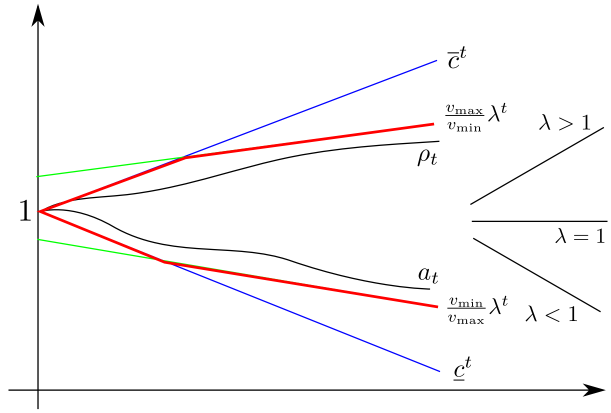

Figure 16: Combined Bounds.

8 Spatially distributed reaction-diffusion kinetics

8.1 Background

Consider the concentration $c(\mathbf{x}, t)$. This is the concentration of some chemical species at $\mathbf{x} \in \mathbb{R}^3$ at time t.

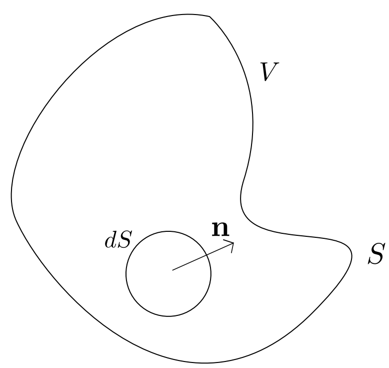

Figure 17: Model setup

Let $f = f(c, \mathbf{x}, t)$ be the source of the chemical in V. Introduce the flux vector $\mathbf{J} = J_1\mathbf{i} + J_2\mathbf{j} + J_3\mathbf{k}$. We define this as, $\mathbf{J} \cdot d\mathbf{S} = \mathbf{J} \cdot \mathbf{n} dS$. This is the rate of movement of chemical across dS per unit time. We can write the following conservation equation,

$$\frac{\partial}{\partial t} \iiint_V c(\mathbf{x}, t) dV = \iiint_V f dV - \iint_S \mathbf{J} \cdot d\mathbf{S}$$

We recall the divergence theorem,

$$\iint_S \mathbf{J} \cdot d\mathbf{S} = \iiint_V \nabla \cdot \mathbf{J} dV$$

Thus,

$$\iiint_V \frac{\partial}{\partial t} c(\mathbf{x}, t) dV = \iiint_V f - \nabla \cdot \mathbf{J} dV$$

This holds for an arbitrary volume V. We can equate the integrands,

$$\frac{\partial c(\mathbf{x}, t)}{\partial t} = -\nabla \cdot \mathbf{J} + f \tag{2}$$

If transport is via diffusion, then,

$$\mathbf{J} = -D\nabla c$$

where D is the diffusion coefficient. In general $D = D(\mathbf{x}, t)$. This is referred to as Fick's law. In $1D$, then $J = -D\frac{\partial c}{\partial x}$. We now substitute into 2. We obtain,

$$\frac{\partial c}{\partial t} = f + \nabla \cdot (D\nabla c). \tag{3}$$

This is the reaction-diffusion equation. We now go further and assume that $D(\mathbf{x}, t) = D$ is constant. Then 3 simplifies to,

$$\frac{\partial c}{\partial t} = f + D\nabla \cdot \nabla c = f + D\nabla^2 c \tag{4}$$

where ∇^2 is just the Laplacian. If $f = 0$, then we obtain the diffusion equation in three dimensions. We consider m reactants, with concentration,

$$u_1(\mathbf{x}, t), \dots, u_m(\mathbf{x}, t)$$

with diffusion constants, $D_1, \dots, D_m$ and source terms $f_1(u_1, \dots, u_m), \dots, f_m(u_1, \dots, u_m)$. We then write the equations as,

$$\frac{\partial u_i}{\partial t} = f_i(u_1, \dots, u_m) + D_i\nabla^2 u_i \qquad 1 \leq i \leq m.$$

