Solutions for assignment 3

Mathematical Ecology

Interacting populations

Exercise 3.1: Consider a model for the interaction of two species with populations N_1 and N_2 described by the system of ODEs

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1} - b_{12}\frac{N_2}{K_1}\right),$$
$$\frac{N_2}{dt} = r_2 N_2 \left(1 - b_{21}\frac{N_1}{K_2}\right),$$

where all the parameters are positive.

a) What type of interaction exists between N_1 and N_2?

b) Non-dimensionalise the system by introducing $u = N_1/K_1$ and $v = N_2/K_2$ as well as a non-dimensional time variable. What are the resulting non-dimensional parameters? Give the ODEs for u and v in terms of these parameters.

c) Determine the steady states in the non-dimensionalised system. Investigate their stability. At what values of the parameters do bifurcations take place?

d) Determine the nullclines and use these to make rough phase-plane sketches (You will need two sketches).

e) Describe under what ecological circumstances N_2 becomes extinct. Do the same for N_1. Show that the principle of competitive exclusion holds irrespective of the size of the parameters.

Solution:

a) Because for both species the growth rate is decreased by the presence of the other species, there is a competition interaction between them.

b) We non-dimensionalise by introducing $u = N_1/K_1$, $v = N_2/K_2$, $\tau = r_1 t$. This gives

$$\frac{du}{d\tau} = u\left(1 - u - b_{12}\frac{K_2}{K_1}v\right),$$
$$\frac{dv}{d\tau} = \frac{r_2}{r_1}v\left(1 - b_{21}\frac{K_1}{K_2}u\right).$$

So we also introduce $R = r_2/r_1$ and $A = b_{12}K_2/K_1$ and $B = b_{21}K_1/K_2$ to simplify further to

$$\frac{du}{d\tau} = u\left(1 - u - Av\right),$$
$$\frac{dv}{d\tau} = Rv\left(1 - Bu\right).$$

Note that this is by no means the only sensible way to non-dimensionalise this system. We could also for example introduce $\tilde{v} = N_2 b_{12}/K_1$ which would remove one more parameter.

c) The steady states are

$$(0,0), \quad (1,0), \quad \left(\frac{1}{B}, \frac{B-1}{AB}\right).$$

The Jacobian matrix is

$$A(u,v) = \begin{pmatrix} 1-2u-Av & -Au \\ -RBv & R(1-Bu) \end{pmatrix}$$

So

$$A(0,0) = \begin{pmatrix} 1 & 0 \\ 0 & R \end{pmatrix}$$

which means that $(0,0)$ is unstable.

$$A(1,0) = \begin{pmatrix} -1 & -A \\ 0 & R(1-B) \end{pmatrix}$$

Thus $(1,0)$ is a saddle if $B < 1$ and a stable node if $B > 1$. Finally,

$$A\left(\frac{1}{B}, \frac{B-1}{AB}\right) = \begin{pmatrix} -\frac{1}{B} & -\frac{A}{B} \\ R\frac{1-B}{A} & 0 \end{pmatrix}$$

Note that in simplifying the entries in the matrix it is useful to reuse some of the relations you found when determining the steady state. I used that for example to simplify the top left entry. The determinant is $R(1-B)/B$ and thus is negative if $B > 1$. So the coexistence fixed point is a saddle. If $B < 1$ the fixed point is not at positive population numbers, so not realistic, but it would be stable as the trace is negative.

