Problem sheet 5

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1   Fixing the logistic map

One of the big problems with the discrete logistic equation is that if your initial population is too high then the population will become negative, namely, you can never start with more than the carrying capacity. Many equations have been suggested to correct for this phenomena. We will be investigating the following:

$$x_{n+1} = f(x_n) = \frac{\mu^3 x_n}{(1+x_n)^3}, \tag{1}$$

where μ is a positive constant.

1. Draw a sketch of $(x, f(x))$ and (x, x) on the same axes. How many non-negative steady states do we expect?

2. Derive the non-negative steady states, noting any parameter dependencies.

3. Derive the stability of the steady states, noting any parameter dependencies.

4. Show that period two oscillatory points, x_p, satisfy

$$(1 + x_p)\left(1 + \frac{\mu^3 x_p}{(1+x_p)^3}\right) = \mu^2. \tag{2}$$

5. Solve for x_p by following the proceeding steps.

   (a) Rewrite equation (2) as a cubic in $y = 1 + x_p$.

   (b) Note that $x_s = \mu - 1$ is a steady state (that should have found in question 2) and remember that any steady state is also a solution of equation (2). Using this knowledge rewrite the cubic in y in the form

   $$(y - \mu)(y^2 + ay + b) = 0 \tag{3}$$

   where a and b should be defined in terms of μ.

   (c) Solve $y^2 + ay + b = 0$ and hence derive x_p, noting any parameter dependencies.

   (d) Calculating the stability of the period two states is very hard to do by hand. However, explain how it would be done. Namely, define the inequality that would have to be calculated.

   (e) The bifurcation diagram of equation (1) is shown in Figure 1, note the logarithmic y-axis. Explain what it shows and how it compares with the results you have generated in this question.

1.1   Answers

1. From Figure 2 we expect 2 steady states, one zero and one positive.

2. The steady states satisfy $x_n = x_s$ for all n. Thus

$$x_s = \frac{\mu^3 x_s}{(1+x_s)^3}, \tag{4}$$

which implies $x_{s0} = 0$ is a steady state and

$$(1 + x_s)^3 = \mu^3, \implies x_{s1} = \mu - 1, \tag{5}$$

is another. Notably, $\mu \geq 1$ is required for the steady state to exist in the positive quadrant.
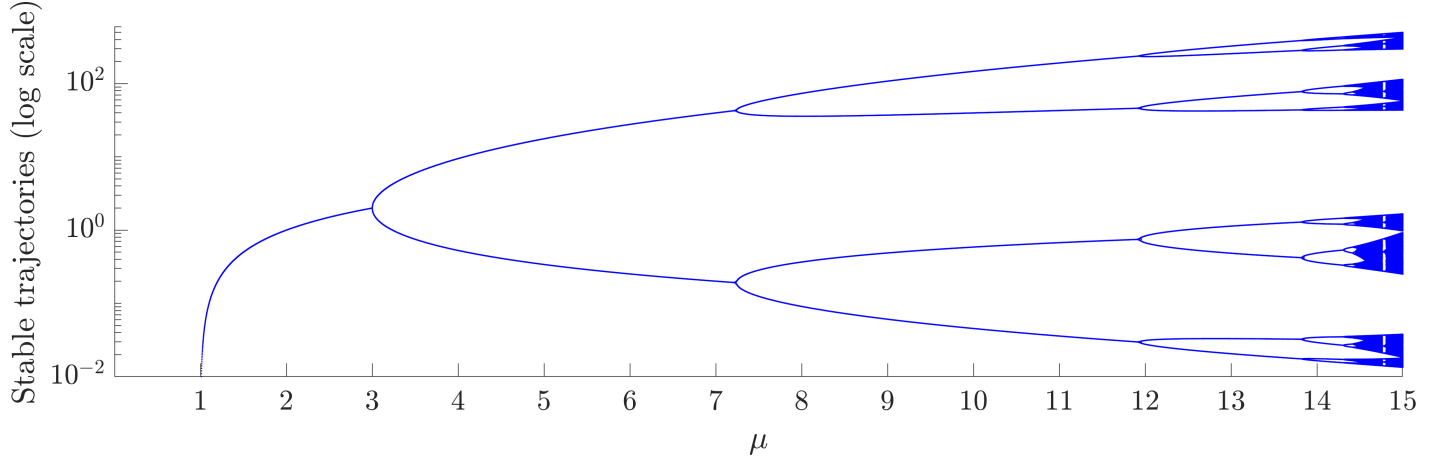
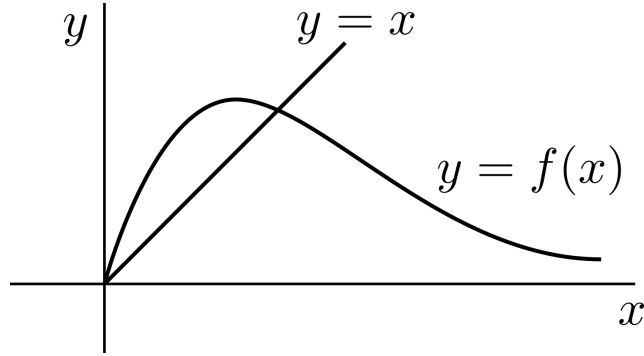Figure 1: Bifurcation diagram of equation (1), note the logarithmic y-axis.

Figure 2: Plot of $(x, f(x))$ and (x, x).

3. To calculate the stability we need to obtain the derivative of f,

$$f'(x) = \frac{\mu^3}{(1+x)^3} - \frac{3\mu^3 x}{(1+x)^4}, \tag{6}$$

then evaluate f' at the steady states and compare $|f'(x_s)|$ to one.