We can write this in vector form,

$$\frac{\partial \mathbf{u}}{\partial t} = \mathbf{f}(\mathbf{u}) + \mathbf{D}\nabla^2\mathbf{u}$$

where,

$$\mathbf{u} = (u_1, \dots, u_m)^T \qquad \mathbf{f} = (f_1, \dots, f_m)^T$$

and,

$$D = \begin{pmatrix} D_1 & & 0 \\ & \ddots & \\ 0 & & D_m \end{pmatrix}$$

First, we consider one reactant, $m = 1$ and $x \in \mathbb{R}$. This gives arise to,

$$\frac{\partial u}{\partial t} = f(u) + D\frac{\partial^2 u}{\partial x^2}.$$

8.2 Fisher Equation

We will consider the Fisher equation. We consider $u(\mathbf{x}, t)$ as the concentration of the gene in a population at spatial location $\mathbf{x}$ at time t,

$$\frac{\partial u}{\partial t} = ku(1-u) + D\frac{\partial^2 u}{\partial x^2}.$$

We assume that $k, D > 0$. We can non-dimensionalise this set of equations with $\tau = kt$, $\xi = \sqrt{\frac{k}{D}}$ to give,

$$\frac{\partial u}{\partial \tau} = u(1-u) + \frac{\partial^2 u}{\partial \xi^2} \tag{5}$$

To analyse systems of this kind we consider the spatially homogenous system, we ignore $\frac{\partial^2 u}{\partial \xi^2}$. It has two steady states, where $\frac{\partial u}{\partial \tau} = 0$. That is $u = 0$ and $u = 1$,

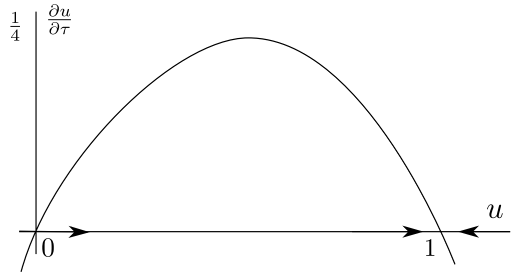

Figure 18: Stability of stable states

We know that 0 is unstable and 1 is stable, that is any profile between 0 and 1 it will asymptotically go to 1. This isn't very interesting. We now consider the system with diffusion. We seek a solution of 5, as,

$$u(\xi,\tau) = U(\xi - c\tau) \qquad c > 0$$

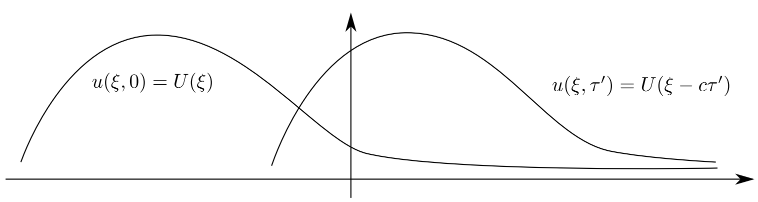

Figure 19: Characteristics of solutions of 5

We introduce the travelling wave coordinate $z = \xi - c\tau$, which now means, $u(\xi,\tau) = U(\xi - c\tau) = U(z)$. Now we can transform this into a system in terms of z. We see by the chain rule,

$$\frac{\partial u}{\partial \tau} = -c\frac{dU}{dz}$$
$$\frac{\partial^2 u}{\partial \xi^2} = \frac{d^2 U}{dz^2}$$

Then substituting this into the PDE (5) we get,

$$\frac{d^2U}{dz^2} + c\frac{dU}{dz} + u(1-u) = 0$$

We seek solutions with respect to the boundary conditions,

$$U(-\infty) = 1 \quad \text{and } U(\infty) = 0$$

These equate to a solution of the form,

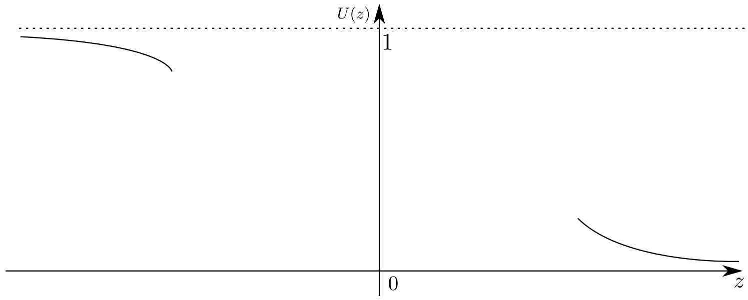

Figure 20: BC of the solution.