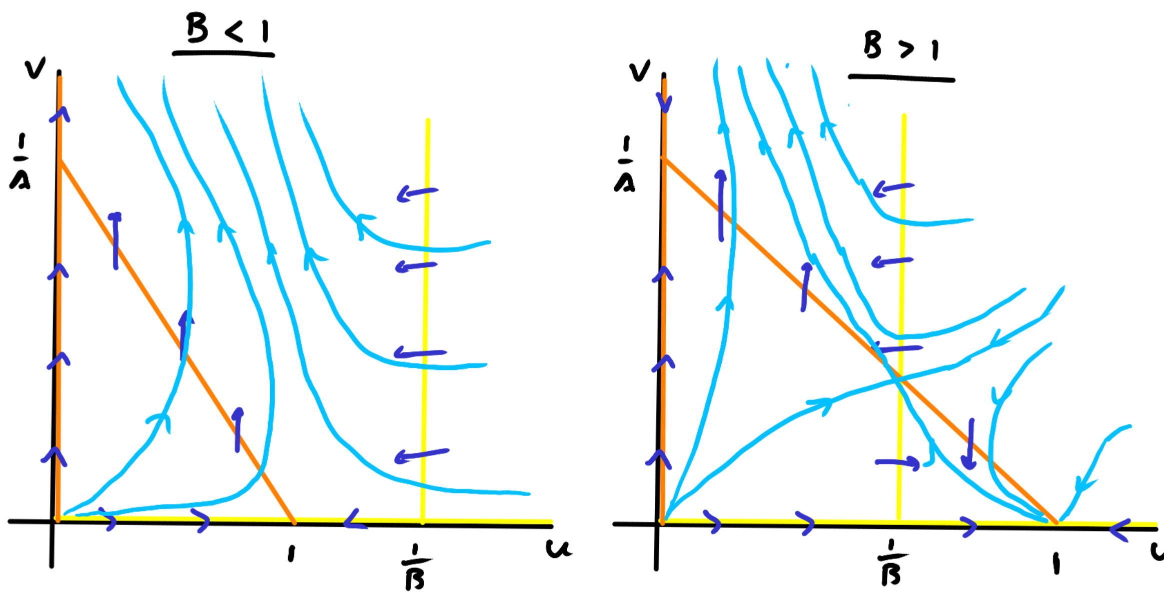

Figure 1: Phase portraits for the competition model in Exercise 3.

d) The $du/d\tau = 0$ nullclines are $u = 0$ and $v = (1-u)/A$. They are indicated in orange in Figure 1. The $dv/d\tau = 0$ nullclines are $v = 0$ and $u = 1/B$. They are indicated in yellow in Figure 1. The arrows on the nullclines indicate the direction of flow. Some rough trajectories are drawn in in light blue.

e) In the case of $B < 1$ species 1 goes extinct and species 2 grows beyond all bounds. In case $B > 1$ whether species 1 or species 2 goes extinct depends on the initial conditions. Species 2 will go extinct if the initial condition lies below the separatrix through the saddle in the second sketch in Figure 1. In all cases, one of the species will exclude the other, so the principle of competitive exclusion holds. To exclude the possibility that both species grow beyond all bounds one just has to observe that dN_1/dt will go negative for sufficiently large N_2.

Geometric mean sex-structured model

Exercise 4.1: Consider the sex-structured population model

$$\frac{dF}{dt} = -\mu_F F + b_F \phi(F, M), \quad \frac{dM}{dt} = -\mu_M M + b_M \phi(F, M),$$

where $F(t)$ denotes the number of females and $M(t)$ the number of males and μ_F, μ_M, b_F, b_M are positive constants. Make the choice

$$\phi(F, N) = \sqrt{FM}.$$

Determine the asymptotic sex ratio

$$s = \lim_{t\to\infty} \frac{M(t)}{F(t)}.$$

What is the numerical value of s when $\mu_F = 2, \mu_M = 1, b_F = 1/2, b_M = 3/2$ per year?

Solution:

To find the asymptotic sex ratio $s = M/F$ we need to solve the fixed-point equation

$$\begin{aligned} 0 = \frac{ds}{dt} &= \frac{d}{dt}\frac{M}{F} = \frac{1}{F^2}\left(\frac{dM}{dt}F - \frac{dF}{dt}M\right) \\ &= \frac{1}{F^2}\left((-\mu_M M + b_M\sqrt{FM})F - (-\mu_F F + b_F\sqrt{FM})M\right). \end{aligned}$$

Multiplying by F/M gives

$$(-\mu_M M + b_M\sqrt{FM})\frac{1}{M} - (-\mu_F F + b_F\sqrt{FM})\frac{1}{F} = 0.$$