Since $f'(0) = \mu^3$ then

$$x_s \text{ is } \begin{cases} \text{stable for } \mu < 1, \\ \text{unstable for } \mu > 1. \end{cases} \tag{7}$$

Equally, we consider

$$|f'(\mu - 1)| < 1,$$
$$\implies -1 < f'(\mu - 1) < 1,$$
$$\implies -1 < 1 - \frac{3(\mu - 1)}{\mu} < 1,$$
$$\implies 2 > \frac{3(\mu - 1)}{\mu} > 0,$$
$$\implies 2\mu > 3\mu - 3 > 0,$$
$$\implies 3 > \mu > 1.$$

Thus, x_{s1} is stable for $1 < \mu < 3$.

4. The period two points satisfy $x_p = f(f(x_p))$,

$$x_p = \frac{\mu^6 x_p}{(1+x_p)^3 \left(1 + \frac{\mu^3 x_p}{(1+x_p)^3}\right)^3}. \tag{8}$$

2

We can cancel the $x_p = 0$ root as it is a steady state x_{s0}. Further, we can take a cube root and multiply by the denominator to get equation (2).

5. (a) Defining $y = 1 + x_p$ gives

$$y \left(1 + \frac{\mu^3 (y - 1)}{y^3} \right) = \mu^2, \tag{9}$$

which is

$$y^3 - \mu^2 y^2 + \mu^3 y - \mu^3 = 0, \tag{10}$$

upon rearrangement.

(b) We now want to factorise equation (10). As mentioned in the question $y = \mu$ is a root (substitute $y = \mu$ into equation (10) to demonstrate this), so we know that we can rewrite equation (10) as

$$(y - \mu)(y^2 + ay + b) = y^3 - \mu^2 y^2 + \mu^3 y - \mu^3. \tag{11}$$

Expanding the left-hand side and comparing terms by inspection we discover that $b = \mu^2$ and $a = \mu - \mu^2$, so

$$(y - \mu)(y^2 + (\mu - \mu^2)y + \mu^2) = y^3 - \mu^2 y^2 + \mu^3 y - \mu^3. \tag{12}$$

(c) Solving the quadratic term in equation (12) gives

$$2y_\pm = \mu^2 - \mu \pm \sqrt{\left(\mu^2 - \mu \right)^2 - 4\mu^2}, \tag{13}$$

or

$$x_{p\pm} = \frac{\mu^2 - \mu - 2 \pm \sqrt{\left(\mu^2 - \mu \right)^2 - 4\mu^2}}{2}. \tag{14}$$

Critically, we require $x_{p\pm}$ to be real and positive. Hence, we require

$$\mu^2 - \mu - 2 > 0, \implies (\mu + 1)(\mu - 2) > 0, \tag{15}$$

so $\mu > 2$. And we require

$$\left(\mu^2 - \mu \right)^2 - 4\mu^2 > 0, \implies \mu^2 - \mu > 2\mu \text{ or } \mu^2 - \mu < -2\mu \tag{16}$$

Since $\mu^2 - \mu < -2\mu$ implies $\mu^2 < -\mu$, which is impossible, we must satisfy

$$\mu^2 - \mu > 2\mu, \implies \mu^2 > 3\mu, \implies \mu > 3. \tag{17}$$

Thus although we derived the inequality $\mu > 2$ through inequality (15) we have to satisfy $\mu > 3$ which is the the stronger requirement. Thus, in conclusion, the periodic two oscillatory states are

$$x_{p\pm} = \frac{\mu^2 - \mu - 2 \pm \sqrt{\left(\mu^2 - \mu \right)^2 - 4\mu^2}}{2}. \tag{18}$$

and appear for $\mu > 3$.

(d) The stability of $x_\pm$ is found by considering the size of $\lambda(x) = |\, \mathrm{d}f(f(x))/\, \mathrm{d}x|$. If $\lambda(x_{p\pm}) > 1$ the oscillatory trajectory is unstable. Alternatively, if $\lambda(x_{p\pm}) < 1$ the oscillatory trajectory is stable.

(e) First we note that since we are on a log scale we cannot visualise the $x_{s0} = 0$ steady state. However, we know that x_{s0} is stable for $\mu < 1$. At $\mu = 1$ there is a bifurcation and x_{s0} becomes unstable whilst x_{s1} becomes stable for $1 < \mu < 3$. At $\mu = 3$ the steady state destabilises to a periodic two trajectory $x_{p\pm}$, which is stable between $3 < \mu \lesssim 7.5$ (by considering the Figure 1). Using an algebraic solver we can find that the period two oscillatory trajectory is stable for $3 < \mu < 3 + 3\sqrt{2} = \approx 7.24$. Continuing on, using Figure 1, we see that the period of the stable oscillations doubles with increasing μ until eventually chaos is seen for $\mu > 14$.
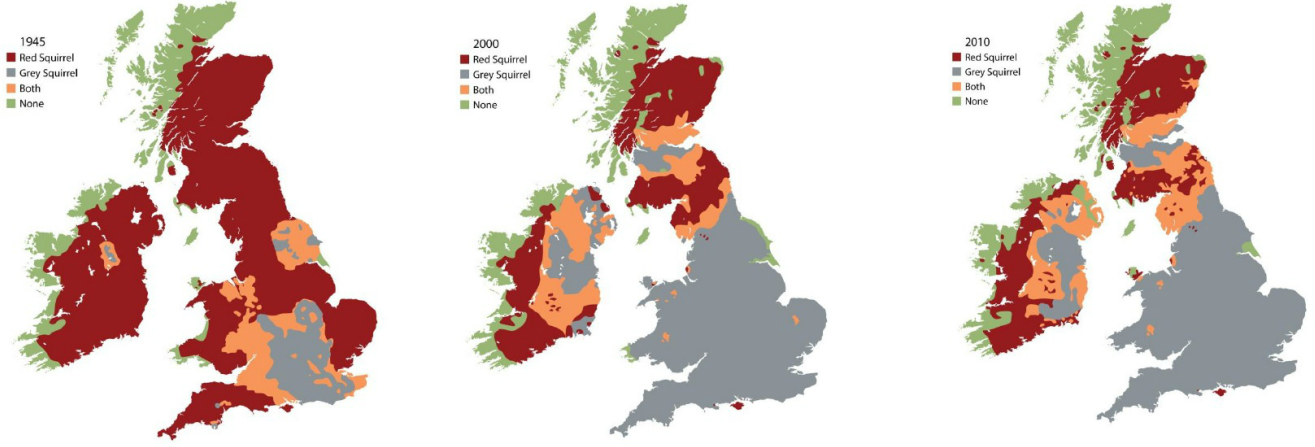
Figure 3: Evolution of the spatial distribution of red and grey squirrels over time from the UK government's science blog.