We now let $v = u'$, which allows us to now present this as a system of two ODEs,

$$\begin{aligned} v = u' &= f(u, v) \\ v' = -cv - u(1-u) &= g(u, v) \end{aligned} \tag{6}$$

Steady states and stabilities
The steady states are where $u' = v' = 0$, that then implies for $v = 0$ we have $u(1-u) = 0$ and so $u = 0$ or $u = 1$. Thus we have two steady states, $(0, 0)$ and $(1, 0)$. To find the stabilities we consider the jacobian at the two steady states,

$$\mathcal{J}(u, v) = \begin{pmatrix} \frac{\partial f}{\partial u} & \frac{\partial f}{\partial v} \\ \frac{\partial g}{\partial u} & \frac{\partial g}{\partial v} \end{pmatrix} = \begin{pmatrix} 0 & 1 \\ -1 + 2u & -c \end{pmatrix}$$

We now consider $\mathcal{J}(0, 0)$. We see,

$$\mathcal{J}(0, 0) = \begin{pmatrix} 0 & 1 \\ -1 & c \end{pmatrix}$$

Then we get the eigenvalues are,

$$\lambda_{\pm} = \frac{1}{2}\left(-c \pm \sqrt{c^2 - 4}\right)$$

Now we consider two cases. If $c^2 \geq 4$, then $\lambda_- \leq \lambda_+ < 0$. This is a stable node. If $c^2 < 4$, then $\lambda_{\pm} \in \mathbb{C}$ and $\text{Re}(\lambda_{\pm}) = -c \leq 0$ and so we have a stable focus.

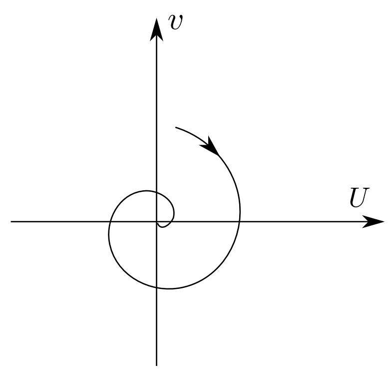

Figure 21: Stability of the origin

We then must have $c^2 \geq 4$ and so $c \geq 2$. This is because $u < 0$ is biologically infeasible. We now have a bound on c. We now consider the other stable state.

$$\mathcal{J}(1, 0) = \begin{pmatrix} 0 & 1 \\ 1 & -c \end{pmatrix}$$

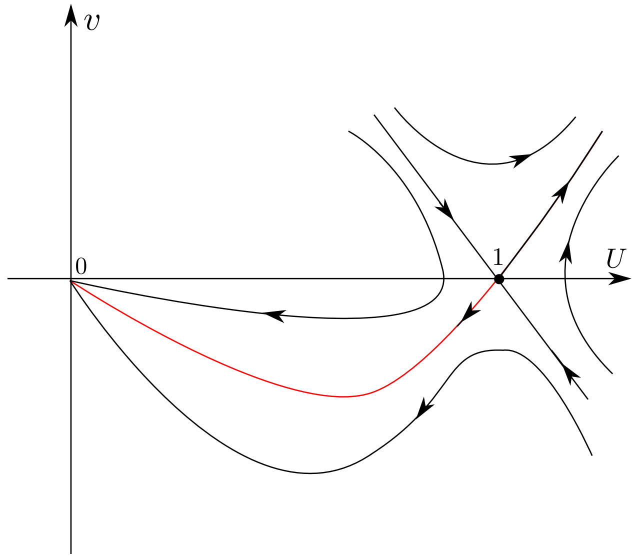

Figure 22: Phase Portrait for the system

where we have eigenvalues of $\lambda_{\pm} = \frac{1}{2}\left(-c \pm \sqrt{c^2-4}\right)$. As $\sqrt{c^2+4} > c$, we have $\lambda_- < 0 < \lambda_+$ and so we have a saddle node. We can now draw a phase portrait of this system,
We see the red trajectory is the only trajectory with the property we are interested in for the boundary conditions. We can now infer the form of $U(z)$.

