Evolutionary Dynamics

Tutorial 2

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1 Multiple variable models: Linear systems

A system is described by n independent quantities $x_1, \ldots, x_n$. For a linear differential equation, the dynamical behaviour can be written in matrix form as

$$\frac{dx}{dt} = \mathbf{M}x, \tag{1}$$

where x is the column vector $x_1, \ldots, x_n$.

1.1 Finding equilibrium points

Analogously to the single variable case, the equilibrium is given by

$$\frac{dx}{dt} = 0 \quad \Leftrightarrow \quad \mathbf{M}\,x = 0, \tag{2}$$

From a simple linear algebra argument, the null vector $x = 0$ is always a solution of equation 2. If $\det\mathbf{M} \neq 0$, it's also the **only** equilibrium point. If $\det\mathbf{M} = 0$, on the other hand, an infinite number of equilibrium points exist.
If the model is described by

$$\frac{dx}{dt} = \mathbf{M}x + c, \tag{3}$$

with c a constant vector (the model is said to be *affine*), then the equilibrium point is given by $x^* = -\mathbf{M}^{-1}c$. Again, this argument is only valid if $\det\mathbf{M} \neq 0$, because the inverse of a matrix is defined only if the determinant is not zero.

1.2 Determining the stability of equilibria

In the following paragraph we will admit that the determinant of matrix $\mathbf{M}$ is different from zero, then we will analyze the stability of the equilibrium point $x^* = 0$. Equation 1 can be, at least formally, integrated and admits the following solution

$$x(t) = e^{\mathbf{M}t}x(0). \tag{4}$$

Consider the transformation of matrix $\mathbf{M}$ to a diagonal matrix of eigenvalues $\mathbf{D}$, i.e., the eigendecomposition

$$\mathbf{M} = \mathbf{A}^{-1}\mathbf{D}\mathbf{A}. \tag{5}$$

Then, the evolution of $x(t)$ can be written as

$$x(t) = \mathbf{A}^{-1}e^{\mathbf{D}t}\mathbf{A}x(0), \tag{6}$$

or

$$v(t) = e^{\mathbf{D}t}v(0), \tag{7}$$

where we have introduced the transformed vector $v(t) = \mathbf{A}x(t)$. Let's also note that $\mathbf{A}$ transforms the null vector into itself. In other words, if we want to analyse the stability of the equilibrium point $x^* = 0$ we have to study the evolution of the vector $v^* = 0$. Since matrix $\mathbf{D}$ is diagonal, each entry of the vector v will be affected by the corresponding eigenvalue only. In symbols

$$v(t) = \begin{pmatrix} v_1(t) \\ \vdots \\ v_n(t) \end{pmatrix} = \begin{pmatrix} e^{\lambda_1 t} v_1(0) \\ \vdots \\ e^{\lambda_n t} v_n(0) \end{pmatrix}. \tag{8}$$

From this it should be clear that in order for the null vector to be a stable equilibrium point *the real parts of all eigenvalues must be negative*. The real part of the eigenvalues represent the decay rate at which each eigenvector is suppressed. If we project the evolution of the system on the different eigenvectors, we see that the dynamics are clearly dominated by the maximum eigenvector. Let's suppose that the eigenvalues $\lambda_1, \dots, \lambda_n$ are ordered in decreasing order according to their real part, so that λ_1 has the maximum real part. The system is at time $t = 0$ in a state $x(t) = \sum_{i=1}^n \alpha_i a_i(t)$, with a_i the eigenvector corresponding to λ_i. The ratio of the contribution of any other eigenvector j with $j \neq 1$ evolves as

$$\frac{\alpha_j(t)}{\alpha_1(t)} = e^{(\lambda_j - \lambda_1)t} \to 0.$$

1.3 An example: the quasispecies equation

The equation can be written

$$\frac{dx}{dt} = \mathbf{M}x - \phi x = \mathbf{T}x.$$

If we consider the eigenvalues of $\mathbf{T}$ we find that they are exactly those of $\mathbf{M}$ shifted by ϕ. The stable fixed point will be the eigenvector corresponding to the maximum eigenvalue of the eigenvalue equation $\mathbf{M}x = \phi x$. Then, the stable fixed point of the system is the one that maximizes the average fitness ϕ.

2 Multivariate models: Non-linear systems

Suppose the general case

$$\frac{dx}{dt} = f(x) \tag{9}$$

with f being differentiable, $f \in C_1(\mathbb{R}^n)$. As in the one-dimensional case, the fixed points x^* are defined as the solution of

$$0 = f(x). \tag{10}$$

In order to determine the *local dynamics* of the system around x^*, consider the linearisation:

$$f(x^* + \varepsilon) = 0 + \mathbf{J}\varepsilon + \dots \tag{11}$$

to find

$$\frac{d\varepsilon}{dt} \approx \mathbf{J}\varepsilon. \tag{12}$$

Here, $\mathbf{J}_{ij} = \partial_j f_i$ is the Jacobian matrix of f. The nature of the fixed point x^* is given by the Jacobian matrix replacing $\mathbf{M}$ in Eq. (1). The fixed point is only stable if all eigenvalues of $\mathbf{J}$ have a negative real part. The dynamical behaviour then depends on the imaginary parts. In the case that the eigenvalues cannot be computed efficiently, it is sufficient to check the *Routh-Hurwitz* conditions. Note that no conclusions can be drawn if $\mathrm{Re}\,\lambda_i = 0$.

Further reading

Murray, J. D. (2002). *Mathematical Biology*, volume 2. Springer.

Otto, S. P. and Day, T. (2007). *A Biologist's Guide to Mathematical Modeling in Ecology and Evolution*, volume 13. Princeton University Press.