2 Squirrels

Consider an infinite one-dimensional domain, in which Grey, G, and red, R, squirrel populations undergo the following interactions:

- Both Grey and Red squirrel populations move randomly through their domains with rates D_G and D_R, respectively.

- Grey squirrels are born at a rate proportional to their population, where the proportionality constant is b_1.

- Red squirrels are born at a rate proportional to their population, where the proportionality constant is b_2.

- Both squirrel populations compete internally with members of their own population (*i.e.* grey compete with grey and red compete with red, respectively). Namely, whenever two members of the same population interact one of the members is suppressed. The constant of proportionality is d_1 for the grey squirrels and d_2 for the red squirrels.

- The squirrels also compete across species. Namely, a grey and a red squirrel interaction can lead to a reduction in red squirrels, or a reduction in grey squirrels. The rate of proportionality for the reduction of grey squirrels is c_1, whilst the rate of proportionality for the reduction of red squirrels is c_2.

1. Ignoring movement for a moment, write down the interaction equations specified by the above description.

2. Show that the interaction equations and movement description lead to the following PDEs,

$$\frac{\partial G}{\partial t} = D_G \frac{\partial^2 G}{\partial x^2} + b_1 G - d_1 G^2 - c_1 RG, \tag{19}$$

$$\frac{\partial R}{\partial t} = D_R \frac{\partial^2 R}{\partial x^2} + b_2 R - d_2 R^2 - c_2 RG. \tag{20}$$

3. Non-dimensionalise the system to produce the following equations,

$$\frac{\partial u}{\partial \tau} = \frac{\partial^2 u}{\partial X^2} + u(1 - u - \alpha_{12} v), \tag{21}$$

$$\frac{\partial v}{\partial \tau} = D \frac{\partial^2 v}{\partial X^2} + \rho v(1 - v - \alpha_{21} u). \tag{22}$$

4. What are the parameter groupings D, ρ, α_{12} and α_{21} in terms of b_1, b_2, d_1, d_2, c_1 and c_2?

5. Find all homogeneous steady states of the system, noting any parameter dependencies that need to be satisfied for the steady state to exist.

6. Calculate the stability of the trivial homogeneous steady states. Namely, those in which one of the populations is zero, noting parameter dependencies of the stability criterion.

   Hint: you should find there are four cases:

(a) $\alpha_{12} < 1$ and $\alpha_{21} < 1$;

(b) $\alpha_{12} < 1$ and $\alpha_{21} > 1$;

(c) $\alpha_{12} > 1$ and $\alpha_{21} < 1$;

(d) $\alpha_{12} > 1$ and $\alpha_{21} > 1$.

Calculating the stability of the fourth steady state,

$$(u_s, v_s) = \frac{1}{1 - \alpha_{12}\alpha_{21}}(1 - \alpha_{12}, 1 - \alpha_{21}), \tag{23}$$

leads to a complicated eigenvalue calculation and we will use curve sketching in the next question to consider the stability of this steady state.

7. Sketch the (u, v) phase plane in each of the cases (a)-(d). You should include: the nullclines; annotations regarding the signs of $\mathrm{d}u/\mathrm{d}\tau$ and $\mathrm{d}v/\mathrm{d}\tau$ in each region delineated by the nullclines; accompanying directional arrows in each region; directional arrows on the nullclines; and, finally, trajectories illustrating the expected evolution with initial conditions taken from each region.

   Use these sketches to determine the stability of (u_s, v_s), when it exists.

8. Describe what happens to the grey and red squirrels in each of the cases (a)-(d).

9. By considering Figure 3 and question 8 what parameter region do you think we are in?

10. Can the non-zero steady state, (u_s, v_s), undergo a Turing instability?

Now suppose we fix some constants and begin to consider the spatial aspects of the problem. Namely let $D = 1$, $\rho = 1$, $\alpha_{12} = 1/2$, $\alpha_{21} = 3/2$. Further, suppose we supply the boundary conditions $u(-\infty) = 1$, $v(-\infty) = 0$ and $u(\infty) = 0$, $v(\infty) = 1$ and initial condition $u = 0$, $v = 1$ almost everywhere.

11. What do these parameters, boundary and initial conditions mean in terms of the biology of the problem?

12. Provide a guess as to how the population will evolve.

13. Convert equations (21) and (22) into a moving frame of reference by converting the coordinates (X, τ) into (z, τ) where $z = X - c\tau$ and c is a positive constant.

14. If we define $s = u + v$ then show that travelling wave with a stationary profile satisfies

$$0 = \frac{\mathrm{d}^2 s}{\mathrm{d}z^2} + c\frac{\mathrm{d}s}{\mathrm{d}z} + s(1 - s), \tag{24}$$

   where you should also specify the boundary and initial conditions.