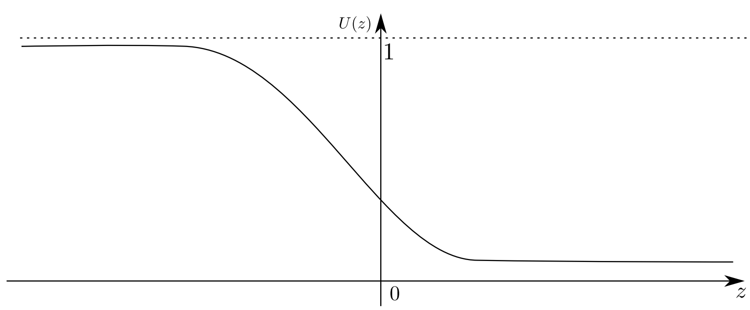

Figure 23: Phase Portrait for the system

8.3 Turing Mechanism

We now consider $n = 2$, we write these as u and v.The application is pattern formation. In absence of diffusion, $u(\mathbf{x}, t) = u_0$ for all $\mathbf{x}, t$. This would produce a uniform pattern. We also assume in the absence of diffusion $v(\mathbf{x}, t) = v_0$. We further assume that steady states are linearly stable. We will focus on deriving conditions such that the introduction of diffusion destabilises this and we get inhomogeneous patterning.

We consider the reaction-diffusion equations for u and v in their normalised form ($\gamma > 0$),

$$\begin{aligned} \frac{\partial u}{\partial t} &= \gamma f(u,v) + \nabla^2 u \\ \frac{\partial v}{\partial t} &= \gamma g(u,v) + \nabla^2 v \end{aligned} \tag{7}$$

We consider some domain Ω with boundary $\partial\Omega$ with outward normal $\mathbf{n}$. Further, we take zero-flux boundary conditions,

$$\mathbf{n} \cdot \nabla u = \mathbf{n} \cdot \nabla v = 0.$$

Suppose we have a spatially uniform steady state of 7, (u_0, v_0). Then, (u_0, v_0) satisfies,

$$f(u_0, v_0) = g(u_0, v_0) = 0.$$

Also note that $\mathbf{n} \cdot \nabla u_0 = \mathbf{n} \cdot \nabla v_0 = 0$. We first linearise these about the steady states (u_0, v_0) in the absence of diffusion, (i.e. when $\nabla^2 u = \nabla^2 v = 0$). Write,

$$\begin{aligned} u &= u_0 + \hat{u} \\ v &= v_0 + \hat{v}. \end{aligned}$$

Substituting into 7, taking a Taylor expansion and considering lowest order terms, we obtain,

$$\begin{aligned} \frac{\partial \hat{u}}{\partial t} &= \gamma(f_u \hat{u} + f_v \hat{v}) \\ \frac{\partial \hat{v}}{\partial t} &= \gamma(g_u \hat{u} + g_v \hat{v}). \end{aligned}$$

In vector form, $\mathbf{w} = (\hat{u} \quad \hat{v})^T$, the equations become,

$$\frac{\partial \mathbf{w}}{\partial t} = L\mathbf{w} \qquad L = \gamma \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix}\Bigg|_{(u_0, v_0)}.$$

Recall that we want the diffusion-free problem to be stable. We want the eigenvalues of L to have negative real part. This is guarenteed if $\operatorname{tr} L < 0$ and $\det L > 0$. Note,

$$\begin{aligned} \operatorname{Tr}(L) &= \gamma(f_u + g_v) \\ \det L &= \gamma(f_u g_v - f_v g_u) \end{aligned}$$

