MSc Computational Methods in Ecology and Evolution

Maths for Biology

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Solvable ODEs in 1 and 2 dimensions

Question 1 Analytical solution to logistic ODE

The following 1st order differential equation for population growth with a limited carrying capacity was studied in the lectures:

$$\frac{\mathrm{d}x}{\mathrm{d}t} = vx\left(1 - \frac{x}{K}\right),$$

where $x(t)$ is the population size at time t, v is the growth rate and K, is the carrying capacity.

a) Use the transformation $\tau = vt$ and $z = x/K$ to simplify the ODE to

$$\frac{\mathrm{d}z}{\mathrm{d}\tau} = z(1 - z)$$

This process is called non-dimensionalisation and is the ODE expressed in natural dimensionless or scaled population size z and dimensionless time τ. Why is this useful?

b) Using separation of variables and then partial fractions find a closed-form analytical solution $z(\tau)$ given the initial condition $z(0) = z_0$.

c) Express the result in terms of the actual population size and time, $x(t)$: check the expression has the correct limit as $t \to 0$.

d) What happens if the initial condition is $x_0 = 0$, or $x_0 = K$? Comment on this result in relation to the fixed points of the system.

e) Show from the analytical expression for $x(t)$ that its limit as $t \to \infty$ is $x(t \to \infty) = K$.

f) In which limit (for what range of times and which initial conditions) does the expression $x(t)$ become approximately exponential? What is this approximate expression?

g) Use the full expression for population growth to show that the time t^*at which the population reaches $\frac{K}{2}$, in terms of v, x_0 & K is

$$t^* = \frac{1}{v}\ln\left(\frac{K - x_0}{x_0}\right)$$

Comment on result for $x_0 > K/2$.
(Hint: It might be less messy to first consider $z(\tau = vt^*) = 1/2$, and then substitute values for z_0)

Question 2 Mutation-selection balance in deterministic population genetics

An ODE that describes both selection on a mutant allele and mutation between mutant and wild type alleles is

$$\frac{\mathrm{d}x}{\mathrm{d}t} = sx(1-x) + \mu(1-2x)$$

Where $x(t)$ is the frequency of the mutant allele that has selective advantage s and μ the mutation rate.

a) The first term on the RHS represents selection; give an intuitive explanation for why this has the form $x(1-x)$ (Hint: refer to the logistic equation)

b) Explain the form for the 2nd term on the RHS, which represents mutation, in terms of the flux of mutations from wild type to mutant + flux of mutants from mutant to wild type.

c) This ODE can't be solved analytically in this form, but we can study its fixed points. i) is $x = 0$ a fixed point? Why not? ii) Set the LHS to zero and show the fixed points x^* are given by

$$x^* = \frac{(s-2\mu)^2 \pm \sqrt{(s-2\mu)^2 + 4\mu s}}{2s}$$

iii) argue that the negative sign solution is unphysical.

d) Rearrange this solution in the following form

$$x^* = \frac{\left(1 - \frac{2\mu}{s}\right) + \sqrt{1 + \frac{4\mu^2}{s^2}}}{2}$$

e) As this solution is only a function of $\frac{\mu}{s}$ we can plot x^* vs $\frac{\mu}{s}$. Do this plot for $0 \le \frac{\mu}{s} \le 10$. What do you notice – explain your result in terms of the balance between mutation and selection.

f) In the case that the mutant is deleterious ($s = -s_d; s_d > 0$), i) why would we *not* expect the mutant to be removed? We would expect $x \ll 1$, and ii) show that the approximate form for the above ODE is

$$\frac{\mathrm{d}x}{\mathrm{d}t} = -s_d x(1-x) + \mu(1-2x) \approx -(s_d + 2\mu)x + \mu.$$

iii) What is the fixed point solution x^* for this ODE?

g) Using the integrating factor method, show the solution to this equation, with initial condition $x(0) = 0$, is

$$x(t) = \frac{\mu}{s_d + 2\mu}\left(1 - e^{-(s_d+2\mu)t}\right)$$

h) Evaluate the limits of this solution for i) $t \to 0$ & ii) $t \to \infty$. Check your answer to ii) agrees with f)ii). Your answer to i) indicates that the initial increase in frequency is independent of selection – why is this so?

i) Typically, in evolution $\mu \ll s_d$. Show that the simplified solution is

$$x(t) = \frac{\mu}{s_d}(1 - e^{-s_d t})$$

and that the fixed point is $x^* \approx \mu/s_d$.

Question 3.

The following system of linear 2D system of ODEs is given by

$$\dot{x} = y$$
$$\dot{y} = x$$

Here, we will find the eigenvalues and eigenvectors of its corresponding 2x2 matrix

$$\boldsymbol{A} = \begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix}$$

a) Find the eigenvalues and eigenvectors of this matrix.
b) Use these to sketch the phase-portrait for this system, indicating the fixed point and its stability.
c) Find the solution for $x(t)$ and $y(t)$ for the initial condition $x(0) = x_0 = -2$ and $y(0) = y_0 = 1$. Sketch this solution on the same phase-plane as t progresses from $t = 0$ to $t \to \infty$.
d) Repeat a) to c) for the linear system

$$\dot{x} = -3x + 2y$$
$$\dot{y} = -2y + x$$

and indicate which are the “fast” and “slow” eigendirections on the phase plot.