15. By inspection offer a simple solution to equation (24).

16. Deduce that, under the given conditions,

$$0 = \frac{\mathrm{d}^2 u}{\mathrm{d}z^2} + c\frac{\mathrm{d}u}{\mathrm{d}z} + (1 - \alpha_{12})u(1 - u). \tag{25}$$

17. Show that equation (25) can support a travelling wave solution if $c \geq 2\sqrt{1 - \alpha_{12}}$.

18. Having looked at equations (19) and (20) in a number of ways return to question 12. Have your thoughts about the spatio-temporal evolution of the red and grey squirrel populations changed? Does this model represent what is happening in Figure 3?

2.1 Answers

1.

$$G \overset{b_1}{\underset{d_1}{\rightleftarrows}} 2G, \quad G + R \overset{c_1}{\to} R. \tag{26}$$

$$R \overset{b_2}{\underset{d_2}{\rightleftarrows}} 2R, \quad G + R \overset{c_2}{\to} G. \tag{27}$$

2. Using the Law of Mass Action on the interactions equations shown in answer 1 and adding diffusive movement to the system we get equations (19) and (20).

3. Using $G = [G]u$, $R = [R]v$, $x = [x]X$ and $t = [t]\tau$ we find that $[G] = b_1/d_1$, $[R] = b_2/d_2$, $[x] = \sqrt{D_G/b_1}$ and $[t] = 1/b_1$.

4. Subsequently, $D = D_R/D_G$, $\rho = b_2/b_1$, $\alpha_{12} = c_1 b_2/(d_2 b_1)$ and $\alpha_{21} = c_2 b_1/(d_1 b_2)$.

5. The steady states are (0,0), (0,1), (1,0) and

$$(u_s, v_s) = \frac{1}{1 - \alpha_{12}\alpha_{21}}(1 - \alpha_{12}, 1 - \alpha_{21}). \tag{28}$$

We note that for (u_s, v_s) to exist then either $\alpha_{12}, \alpha_{21} < 1$ or $\alpha_{12}, \alpha_{21} > 1$.

6. The Jacobian of the system is

$$J(u, v) = \begin{bmatrix} 1 - 2u - \alpha_{12}v & -\alpha_{12}u \\ -\rho\alpha_{21}v & \rho(1 - 2v - \alpha_{21}u) \end{bmatrix}. \tag{29}$$

Thus,

$$J(0,0) = \begin{bmatrix} 1 & 0 \\ 0 & \rho \end{bmatrix}. \tag{30}$$

The eigenvalues are the diagonal elements, which are both positive. Hence (0,0) is an unstable node.

$$J(1,0) = \begin{bmatrix} -1 & -\alpha_{12} \\ 0 & \rho(1 - \alpha_{21}) \end{bmatrix}. \tag{31}$$

The eigenvalues are the diagonal elements. Hence, (1,0) is a stable node if $\alpha_{21} > 1$ and a saddle point if $\alpha_{21} < 1$.

$$J(0,1) = \begin{bmatrix} 1 - \alpha_{12} & 0 \\ -\rho\alpha_{21} & -\rho \end{bmatrix}. \tag{32}$$

The eigenvalues are the diagonal elements. Hence, (0,1) is a stable node if $\alpha_{12} > 1$ and a saddle point if $\alpha_{12} < 1$.

In summary (0,0) always exists and is always unstable, (1,0) and (0,1) always exist but their stability depends on $(\alpha_{12}, \alpha_{21})$ and, finally, existence and stability of (u_s, v_s) depends on $(\alpha_{12}, \alpha_{21})$. Specifically,

(a) when $\alpha_{12} < 1$ and $\alpha_{21} < 1$ (1,0) is unstable, (0,1) is unstable and (u_s, v_s) exists, stability to be considered in the next question.

(b) when $\alpha_{12} < 1$ and $\alpha_{21} > 1$ (1,0) is stable, (0,1) is unstable and (u_s, v_s) does not exist.

(c) when $\alpha_{12} > 1$ and $\alpha_{21} < 1$ (1,0) is unstable, (0,1) is stable and (u_s, v_s) does not exist.

(d) when $\alpha_{12} > 1$ and $\alpha_{21} > 1$ (1,0) is stable, (0,1) is stable and (u_s, v_s) exists, stability to be considered in the next question.

7. From the bottom left sketch of Figure 4 we see that when $\alpha_{12}, \alpha_{21} > 1$ (u_s, v_s) is unstable, specifically, it is a saddle point. Equally, the bottom right sketch of Figure 4 shows that when $\alpha_{12}, \alpha_{21} < 1$ (u_s, v_s) is stable.