This simplifies to

$$-\mu_M + b_M\sqrt{\frac{F}{M}} + \mu_F - b_F\sqrt{\frac{M}{F}} = 0.$$

If we introduce $r = \sqrt{s} = \sqrt{M/F}$ and multiply the above equation by $-r$ we get the quadratic equation

$$b_F r^2 - (\mu_F - \mu_M)r - b_M = 0.$$

The positive solution is

$$r = \frac{\mu_F - \mu_M + \sqrt{(\mu_F - \mu_M)^2 + 4b_M b_F}}{2b_F}.$$

Therefore the asymptotic sex ratio is

$$s = \left(\frac{\mu_F - \mu_M + \sqrt{(\mu_F - \mu_M)^2 + 4b_M b_F}}{2b_F}\right)^2.$$

For the given numerical values we get

$$s = \left(\frac{2 - 1 + \sqrt{1+3}}{1}\right)^2 = \left(1 + \sqrt{4}\right)^2 = 3^2 = 9.$$

Fibonacci population

Exercise 5.2: Consider a population in which individuals on average produce one offspring when they turn 1 year old and another offspring when they turn 2 years old. After that they die. Assume that there is no mortality before they turn 2 year old.

1. Formulate the above information in terms of values for the reproduction numbers b_a and the survival probabilities S_a.
2. Write down the Leslie matrix for this population.
3. Assume that at $t = 0$ we start with 1 individual of age 0. By hand, calculate the numbers of individuals at each age at time $t = 1, 2, 3, 4$ and 5.
4. Draw the directed graph associated with this Leslie matrix. Is the Leslie matrix irreducible? Is it primitive? What does this tell you about the long-term behaviour of the population?
5. Using the Leslie matrix, calculate the long-term growth factor (the factor by which the total population changes from one year to the next) and the stable age distribution.

Solution:

1. The nonzero reproduction numbers are $b_1 = 1$ and $b_2 = 1$. The nonzero survival probabilities are $S_0 = 1$ and $S_1 = 1$.
2. The non-zero fecundities are $F_0 = b_1 S_0 = 1$ and $F_1 = b_2 S_1 = 1$. The Leslie matrix is
$$L = \begin{pmatrix} F_0 & F_1 \\ S_0 & 0 \end{pmatrix} = \begin{pmatrix} 1 & 1 \\ 1 & 0 \end{pmatrix}.$$
3. The Leslie matrix multiplies the population vector at time t to give the population vector at time $t + 1$.
$$\mathbf{N}_{t+1} = \begin{pmatrix} N_0 \\ N_1 \end{pmatrix}_{t+1} = L\mathbf{N}_t = \begin{pmatrix} 1 & 1 \\ 1 & 0 \end{pmatrix} \begin{pmatrix} N_0 \\ N_1 \end{pmatrix}_t .$$
This gives
$$\begin{aligned} \mathbf{N}_1 = L\mathbf{N}_0 &= \begin{pmatrix} 1 & 1 \\ 1 & 0 \end{pmatrix} \begin{pmatrix} 1 \\ 0 \end{pmatrix} = \begin{pmatrix} 1 \\ 1 \end{pmatrix}, \\ \mathbf{N}_2 = L\mathbf{N}_1 &= \begin{pmatrix} 1 & 1 \\ 1 & 0 \end{pmatrix} \begin{pmatrix} 1 \\ 1 \end{pmatrix} = \begin{pmatrix} 2 \\ 1 \end{pmatrix}, \\ \mathbf{N}_3 = L\mathbf{N}_2 &= \begin{pmatrix} 1 & 1 \\ 1 & 0 \end{pmatrix} \begin{pmatrix} 2 \\ 1 \end{pmatrix} = \begin{pmatrix} 3 \\ 2 \end{pmatrix}, \\ \mathbf{N}_4 = L\mathbf{N}_3 &= \begin{pmatrix} 1 & 1 \\ 1 & 0 \end{pmatrix} \begin{pmatrix} 3 \\ 2 \end{pmatrix} = \begin{pmatrix} 5 \\ 3 \end{pmatrix}, \\ \mathbf{N}_5 = L\mathbf{N}_4 &= \begin{pmatrix} 1 & 1 \\ 1 & 0 \end{pmatrix} \begin{pmatrix} 5 \\ 3 \end{pmatrix} = \begin{pmatrix} 8 \\ 5 \end{pmatrix}. \end{aligned}$$

To get the population at age 2 we use $N_{2,t+1} = S_2 N_{1,t}$. With $S_2 = 1$ this gives
$$\begin{aligned} &N_{2,1} = N_{1,0} = 0, \quad N_{2,2} = N_{1,1} = 1, \quad N_{2,3} = N_{1,2} = 1, \\ &N_{2,4} = N_{1,3} = 2, \quad N_{2,5} = N_{1,4} = 3. \end{aligned}$$

4. The directed graph associated with the Leslie matrix is shown in Figure 2. The Leslie matrix is irreducible as there is a directed path from any age class to any other age class. The Leslie matrix is primitive as there are cycles of length 2 and of length 1, so the greatest common divisor of the cycle lengths is 1. This means that the age-distribution of the population will converge to a stable age distribution as $t \to \infty$.

