix} e & f \\ g & h \end{pmatrix}$ is given by $e\,h - f\,g$. Therefore, Eq. (15), the characteristic polynomial, reads

$$\mathrm{Det}(\mathbf{M} - \mathbf{I}\,r) = (a - r)\,(d - r) - b\,c = r^2 - (a + d)\,r + (a\,d - b\,c) = 0. \tag{16}$$

Equation (16) is a quadratic equation in r, and the two solutions are

$$\begin{aligned} r_1 &= \frac{a + d + \sqrt{(a + d)^2 - 4\,(a\,d - b\,c)}}{2}, \\ r_2 &= \frac{a + d - \sqrt{(a + d)^2 - 4\,(a\,d - b\,c)}}{2}. \end{aligned} \tag{17}$$

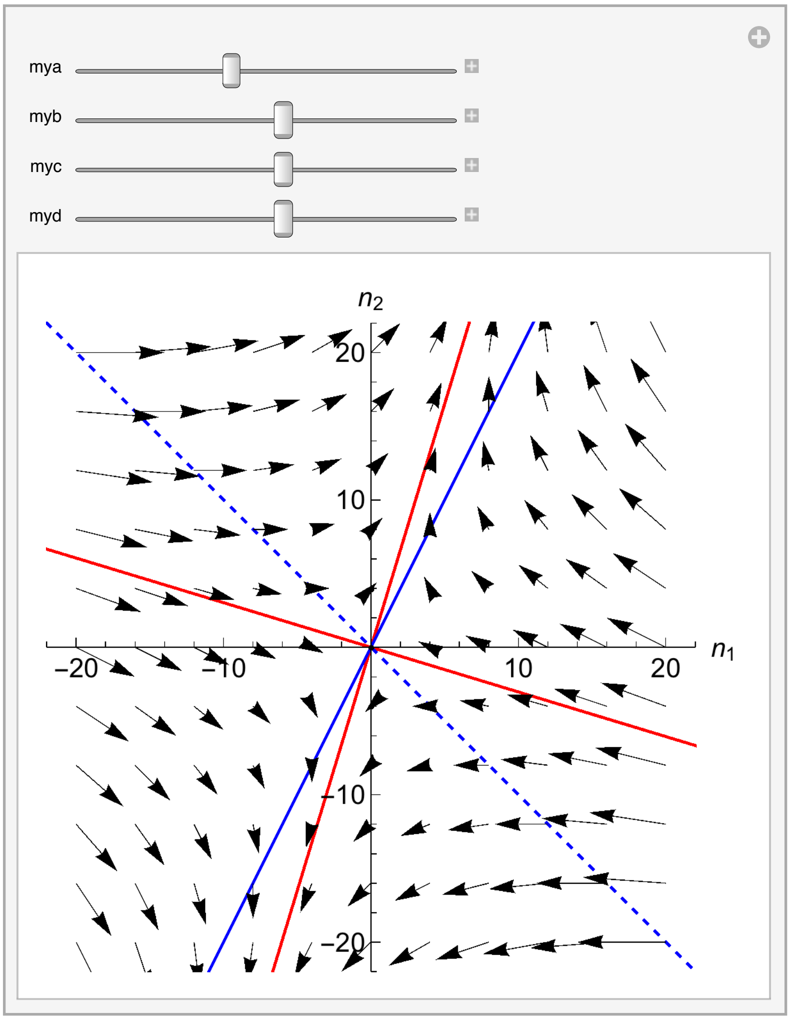
Equation (17) gives the two eigenvalues for the general two-dimensional linear model.

Illustration: Eigenvalues and null clines

In the figure below, the two null clines in blue (solid for n_1, and dashed for n_2), and the eigenvectors are shown in red. The arrows point in the direction of change, and their length is proportional to the rate of change.

In[7]:=
```
Manipulate[
 Show[vectorFieldPlot[mya, myb, myc, myd, 0.1]],
 {{mya, -2}, -10, 10}, {{myb, 1}, -10, 10},
 {{myc, 1}, -10, 10}, {{myd, 1}, -10, 10}
]
```

Out[7]=



Example: Metastasis of malignant tumors (adapted from Glass and Kaplan 1995)

Concider the case of a cancer forming metastases. Let the number of cancer cells in the capillaries of an organ be C, and the number of cancer cells that have actually invaded the organ be I.