8. In this model we see four possible outcomes. In three of these cases only one of the populations survives and exists at the expense of the other, *e.g.* the red squirrel population survives, but the grey squirrel population dies out. Only in the case that $\alpha_{12}, \alpha_{21} < 1$ are both populations able to live together. In ecology this concept is called competitive exclusion. It suggests that two species competing for exactly the same resources cannot stably coexist. One of the two competitors will always have an ever so slight advantage over the other that leads to extinction of the second competitor in the long run (or evolution into distinct ecological niches).
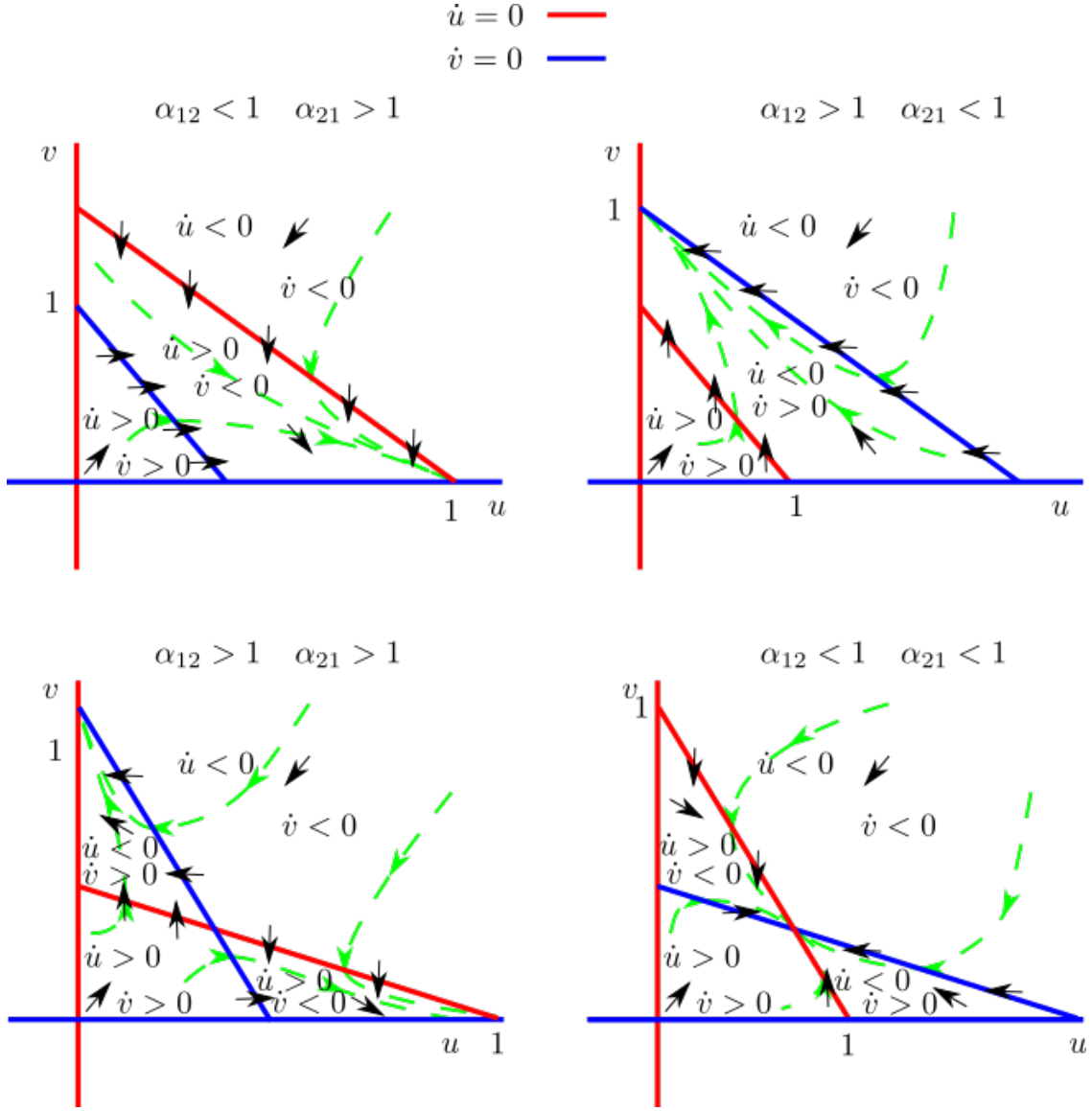
Figure 4: Phase planes in all possible configurations.

9. Figure 3 shows that the squirrels are being pushed further and further north. Thus, it seems like the grey squirrels are winning out, thus, we would expect to be in the case that at least (1,0) is stable, *i.e.* $\alpha_{21} > 1$.

10. First we need (u_s, v_s) to exist and be stable. This work has already been done above and, thus, we are in the case that $\alpha_{12}, \alpha_{21} < 1$. Then either by linearising the system using a perturbation of the form

$$\begin{pmatrix} u \\ v \end{pmatrix} = \frac{1}{1 - \alpha_{12}\alpha_{21}} \begin{pmatrix} 1 - \alpha_{12} \\ 1 - \alpha_{21} \end{pmatrix} + \begin{pmatrix} \epsilon_1 \\ \epsilon_2 \end{pmatrix} \exp(\lambda t)\cos(kx), \tag{33}$$

or by writing the Turing inequalities down we find that we need to satisfy

$$g_v + Df_u > 2\sqrt{D(f_u g_v - f_v g_u)}, \tag{34}$$

substituting in $f = u(1 - u - \alpha_{12})$ and $g = \rho v(1 - v - \alpha_{21}u)$ and the steady state (u_s, v_s) we derive

$$\frac{1}{\alpha_{12}\alpha_{21} - 1}\left(2(1 - \alpha_{12}\alpha_{21})\sqrt{\frac{D\rho(1 - \alpha_{12})(1 - \alpha_{21})}{1 - \alpha_{12}\alpha_{21}}} + D(1 - \alpha_{12}) + \rho(1 - \alpha_{21})\right) > 0. \tag{35}$$

Since $\alpha_{12}, \alpha_{21} < 1$ the $\alpha_{12}\alpha_{21} - 1 < 0$ and, so,

$$\underbrace{2\left(1 - \alpha_{12}\alpha_{21}\right)\sqrt{\frac{D\rho\left(1 - \alpha_{12}\right)\left(1 - \alpha_{21}\right)}{1 - \alpha_{12}\alpha_{21}}}}_{>\,0} + \underbrace{D(1 - \alpha_{12})}_{>0} + \underbrace{\rho(1 - \alpha_{21})}_{>0} < 0. \tag{36}$$

However, as shown in inequality (36), all the terms on the left-hand side are positive, thus, the inequality cannot be satisfied, meaning that the interacting squirrel model cannot produce Turing patterns.