Question 4.

Consider the following linear 2D system of ODEs:

$$\dot{x} = -y$$
$$\dot{y} = x$$

The matrix representation gives rise to the following 2x2 matrix:

$$\boldsymbol{A} = \begin{pmatrix} 0 & -1 \\ 1 & 0 \end{pmatrix}$$

a) Show that the eigenvalues of $\boldsymbol{A}$ are given by $\lambda = \pm i$.
b) Sketch the phase-portrait.
c) The imaginary eigenvalues indicate the nature of $\boldsymbol{A}$ is to rotate vectors and so we cannot define eigenvectors in the conventional sense – we can have complex eigenvectors, but we cannot associate it with a fixed direction on a 2D plane. However, this rotational nature suggests the solution:

$$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = \begin{pmatrix} \cos t & -\sin t \\ \sin t & \cos t \end{pmatrix} \begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$$

where you should recognise the familiar rotation matrix. Verify that this indeed is the solution for the initial condition $x(0) = x_0$ and $y(0) = y_0$, by separately calculating $\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix}$ and $\boldsymbol{A}\underline{x}$ and showing them to be equal.
d) Without calculation what would the dynamics for the following matrix look like

$$\boldsymbol{B} = \begin{pmatrix} 0 & 1 \\ -1 & 0 \end{pmatrix}$$

Give your reasoning. (Hint: this matrix is effectively like swapping the x and y-axis and then relabelling them, so in which case what would happen to an anti-clockwise rotation, which occurs with $\boldsymbol{A}$).

Question 5.

Consider the following linear 2D system of ODEs:

$$\dot{x} = -x - y$$
$$\dot{y} = x - y$$

Which we studied in the lectures. The matrix representation gives rise to the following 2x2 matrix:

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

a) Show that the eigenvalues of $\boldsymbol{A}$ are given by $\lambda = -1 \pm i$.
b) What is the real part of the eigenvalue and what does it indicate about the dynamics?
c) What does the presence of an imaginary part indicate?
d) Sketch the phase portrait.
e) The solution to this as shown in the lectures is

$$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = e^{-t} \begin{pmatrix} \cos t & -\sin t \\ \sin t & \cos t \end{pmatrix} \begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$$

where you should recognise the familiar rotation matrix. Verify that this indeed is the solution for the initial condition $x(0) = x_0$ and $y(0) = y_0$, by separately calculating $\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix}$ and $\boldsymbol{A}\underline{x}$ and showing them to be equal.
f) If the matrix is now

$$\boldsymbol{B} = \begin{pmatrix} 1 & -1 \\ 1 & 1 \end{pmatrix}$$

Without calculation can you predict what the dynamics of this matrix look like? Give your reasoning and sketch the phase portrait. Confirm that the real part of the eigenvalues of this matrix are positive ($\mathrm{Re}(\lambda) > 0$).

Integration Practice

Integrate the following by finding the appropriate substitution

a) $\int 2x\sqrt{x^2+1}\mathrm{d}x$; b) $\int 3x^2\sqrt{x^3+1}\mathrm{d}x$; c) $\int ax^{\alpha-1}(bx^{\alpha}+c)^{\beta}\mathrm{d}x$; d) $\int x\cos(x^2+3)\,\mathrm{d}x$

e) $\int_0^{\infty} xe^{-x^2}\mathrm{d}x$; f) $\int_0^{\infty} x^2e^{-x^3}\mathrm{d}x$; g) $\int \frac{x+2}{x^2+4x}\mathrm{d}x$; h) $\int_0^{\pi/2} \frac{\cos x}{1+\sin^2 x}\mathrm{d}x$ (Hint: $\frac{\mathrm{d}\tan^{-1}(x)}{\mathrm{d}x} = \frac{1}{1+x^2}$)

What is the general rule that allows integration by substitution to work? Why can't we integrate $\int 2x^2\sqrt{x^2+1}\mathrm{d}x$ this way?

Integrate by parts the following integral

i) $\int xe^{-x}\mathrm{d}x$; j) $\int x\ln x\,\mathrm{d}x$; k) $\int \ln x\,\mathrm{d}x$ (Hint: $\ln x = 1\times\ln x$); l) $\int \cos^2 x\,\mathrm{d}x$; m) $\int e^{-x}\cos x\,\mathrm{d}x$

Integrate the following using partial fractions

n) $\int \frac{\mathrm{d}x}{x(1-x)}$; o) $\int \frac{\mathrm{d}x}{x(1-x)(x+1)}$; p) $\int \frac{x\mathrm{d}x}{(x+1)^2}$