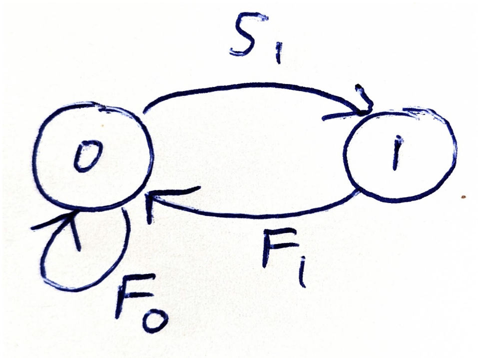

Figure 2: Leslie graph for the Fibonacci population.

5. The stable age distribution is the eigenvector of the Leslie matrix corresponding to the dominant eigenvalue, i.e., the eigenvalue with the largest magnitude. We know that there is a unique such eigenvalue because the Leslie matrix is irreducible and primitive. We determine the eigenvalues of the Leslie matrix by solving

$$0 = \det(L - \lambda I) = \det \begin{pmatrix} 1-\lambda & 1 \\ 1 & -\lambda \end{pmatrix} = \lambda^2 - \lambda - 1.$$

Solving this quadratic equation tells us that the eigenvalues are $\lambda_\pm = (1 \pm \sqrt{5})/2$. The dominant eigenvalue is $\lambda_+ = (1+\sqrt{5})/2 = \phi$, which we recognise as the golden ratio.

In the stable age distribution we have $n_1^* = \phi n_0^*$ and $n_2^* = \phi n_1^* = \phi^2 n_0^*$.

Age-independent rates

Exercise 5.5: In the continuous-time age-structured population model consider the case where $b(a) = b$ and $\mu(a) = \mu$ are both constant. Repeat all steps of the analysis but simplifying the expressions at each step by using the constant values for birth and death rates.

1. Solve the partial differential equation of the age-structured model by making the Ansatz $n(t, a) = f(t)r(a)$ and introducing the separation constant γ.
2. Use the boundary condition at $a = 0$ to obtain an equation for γ.
3. Give the condition under which the population goes extinct and compare it to the condition in the exponential model from chapter 1.

Solution:

1. If we substitute the Ansatz $n(t, a) = f(t)r(a)$ into the PDE

$$\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} = -\mu(a)n,$$

and divide by $f(t)r(a)$ we get

$$\frac{f'(t)}{f(t)} + \frac{r'(a)}{r(a)} = -\mu.$$

Separating variables and introducing the separation constant γ gives

$$\frac{f'(t)}{f(t)} = \gamma, \quad \frac{r'(a)}{r(a)} = -\gamma - \mu.$$

So

$$f(t) = f(0)e^{\gamma t} \quad \text{and} \quad r(a) = r(0)e^{-(\mu+\gamma)a}.$$

and thus

$$n(t,a) = n(0,0)e^{\gamma t}e^{-(\mu+\gamma)a}.$$

2. Substituting this into the boundary condition

$$n(t,0) = \int_0^\infty b\, n(t,a)da$$

and dividing both sides by $n(0,0)e^{\gamma t}$ gives

$$1 = \int_0^\infty b\, e^{-(\mu+\gamma)a}da = -\frac{b}{\mu+\gamma}\left[e^{-(\mu+\gamma)a}\right]_0^\infty = \frac{b}{\mu+\gamma}.$$

and hence

$$\gamma = b - \mu.$$

3. As the time dependence of $n(t,a)$ is given by $e^{\gamma t}$, the population will go extinct if $\gamma < 0$, i.e, if the death rate μ is greater than the birth rate b. This is the same condition as in the exponential growth model.