Thus we obtain stability if,

$$f_u + g_v < 0 \tag{I}$$

$$f_u g_v - f_v g_u > 0. \tag{II}$$

Let us consider the full equations with diffusion,

$$\begin{aligned} \frac{\partial u}{\partial t} &= \gamma f(u, v) + \nabla^2 u \\ \frac{\partial v}{\partial t} &= \gamma g(u, v) + \nabla^2 v \end{aligned}$$

We introduce again $u = u_0 + \hat{u}$ and $v = v_0 + \hat{v}$ and we then obtain the linearisation,

$$\begin{aligned} \frac{\partial \hat{u}}{\partial t} &= \gamma(f_u \hat{u} + f_v \hat{v}) + \nabla^2 \hat{u} \\ \frac{\partial \hat{u}}{\partial t} &= \gamma(g_u \hat{u} + g_v \hat{v}) + d\nabla^2 \hat{v} \end{aligned}$$

In vector form, $\mathbf{w} = (\hat{u} \quad \hat{v})^T$, obtaining,

$$\frac{\partial \mathbf{w}}{\partial t} = L\mathbf{w} + D\nabla^2 \mathbf{w} \qquad D = \begin{pmatrix} 1 & 0 \\ 0 & d \end{pmatrix} \tag{8}$$

To solve 8 we are going to separate space and time. First, let $\mathbf{w}_k(\mathbf{x}) = (\hat{u}_k(\mathbf{x}) \quad \hat{v}_k(\mathbf{x}))^T$ be the solution to the spatial eigenvalue problem,

$$\nabla^2 \mathbf{w}_k = -k^2 \mathbf{w}_k.$$

Subject to the following boundary conditions $\mathbf{n} \cdot \nabla \hat{u}_k = \mathbf{n} \cdot \hat{w}_k = 0$.

Example. Consider the 1D domain $\Omega = \{0 \leq x \leq a\}$, then $\partial\Omega = \{0\} \cup \{a\}$. The eigenvalue problem is then,

$$\frac{\partial^2 \mathbf{w}_k}{\partial x^2} = -k^2 \mathbf{w}_k$$

which we can write as the shorthand for $w_k = \hat{u}_k$ or $\hat{v}_k$. The boundary conditions are,

$$\frac{\partial w_k}{\partial x} = 0 \text{ at } x = o \text{ and } x = a.$$

The general solution is,

$$w_k(x) = A_k \cos(kx) + B_k \sin(kx) \qquad A_k, B_k \in \mathbb{R}.$$

Imposing the boundary conditions, the solution are,

$$w_k(x) = A_k \cos\left(\frac{n\pi x}{a}\right)$$

Thus we have shown,

$$\mathbf{w}_k(x) = \begin{pmatrix} A_{k_1} \\ A_{k_2} \end{pmatrix} \cos\left(\frac{n\pi x}{a}\right)$$

where $A_{k_1}, A_{k_2} \in \mathbb{R}$.

In general we see a solution to (8) in the following form,

$$\mathbf{w}(\mathbf{x}, t) = \sum_k c_k e^{\lambda_k t} \mathbf{w}_k(\mathbf{x}) \tag{9}$$

The stability of the solutions in time will be determined by the spatial eigenvalues. If $\lambda_k < 0$ then we get the perturbation dying out, but if $\lambda_k > 0$ then we have a growing solution with the trig function in space with a periodic solution. Hence for instability we want some $\lambda_k > 0$. We are going to substitute this (9) back into (8),

$$\sum_k c_k \lambda_k e^{\lambda_k t} \mathbf{w}_k = \sum_k c_k e^{\lambda_k t} (\gamma A - k^2 D) \mathbf{w}_k$$

where A is just the Jacobean at (u_0, v_0). But the $\mathbf{w}_k$'s are linearly independent, and so

$$(\gamma A - k^2 D)\mathbf{w}_k = \lambda_k \mathbf{w}_k$$

and so,

$$(\lambda_k I - \gamma A + k^2 D)\mathbf{w}_k = 0$$

We are interested in the temporal eigenvalues λ_k. For non-trivial solutions, we require that,