11. $D = 1$ means that both squirrel populations spread out at the same rate. $\rho = 1$ means that the interaction time scales are the same. Namely, each interactions takes the same time. $\alpha_{12} = 1/2 < 3/2 = \alpha_{21}$ means that the grey squirrels out compete the red squirrels 3 out of 4 times. The initial condition means that we are initially in a system that is full of red squirrels only. However, the boundary conditions means that grey squirrels are being released at $x = -\infty$ and red squirrels are being destroyed. Equally, at $x = \infty$ red squirrels are being released and grey squirrels are being destroyed. Of course an infinitely long domain is physically impossible. The domain size just has to be large compared to the movement length scale of the squirrels.

12. Considering the results above heterogeneous patterning will not occur and the parameter values put us in the case of $(0,0)$, $(0,1)$ and (u_s, v_s) being unstable, whilst $(1,0)$ is stable. Namely, since the grey squirrels out compete the red we expect that the grey squirrels will invade the entire territory and wipe the red squirrels out.

13. using $z = X - c\tau$ means that

$$\frac{\partial}{\partial X} = \frac{\partial}{\partial z}\frac{\partial z}{\partial X} = \frac{\partial}{\partial z}. \tag{37}$$

and

$$\frac{\partial}{\partial \tau} = \frac{\partial}{\partial \tau}\frac{\partial \tau}{\partial \tau} + \frac{\partial}{\partial z}\frac{\partial z}{\partial \tau} = \frac{\partial}{\partial \tau} - c\frac{\partial}{\partial z}. \tag{38}$$

Upon substitution we generate

$$\frac{\partial u}{\partial \tau} - c\frac{\partial u}{\partial z} = \frac{\partial^2 u}{\partial z^2} + u\left(1 - u - \frac{1}{2}v\right), \tag{39}$$

$$\frac{\partial v}{\partial \tau} - c\frac{\partial v}{\partial z} = \frac{\partial^2 v}{\partial z^2} + v\left(1 - v - \frac{3}{2}u\right). \tag{40}$$

14. First, we are dealing with a stationary profile in the travelling frame of reference so derivatives with respect to τ disappear. Now we add together equations (39) and (40) to get

$$0 = \frac{\partial^2 u + v}{\partial z^2} + c\frac{\partial u + v}{\partial z} + u + v - 2uv - u^2 - v^2. \tag{41}$$

Letting $s = u + v$ this simplifies to

$$0 = \frac{\partial^2 s}{\partial z^2} + c\frac{\partial s}{\partial z} + s - s^2. \tag{42}$$

The boundary conditions and initial conditions are $s(-\infty, t) = s(\infty, t) = s(x, 0) = 1$.

15. $s \equiv 1$

16. Since $1 = s = u + v$ we can substitute $v = 1 - u$ into equation (39). Rearranging and cancelling the τ derivative once again leads to equation (25).

17. To show a travelling wave is possible we need to consider the stability of $u = 0$ and $u = 1$. Since u corresponds to grey squirrels we expect the wave to invade from the $u = 1$ boundary towards the $u = 0$ boundary. Thus, we need to show that $u = 0$ is stable and $u = 1$ is unstable. First we perturb around $u = 0$ with $u = \epsilon\exp(\lambda z)$. Substituting this into equation (25) gives

$$0 = \lambda^2 + c\lambda + 1 - \alpha_{12}. \tag{43}$$

So,

$$2\lambda_{\pm} = -c \pm \sqrt{c^2 - 4(1 - \alpha_{12})}. \tag{44}$$

As mentioned we need $u = 0$ to be stable, implying $\mathrm{Re}(\lambda_{\pm}) < 0$. Further, because u is a physical population, $u > 0$. Thus, $u = 0$ cannot be a spiral point. Hence, the eigenvalues must be real and negative implying that $1 > \alpha_{12}$, which is already satisfied, and $c^2 - 4(1 - \alpha_{12}) > 0$, or $c > 2\sqrt{(1 - \alpha_{12})}$.

We next check the stability of $u = 1$ using $u = 1 + \epsilon \exp(\lambda t)$

$$0 = \lambda^2 + c\lambda - 1 + \alpha_{12}. \tag{45}$$

So,

$$2\lambda_{\pm} = -c \pm \sqrt{c^2 + 4(1 - \alpha_{12})}. \tag{46}$$

Since $\alpha_{12} < 1$ we have that $\lambda_- < 0 < \lambda_+$ and, thus, $u = 1$ is unstable. Thus, a travelling wave with a stationary profile can exist.

18. The suggested model dynamics are that due to grey squirrels being "fitter" (in a Darwinian sense) than the red squirrels we should see a travelling wave of grey squirrel population pushing the red squirrel out. This is what is seen in Figure 3 between 1945 and 2000. However, after 2000 the wave seems to halt. This is due to conservation programmes that enable the red squirrel population to survive in certain carefully protected regions. Such external conservation factors are not included in the above model.