- Suppose that cells are lost from the capillaries by death at a per capita rate δ_1.
- Assume that cells from the capillaries invade the organ at a per capita rate β.
- Let the per capita rate of death of cells in the organ be δ_2.
- Last, assume that cancer cells that have invaded the organ replicate at a per capita rate ρ.

- Draw a flow diagram.
- Derive the differential equations for C and I, and write the dynamics in matrix form.
- Determine under which condition the tumor will take hold and grow.

When eigenvalues are complex

Looking at Eq. (17), we note that the eigenvalues are complex if $(a-d)^2 < 4\,(a\,d - b\,c)$. Shrinkage or growth of the system along the eigenvectors is now cyclic, with an amplitude determined by the real part of the eigenvalues. Therefore, if the eigenvalues are complex, then it is their real part that determines whether or not the equilibrium is stable.

When eigenvalues are complex, the eigenvectors are complex, too. They can no longer be represented on a plane.

This brings us to the definition of the **leading eigenvalue**:

Leading eigenvalue

The **leading eigenvalue** of a continuous-time model is *the one with the largest real part*. The leading eigenvalue *dominates the long-term dynamics* of a system, and is therefore crucial for determining the stability of an equilibrium.

Rule 7.2: Stability of an equilibrium in a linear continuous-time model

- For an equilibrium to be stable in *continuous time*, the *real parts of all eigenvalues* of the matrix **M** must be *negative*.
- Equivalently, the *real part of the leading eigenvalue must be negative*. The leading eigenvalue of a continuous-time model is the eigenvalue with the largest real part.

Equilibria and stability for linear multivariable models in discrete time

A linear multivariable model in discrete time can be expressed as a recursion equation in matrix form as follows:

$$\vec{n}(t+1) = \mathbf{M}\,\vec{n}(t), \tag{18}$$

where, in the case of just two variables,

$$\vec{n}(t+1) = \begin{pmatrix} n_1(t+1) \\ n_2(t+1) \end{pmatrix},$$

$$\vec{n}(t) = \begin{pmatrix} n_1(t) \\ n_2(t) \end{pmatrix}, \text{ and}$$

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

The matrix **M** is sometimes called the *transition matrix*, as it describes the transition from one to the next time step.

Finding the equilibrium

The equilibrium for the model in Eq. (18) must satisfy the *equilibrium condition*

$$\hat{\vec{n}} = \mathbf{M}\,\hat{\vec{n}}, \tag{19}$$

or

$$\vec{0} = (\mathbf{M} - \mathbf{I})\,\vec{n}. \tag{20}$$

To solve Eq. (20), we note that there are two possibilities: (i) the determinant of the matrix $\mathbf{M} - \mathbf{I}$ is nonzero, i.e. $\mathbf{M} - \mathbf{I}$ can be inverted, in which case the only equilibrium is $\vec{0}$; (ii) the determinant of $\mathbf{M} - \mathbf{I}$ is zero, in which case there is an infinite number of equilibria, which reflects a special case of parameters. Rule 7.3 gives a formal recipe.

Rule 7.3: Equilibrium of linear multivariable models in discrete time

As long as the determinant of $\mathbf{M} - \mathbf{I}$ is not zero (i.e. $\mathbf{M} - \mathbf{I}$ is invertible), a linear model in discrete time has only one equilibrium, regardless of the number of variables.

- For a linear model of the form $\vec{n}(t+1) = \mathbf{M}\,\vec{n}(t)$, the equilibrium point is the origin, $\hat{\vec{n}} = \vec{0}$.
- For an affine model of the form $\vec{n}(t+1) = \mathbf{M}\,\vec{n}(t) + \vec{c}$, the equilibrium point is $\hat{\vec{n}} = -(\mathbf{M} - \mathbf{I})^{-1}\,\vec{c}$.

If the determinant of $\mathbf{M} - \mathbf{I}$ is zero, then there are an infinite number of equilibria.