$$|\lambda_k I - \gamma A + k^2 D| = 0$$

This is equivalent to the following,

$$\lambda_k^2 + (k^2(1+d) - \gamma(f_u + g_v))\lambda_k + h(k^2) = 0$$

where

$$h(k^2) = dk^4 - \gamma(df_u + g_v)k^2 + \gamma(f_u g_v - f_v g_u).$$

We want stable eigenvalues and so we will use (I) and (II) to find new conditions on this problem. From condition **??**, $f_u + g_v < 0$. Hence, for $\mathrm{Re}(\lambda_k) > 0$, we must $h(k^2) < 0$. From condition **??**, we have that $f_u g_v - f_v g_u > 0$, so for $h(k^2) < 0$, require

$$df_u + g_v > 0 \tag{III}$$

Further we can write $h(k^2)$ as,

$$h(k^2) = d\left[(k^2 - \frac{\gamma}{2d}(f_u + g_v)) + \frac{\gamma^2}{d}\left(f_u g_v - f_v g_u\right) - \frac{\gamma^2}{4d^2}\left(df_u + g_v\right)^2\right].$$

The last two terms are independent of k^2, hence $h(k^2)$ is minimised when,

$$k^2 = \frac{\gamma}{2d}\left(f_u + g_v\right) \tag{10}$$

and $h(k^2)$ has the following minimum value,

$$h_{\min} = \gamma^2\left(f_u g_v - f_v g_u\right) - \frac{\gamma^2}{4d}\left(df_u + g_v\right)^2$$

Then $h_{\min} < 0$ and so $h(k^2) < 0$, so for instability we require,

$$(df_u + g_v)^2 < 4d(f_u g_v - f_v g_u) \tag{IV}$$

To recap. We have show that conditions required for diffusion driven instability are,

$$f_u + g_v < 0 \tag{I}$$
$$f_u g_v - f_v g_u > 0 \tag{II}$$
$$df_u + g_v > 0 \tag{III}$$
$$(df_u + g_v)^2 > 4d(f_u g_v - f_v g_u) \tag{IV}$$

The first two will guarantee that without diffusion it is stable and the last two guarantee it is unstable with diffusion. Note, each partial derivatives are evaluated at (u_0, v_0).

This is obviously a bifurcation. Let us thing about d as a parameter. Then there is a critical value of d, d_c at which instability occurs (When $h_{\min}$). The derivation for condition IV tells us it is,

$$(d_c f_u + g_v)^2 = 4d_c(f_u g_v - f_v g_u) \tag{11}$$

We can plot this as,

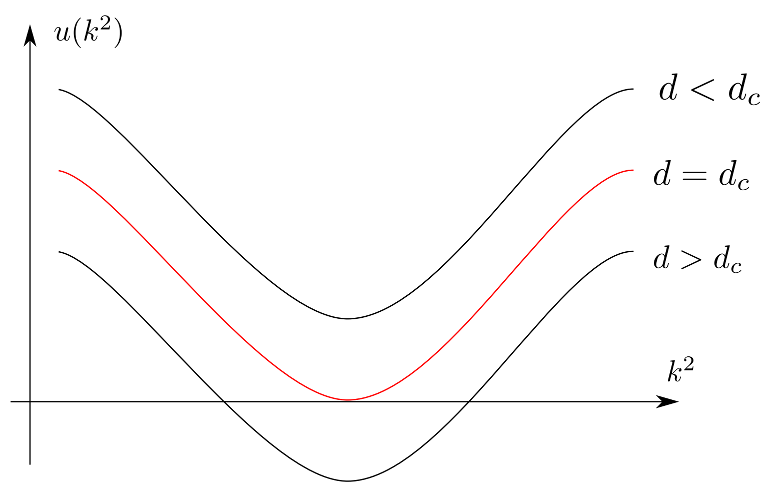

Figure 24: Different values of d with respect to d_c.

We consider the the perturbation from the steady states was,

$$\mathbf{w}(\mathbf{x},t) = \sum_k c_k e^{\lambda_k t}\mathbf{w}_k(\mathbf{x}).$$

This tells is that for all $k_1^2 k^2 < k_2^2$ we have $\mathrm{Re}(\lambda_k) > 0$. For $d < d_c$ we have all the $\mathrm{Re}(\lambda_k) < 0$ and so $\mathbf{w}(\mathbf{x},t) \to 0$, but for $d > d_c$ we will have $\mathbf{w}_k$ grow to an inhomogeneous solution.