3   Amoebae movement

The amoebae of the slime mould *Dictyostelium discoideum* secretes a chemical attractant, cyclic-AMP. The attractant diffuses away from the amoebae source and attracts other amoebae to it, causing spatial aggregations to form, see Figure 5 and the linked YouTube video.
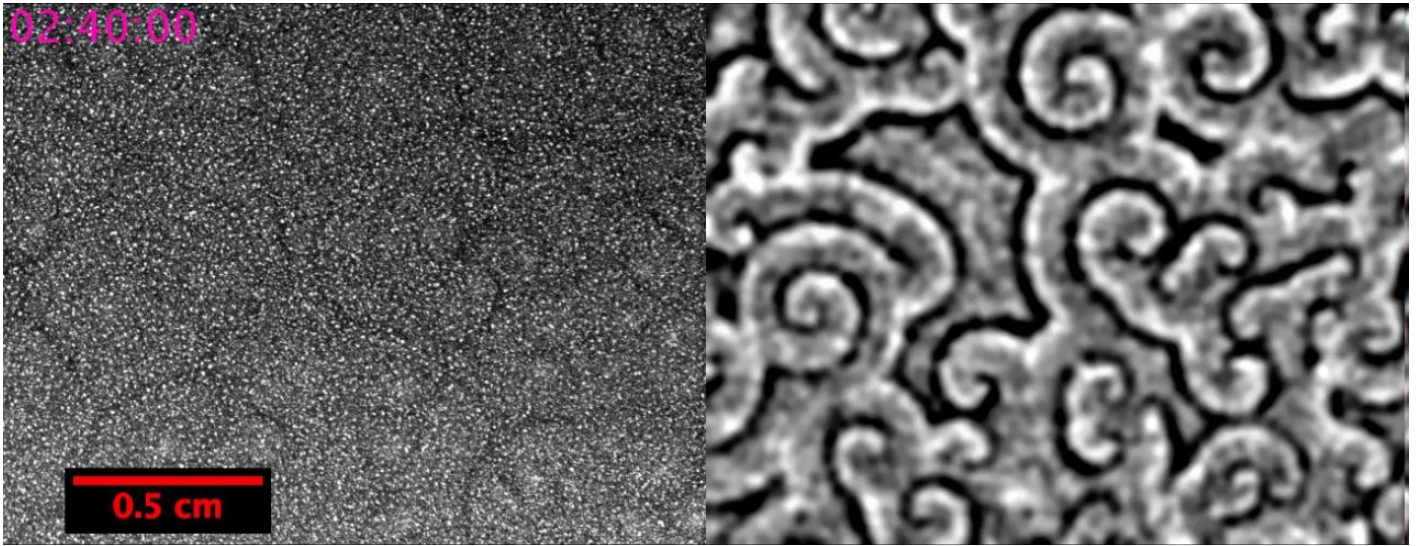

Figure 5:   Single frame of the a spatio-temporal wave pattern made by Dictyostelium discoideum. The full video can be found on YouTube. Have a watch to see how the pattern is generated from randomness.

In the following assume that we are on a infinite, one-dimensional domain so that we can be loose with boundary conditions.

The attractant (concentration denoted a) is secreted by the amoebae (concentration denoted c) at a rate proportional to the amoebae concentration. The attractant is able to diffuse and the attractant decays at a rate proportional to the attractant's concentration.

1. Justify the following equation for the attractant population,

$$\frac{\partial a}{\partial t} = D_a \frac{\partial^2 a}{\partial x^2} + k_1 n - k_2 a. \tag{47}$$

The amoebae do not reproduce or degrade, however, alongside their diffusive motion (Figure 6(a)) they also undergo attractant controlled motion (chemotaxis, as shown in Figure 6(b)) .

2. Using the process of considering an infinite discretised domain, derive the equation of the amoebae movement. Show that, upon taking a continuum spatial limit the equations can be simplified to

$$\frac{\partial n}{\partial t} = D_n \frac{\partial^2 n}{\partial x^2} - \chi \frac{\partial}{\partial x}\left(n \frac{\partial a}{\partial x}\right). \tag{48}$$

where D_n and χ should be defined in terms of D_n', χ' and Δx.

(a) Schematic of diffusive motion
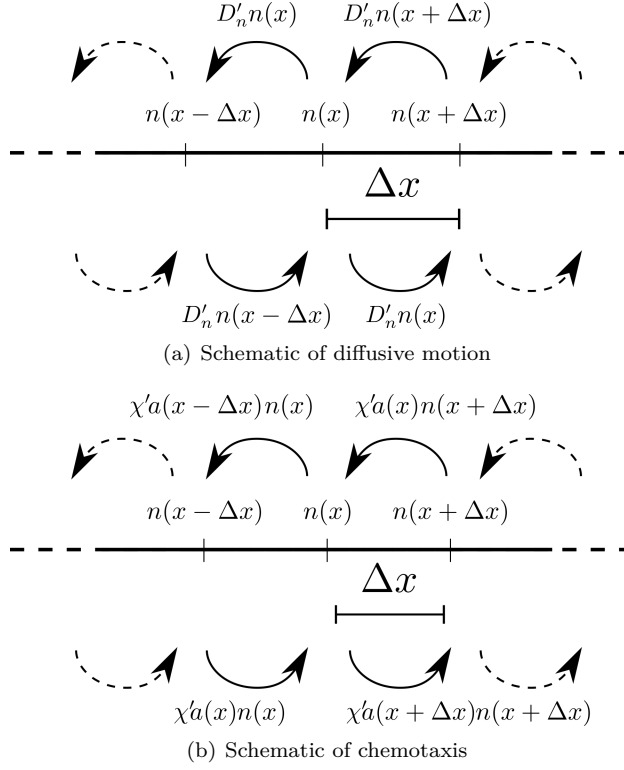

(b) Schematic of chemotaxis

Figure 6: Different motion types of the amoebae.

We now consider the system

$$\frac{\partial n}{\partial t} = D_n \frac{\partial^2 n}{\partial x^2} - \chi \frac{\partial}{\partial x}\left(n\frac{\partial a}{\partial x}\right), \tag{49}$$

$$\frac{\partial a}{\partial t} = D_a \frac{\partial^2 a}{\partial x^2} + n - a. \tag{50}$$

where we have set $k_1 = 1 = k_2$. The system is on an infinite one-dimensional domain. The boundary conditions are zero-flux and the initial conditions are uniformly distributed random perturbations about a mean of $n = a = 1$ and range $1/10$.