Determining stability

Let us focus on the case where the determinant of **M – I** is nonzero, i.e. where there is a single equilibrium at the origin $\vec{0}$. As for continuous-time linear multivariable models, the key here is to determine the **eigenvalues**.

- Recall: In the case of *continuous time*, we had to compare the **real parts** of the eigenvalues **to zero**.
- In contrast to continuous-time models, in *discrete time* we must now compare the **absolute values** of the eigenvalues to **one**, regardless of whether the eigenvalues are real or complex.

In general, the eigenvalue associated with the *j*th eigenvector will take the form

$$\lambda_j = A_j + B_j\, i.$$

The absolute value (also called *modulus*) of such an eigenvalue is

$$|\lambda_j| = \sqrt{A_j^2 + B_j^2}\ .$$

Stability of $\vec{0}$ requires that $|\lambda_j| < 1$ for all j, which implies that stability hinges on the absolute value of the eigenvalue with the largest absolute value.

The **leading eigenvalue** of a *discrete-time model* is the one with the **largest absolute value**. The leading eigenvalue dominates the long-term dynamics of a system.

Rule 7.4: Stability of an equilibrium in a linear discrete-time model

For stability of an equilibrium in discrete time, all eigenvalues must be less than one in absolute value. Equivalently, the absolute value of the leading eigenvalue must be less than one.

- For complex eigenvalues $\lambda = A \pm B\,i$, stabilit requires that the value $\sqrt{A^2 + B^2}$ be less than one.
- For real eigenvalues, stability requires that $|\lambda| < 1$, i.e. that both $\lambda < 1$ and $-1 < \lambda$.

Concluding remark

While models in biology are rarely linear, the concepts visited in this unit will be helpful for non-linear models to be discussed later.

Initialisation cells

In[8]:=
```
vectorFieldPlot[α_, β_, χ_, δ_, σ_] :=
 Module[{mya = α, myb = β, myc = χ, myd = δ, mys = σ, n1Min, n2Min, n1Max, n2Max,
   gridStep1, gridStep2, arrowCoord, vFieldPlot, eVecs, nullClines},
  n1Min = -20;
  n1Max = 20;
  n2Min = -20;
  n2Max = 20;
  gridStep1 = 4;
  gridStep2 = 4;
  arrowCoord = Table[Table[{{x, y},
       {x + s ({{a, b}, {c, d}}.{x, y})[[1]], y + s ({{a, b}, {c, d}}.{x, y})[[2]]}},
      {y, n2Min, n2Max, gridStep2}], {x, n1Min, n1Max, gridStep1}];
  vFieldPlot = ListPlot[
    {{n1Min, n2Min}, {n1Max, n2Max}},
    PlotStyle → None,
    Epilog → {Black, Arrow[
       Flatten[arrowCoord, 1] /. {a → mya, b → myb, c → myc, d → myd, s → mys}]},
    PlotRange → {{n1Min - 2, n1Max + 2}, {n2Min - 2, n2Max + 2}},
    AxesLabel → {"n₁", "n₂"},
    LabelStyle → Directive[FontSize → 14],
    AspectRatio → 1
   ];
  eVecs =
   Plot[{N[-(2 c)/(-a + d + Sqrt[a^2 + 4 b c - 2 a d + d^2])] * n1 /. {a → mya, b → myb, c → myc, d → myd},
     N[-(2 c)/(-a + d - Sqrt[a^2 + 4 b c - 2 a d + d^2])] * n1 /. {a → mya, b → myb, c → myc, d → myd}},
    {n1, n1Min - 100, n1Max + 100},
    PlotRange → {{n1Min - 5, n1Max + 5}, {n2Min - 5, n2Max + 5}},
    PlotStyle → {Red, {Red}}
   ];
  nullClines = Plot[{-a n1 / b /. {a → mya, b → myb, c → myc, d → myd},
     -c n1 / d /. {a → mya, b → myb, c → myc, d → myd}}, {n1, n1Min - 100, n1Max + 100},
    PlotRange → {{n1Min - 5, n1Max + 5}, {n2Min - 5, n2Max + 5}},
    PlotStyle → {{Blue}, {Blue, Dashed}}
   ];
  Return[{vFieldPlot, eVecs, nullClines}]
 ]
```