Elgersburg Summer School, March 2014
Mathematical Biology
Exercise Sheet 4– Turing Instabilities

(1) Diffusion driven instability of a uniform steady state (u^*, v^*) requires that the linearised matrix

$$A = \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix}$$

has only eigenvalues with negative real part, and

$$A - k^2 \begin{pmatrix} 1 & 0 \\ 0 & d \end{pmatrix}$$

has at least one eigenvalue with positive real part for some k.

(i) Show that diffusion driven instability is possible, in general, only if

$$f_u + g_v < 0, \qquad f_u g_v - f_v g_u > 0,$$

and

$$d f_u + g_v > 0, \qquad (d f_u + g_v)^2 > 4d(f_u g_v - g_u f_v)\,.$$

(ii) Suppose that

$$\begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix} = \begin{pmatrix} -1 & 1 \\ a & b \end{pmatrix}$$

Show that diffusion driven instability is possible only if

$$b < 1, \quad a + b < 0, \quad d < b, \quad (a + b) > -\frac{(b-d)^2}{4d}\,.$$

Verify, in the case

$$b = 0.5, a = -0.55, d = 0.25$$

that diffusion driven instability occurs if there are wave numbers k which satisfy

$$0.5 - \frac{1}{10}\sqrt{5} < k^2 < 0.5 + \frac{1}{10}\sqrt{5}\,. \tag{1}$$

Typically, the wave number k decreases as the size of the spatial domain increases. What does the condition (1) require of the size of the domain if diffusion driven instability is to occur?

(2) A dimensionless reaction diffusion system for two chemicals with concentrations u and v is formally described by

$$u_t = f(u, v) + u_{xx}, \qquad v_t = g(u, v) + d v_{xx}\,.$$

Here d is a positive constant, f and g are the nonlinear reaction kinetics and subscripts denote partial derivatives. Assume that a single positive uniform steady state (u_0, v_0) exists.

(i) Suppose that u inhibits v and v inhibits u. Describe what this means. What does this imply about the signs of some of the partial derivatives f_u, f_v, g_u, g_v?

(ii) Show that such an "inhibitor–inhibitor" reaction diffusion system **cannot** be driven unstable by diffusion.

(3) Consider the non–dimensionalised reaction diffusion system

$$\begin{aligned}\frac{\partial X}{\partial t} &= a - X - \frac{4XY}{1+X^2} + \nabla^2 X\,,\\ \frac{\partial Y}{\partial t} &= \gamma\left[b\left(X - \frac{XY}{1+X^2}\right) + c\nabla^2 Y\right],\end{aligned} \tag{2}$$

developed by Lengyle and Epstein. Here X and Y refer to the concentrations of Iodine and Chlorine respectively. All the parameters a,b, and c are positive constants.

(i) Show that, without diffusion, the system (2) has the homogeneous steady state

$$X^* = \frac{a}{5}, \quad Y^* = 1 + \frac{a^2}{25}.$$

(ii) Show that the Jacobian around (X^*, Y^*) is given by

$$A = \frac{1}{1+\frac{a^2}{25}}\begin{pmatrix} -5+\frac{3a^2}{25} & \frac{-4a}{5} \\ \frac{2\gamma a^2 b}{25} & -\frac{\gamma ab}{5}\end{pmatrix} = \frac{1}{1+\beta^2}\begin{pmatrix} -5+3\beta^2 & -4\beta \\ 2\gamma\beta^2 b & -\gamma\beta b\end{pmatrix},$$

where $\beta = \frac{a}{5}$.

(iii) Show that this steady state is asymptotically stable if, and only, if

$$-5 + 3\beta^2 - \gamma\beta b < 0.$$

(iv) Show that the necessary conditions for Turing instability are

$$\begin{cases} -5+3\beta^2-\gamma\beta b < 0, \\ 3\beta^2 c - \gamma\beta b - 5c > 0, \\ \frac{3\beta^2 c-\gamma\beta b-5c}{(1+\beta^2)^2} + 4\gamma c\det(A) > 0. \end{cases} \tag{3}$$

(v) Sketch the region for DDI in the parameter space (a, b), where Turing pattern can be exhibited in the case $\gamma = 9$ and $c = 1.2$.

(4) Suppose that A and B admit a common Lyapunov function P. Show that P is also a common Lyapunov function for A and B^{-1}.

(5) Let A and B be stable matrices. Show that $A + \alpha B$ is unstable for some positive α only if $A - B$ is large enough.

(6) Suppose that A is stable and ρ is such that the Riccati equation

$$A^T P + PA + \rho^2 E^T E + PDD^T P = 0\,,$$

has a positive definite solution $P = P^T$. Show that if $\|\Delta\| < \rho$, then P is a CLF for all $A_\Delta = A + D\Delta E$.

(7) Gierer and Meinhardt proposed an inhibitor–activator model to explain the regenerative properties of *Hydra*.

Let $a(t,x)$ and $h(t,x)$ denote the concentrations of the activator and the inhibitor at time t and position x, respectively. The spatio–temporal dynamics of a and h are given by the reaction diffusion system:

$$\begin{cases} \frac{\partial a}{\partial t} &= \rho\rho_0 + c_1\rho\frac{a^2}{h} - \mu a + d_1\nabla_x^2 a \\ \frac{\partial h}{\partial t} &= c_2\rho' a^2 - \nu h + d_2\nabla_x^2 h. \end{cases}$$

Here d_1 and d_2 are the diffusivities of the activator and the inhibitor; ρ_0 is the basic production of the activator and ρ and ρ' are the source concentrations for the activator and the inhibitor respectively; μ and ν are the degradation rates of the activator and the inhibitor. The parameters c_1 and c_2 are connected with the activator and inhibitor production.