3. What is the spatially homogeneous steady states (n_s, a_s) of system (49)-(50)?

4. Perturb around this homogeneous steady state using a spatial perturbation and derive conditions under which the homogeneous steady state will evolve to a patterned state.

5. Experimentally, χ is seen to increase during the life cycle of the slime mould. What does this mean? What would you expect to see over the course of the experiment?

3.1 Answers

1.

$$\underbrace{\frac{\partial a}{\partial t}}_{\substack{\text{Evolution of the} \\ \text{morphogen}}} = \underbrace{D_a \frac{\partial^2 a}{\partial x^2}}_{\substack{\text{Diffusion of the} \\ \text{morphogen}}} + \underbrace{k_1 n}_{\substack{\text{Creation of the} \\ \text{morphogen}}} - \underbrace{k_2 a}_{\substack{\text{Degradation of} \\ \text{the morphogen}}}. \tag{51}$$

2. From Figure 6 we can right down the evolution of $n_i = n(x)$ in terms of $n_{i\pm1} = n(x \pm \Delta x)$ and $a_{i\pm1} = a(x \pm \Delta x)$,

$$\dot{n}_i = D_n'\left(n_{i-1} - 2n_i + n_{i+1}\right) + \chi'\left(a_i n_{i+1} - a_{i-1} n_i + a_i n_i - a_{i+1} n_{i+1}\right). \tag{52}$$

Using

$$u_{i\pm1} = u_i \pm \frac{\partial u_i}{\partial x} + \frac{1}{2}\frac{\partial^2 u_i}{\partial x^2} + O(\Delta x^3) \tag{53}$$

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to expand all the terms we find that

$$\dot{n}_i = D'_n \Delta x^2 \frac{\partial^2 n_i}{\partial x^2} - \chi' \Delta x^2 \left(n_i \frac{\partial^2 a_i}{\partial x^2} + \frac{\partial n_i}{\partial x} \frac{\partial a_i}{\partial x} \right). \tag{54}$$

Letting $D_n = D'_n \Delta x^2$ and $\chi = \chi' \Delta_x^2$ be finite we take $\Delta x \to 0$ and simplify to

$$\frac{\partial n}{\partial t} = D_n \frac{\partial^2 n}{\partial x^2} - \chi \frac{\partial}{\partial x} \left(n \frac{\partial a}{\partial x} \right). \tag{55}$$

3. Searching for the homogeneous steady state means we ignore all derivatives. However, that means equation (49) does not provide any information. However, the zero-flux boundary conditions means that the n population is neither created, degraded, nor is it able to leave the domain. Thus, the homogeneous steady state is found by averaging out the total initial density across the entire domain,

$$n_s = \lim_{L \to \infty} \frac{1}{2L} \int_{-L}^{L} n(x,0) \, \mathrm{d}x. \tag{56}$$

Call this n_0. From equation (50) we find that the steady state satisfies $a_s = n_s = n_0$.

4. We substitute the perturbation

$$\begin{pmatrix} n \\ a \end{pmatrix} = \begin{pmatrix} n_0 \\ n_0 \end{pmatrix} + \begin{pmatrix} \epsilon_1 \\ \epsilon_2 \end{pmatrix} \exp(\lambda t) \cos(kx). \tag{57}$$

into equations (49) and (50) and derive

$$\lambda \cos(kx) \exp(\lambda t) \begin{pmatrix} \epsilon_1 \\ \epsilon_2 \end{pmatrix} = -k^2 \cos(kx) \exp(\lambda t) \begin{pmatrix} D_c & 0 \\ 0 & D_a \end{pmatrix} \begin{pmatrix} \epsilon_1 \\ \epsilon_2 \end{pmatrix} + \cos(kx) \exp(\lambda t) \begin{pmatrix} n_0 \chi k^2 \epsilon_2 \\ \epsilon_1 - \epsilon_2 \end{pmatrix}. \tag{58}$$

Upon simplification

$$\begin{pmatrix} -k^2 D_c - \lambda & n_0 \chi k^2 \\ 1 & -k^2 D_a - \lambda - 1 \end{pmatrix} \begin{pmatrix} \epsilon_1 \\ \epsilon_2 \end{pmatrix} = \mathbf{0}. \tag{59}$$

We now invoke the result that the determinant of the matrix must be zero in order to have a non-trivial solution for (ϵ_1, ϵ_2). Thus,

$$0 = (-k^2 D_c - \lambda)(-k^2 D_a - \lambda - 1) - n_0 \chi k^2 = \lambda^2 + \lambda(k^2 D_a + k^2 D_c + 1) + k^4 D_c D_a + k^2 (D_c - n_0 \chi). \tag{60}$$

For an instability to happen at least one root, λ, must be positive,

$$2\lambda_\pm = -(k^2 D_a + k^2 D_c + 1) \pm \sqrt{(k^2 D_a + k^2 D_c + 1)^2 - 4 \left(k^4 D_c D_a + k^2 (D_c - n_0 \chi) \right)}. \tag{61}$$

Thus, we require

$$0 > k^4 D_c D_a + k^2 (D_c - n_0 \chi) = k^2 D_c D_a \left(k^2 + \frac{(D_c - n_0 \chi)}{D_c D_a} \right). \tag{62}$$

Since inequality (62) is a positive quartic then we need

$$\frac{(D_c - n_0 \chi)}{D_c D_a} < 0, \implies D_c < n_0 \chi \tag{63}$$

5. χ is the chemotactic parameter, increasing it means that the cells become more attracted to the diffusing morphogen. Thus, even if initially the cells do not pattern eventually χ will increase to a point that satisfies the condition $D_c < n_0 \chi$. Thus, the population will eventually pattern.