The bifurcation we see is sometimes called the Turing bifurcation, we call the k's the wave numbers. There is a critical wave number, k_c, the wave number we get at the bifurcation. This is the first node to lose stability. From 10, we can see this is,

$$k_c^2 = \frac{\gamma}{2d_c}(d_c f_u + g_v).$$

Then 11 then gives us,

$$k_c^2 = \gamma\sqrt{\frac{f_u g_v - f_v g_u}{d_c}}$$

8.4 Turing Mechanism: Example

Consider the following system in $\mathbb{R}$ ($u = u(x,t)$ and $v = v(x,t)$). Then the system is,

$$u_t = \frac{u^2}{v} - bu + u_{xx}$$
$$v_t = u^2 - v + du_{xx}$$

where $b, k > 0$. The reaction terms in this case are the following,

$$f(u,v) = \frac{u^2}{v} - bu \qquad g(u,v) = u^2 - v$$

This define the system as an activator-inhibitor system because, an increase of u increases v, that is u is having a positive increasing affect on v. Increasing v decreases the amount of u created. Hence we have an activator coupled with an inhibitor. We can take partial derivatives,

$$f_u = \frac{2u}{v} - b \qquad f_v = -\frac{u^2}{v^2}$$

$$g_u = 2u \qquad g_v = -1$$

We are interested in spatially homogenous steady states $u = u_0$ and $v = v_0$ satisfy,

$$f(u_0,v_0) = g(u_0,v_0) = 0$$

That gives,

$$\frac{u_0^2}{v^2} - bu_0 = 0 \qquad u_0^2 = v_0$$

This is pretty easy to solve and we get,

$$u_0 = \frac{1}{b} \qquad v_0 = \frac{1}{b^2}.$$

So we have the steady state of $\left(\frac{1}{b}, \frac{1}{b^2}\right)$. At the steady state,

$$f_u = b \qquad g_v = -b^2 \qquad g_u = \frac{2}{b} \qquad g_v = -1$$

Stability in the presence of diffusion requires,

$$f_u + g_v < 0 \implies b < 1 \tag{I}$$
$$f_u g_v - f_v g_u > 0 \implies b > 0 \tag{II}$$

Therefore, stability in the presence of diffusion happens when $0 < b < 1$. For diffusion-driven instability, requires,

$$df_u + g_v > 0 \implies db > 1 \tag{III}$$
$$(df_u + g_v)^2 > 4d(f_u g_v - f_v g_u) \implies (db - 1)^2 > 4db \tag{IV}$$

To simplify the analysis, we let $x = db$. Then (IV) becomes,

$$(x - 1)^2 > 4x$$

This can be manipulated to find that $(x - 3) > 8$ and further $3 + 2\sqrt{2} < x < 3 - 2\sqrt{2}$. We let $x = db$ and (III) said that $db > 1$, we see that the later half of the above inequality violated that. This $db > 3 + 2\sqrt{2}$. So for diffusion-driven instability we require,