(i) Show that the Gierer and Meinhardt systems has a positive homogeneous steady state given by:

$$(a^*,h^*) = (\frac{c_2\rho'\rho\rho_0 + c_1\rho\nu}{c_2\rho'\mu}, \frac{c_2\rho'(a^*)^2}{\nu}).$$

Show that the Jacobian of the system around this homogeneous steady state is given by

$$A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix},$$

where

$$\begin{cases} a_{11} &= \frac{2c_1\mu\nu}{c_1\nu + c_2\rho'\rho_0} - \mu\,, & a_{12} &= \frac{-c}{\rho}(\frac{\mu\nu}{c_1\nu + c_2\rho'\rho_0})^2\,, \\ a_{21} &= \frac{2\rho(c_1\nu + c_2\rho'\rho_0)}{\mu}\,, & a_{22} &= -\nu\,. \end{cases}$$

(ii) Show that A is stable when

$$\mu\nu > 0 \quad \text{and} \quad \frac{2c_1\nu}{c_1\nu + c_2\rho'\rho_0} - \mu - \nu < 0.$$

(iii) For a general 2 by 2 matrix A, show that $P = I$ is a Lyapunov function for A if, and only if,

$$a_{11} \leq 0 \quad \text{and} \quad 4a_{11}a_{22} - (a_{12} + a_{21})^2 \geq 0.$$

We now return to the specific A arising from lineariastion of the Gierer and Meinhardt system. We consider two sets of parameters. The first set of parameters is used to illustrate the differences between when I is a CLF, when there is a CLF (not necessarily I) and when there is DDI.

(iv) Set

$$c_1 = 0.005, \quad c_2 = 0.035, \quad d_1 = 0.03, \quad d_2 = 0.45, \quad \rho' = 0.075 \quad \text{and} \quad \rho = \rho_0 = 3.2$$

Using the `cvx` package, show that the parameter space (μ,ν) splits into three distinct regions: where I is a CLF; where there is a CLF; and where there is DDI. Sketch these regions in the plane. Show that there is a significant part of the stable region of parameter space in which the I-reactive test is inconclusive and that the test for no-DDI based on the existence of a CLF captures all of the no DDI region.

(v) The second set of parameters is taken directly from the original paper by Gierer and Meinhardt; specifically

$$c_1 = 0.05, \quad c_1 = 0.025, \quad d_1 = 0.03, \quad d_2 = 0.45, \quad \rho' = 0.00075 \quad \text{and} \quad \rho = \rho_0 = 3.2\,.$$

Use the `cvx` package to explore the possibility of DDI in the parameter space (μ, ν). Sketch the regions according to I is a Lyapunov for A, there is a CLF for A and D and there is no DDI.

(8) **Reaction–Diffusion–Chemotaxis Models** The non–dimensional dynamics of a multi-species, host–parasitoid community system are given by

$$\begin{aligned} \frac{\partial u}{\partial t} &= \gamma(a - u + u^2 v) + \nabla^2 u - \alpha \nabla.(u \nabla v), \\ \frac{\partial v}{\partial t} &= \gamma(b - u^2 v) + d\nabla^2 v\,. \end{aligned}$$

Here the parameters a and b are species growth rates. The parameter γ is non–dimensional and is essentially related to nature of the space. Here α is assumed to be positive which means that species u is attracted to species v.

(i) Show that $(a + b, b/(a + b)^2)$ is an equilibrium and that around this equilibrium the Jacobian for a wave number k is given by

$$A - k^2 D_\alpha,$$

where

$$A = \begin{pmatrix} \frac{b-a}{a+b} & (a+b)^2 \\ \frac{-2b}{a+b} & -(a+b)^2 \end{pmatrix}, \quad D_\alpha = \begin{pmatrix} 1 & -\alpha(a+b) \\ 0 & d \end{pmatrix}.$$

(ii) Show that the uniform steady state is stable when

$$b - a - (a + b)^3 < 0.$$

(iii) Show that I is a CLF for A and D_α in a region determined by the inequalities:

$$b < 1, \quad (a+b)(2b-1) > 0 \quad \frac{2d}{\alpha} > (a+b) \quad (\text{for } A) \quad \text{and} \quad 4d > \alpha^2 (a+b)^2 \quad (\text{for } D_\alpha)\,.$$

(iv) Use the `cvx` package to determine a region in (a, b)–parameter space when A and D_α have a CLF in the case $d = 100$ and $\alpha = 20$.

(v) Show that when $a = 0.15$ and $b = 0.7$ then A and D_{20} have no CLF (where CDDI might be expected). Show that

$$A = \begin{pmatrix} 0.6471 & 72.25 \\ -1.6471 & -0.7225 \end{pmatrix}, \quad D_\alpha = \begin{pmatrix} 1 & -17 \\ 0 & 100 \end{pmatrix},$$

and that for the wave number $k = \sqrt{0.3}$, the matrix pencil $A - \omega^2 D_{20}$ has positive eigenvalues.