$$0 < b < 1 \quad \text{and } d > \frac{3 + 2\sqrt{2}}{b}.$$

In the (b, d) parameter plane,

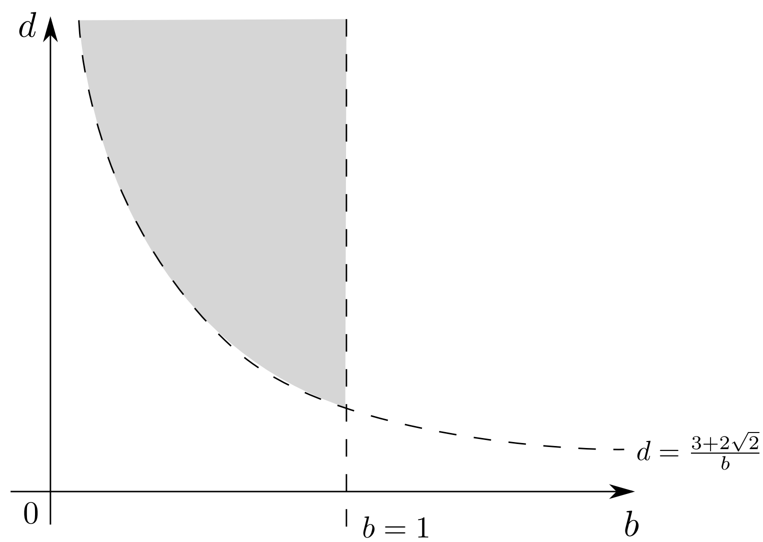

Figure 25: Parameter variation for activator-inhibitor model.

The shaded value shows where diffusion-driven instability can occur. If we think of d as a bifurcation parameter. For each fixed b, f we move d through the curved dotted line a Turing bifurcation will occur. That is, as d increases through,

$$d_c = \frac{3 + 2\sqrt{2}}{b}, \tag{$*$}$$

(u_0, v_0) loses stability in a Turing bifurcation. Now,

$$k_c^2 = \gamma\sqrt{\frac{f_u g_v - f_v g_u}{d_c}} = \sqrt{\frac{b}{d_c}}.$$

So from $*$,

$$k_c = \sqrt{\frac{3 + 2\sqrt{2}}{d_c^2}} = \frac{\sqrt{3 + 2\sqrt{2}}}{d_c} = \frac{1 + \sqrt{2}}{d_c}.$$

8.5 Biological Pattern Formation (Non-examinable)

We have been examining,

$$u_t = \gamma f(u,v) + \nabla^2 u$$
$$v_t = \gamma g(u,v) + d\nabla^2 v$$

involving two reactants and two zero-flux conditions,

$$\frac{\partial u}{\partial n} = \mathbf{n}\cdot\nabla u = 0 \quad \frac{\partial v}{\partial n} = \mathbf{n}\cdot\nabla v = 0$$

and then the linearisation,

$$\mathbf{w}_t = L\mathbf{w} + D\nabla^2\mathbf{w}.$$

This has solutions,

$$\mathbf{w}(\mathbf{x},t) = \sum_k c_k e^{\lambda_k t}\mathbf{w}_k(\mathbf{x})$$

and we have the usual $I - IV$ conditions. So let us now consider $\Omega = \{0 < x < p, 0 < y < q\}$. The spatial eigenvalue problem is,

$$\nabla^2\mathbf{w} = -k^2\mathbf{w}$$

with boundary conditions,

$$\frac{\partial \mathbf{w}}{\partial x} = 0 \text{ at } x = 0, p \qquad \frac{\partial \mathbf{w}}{\partial y} = 0 \text{ at } y = 0, q$$

Thus,

$$\frac{\partial^2 w}{\partial x^2} + \frac{\partial^2 w}{\partial y^2} = -k^2 w$$

with,

$$\frac{\partial w}{\partial x} = 0 \text{ at } x = 0, p \qquad \frac{\partial w}{\partial y} = 0 \text{ at } y = 0, q,$$

where $w = \hat{u}, \hat{v}$. We seek separable solutions $w(x,y) = X(x)Y(y)$. These satisfy,

$$X''Y + XY'' + k^2XY = 0$$

that is,

$$-\frac{X''}{X} = k^2 + \frac{Y''}{Y} = \alpha^2,$$

for some $\alpha \in \mathbb{R}$. This then yields,

$$X(x) = A\cos(\alpha x) + B\sin(\alpha x).$$

Now, $\frac{\partial w}{\partial x} = X'Y$ and $\frac{\partial w}{\partial y} = XY'$. The boundary conditions say,

$$X' = 0 \text{ at } x = 0, p \qquad Y' = 0 \text{ at } y = 0, q.$$

Imposing boundary conditions,

$$\alpha = \frac{m\pi}{p} \qquad \beta = \frac{n\pi}{q} \qquad m, n \in \mathbb{Z}$$

This,

$$w = XY = A\cos\left(\frac{m\pi x}{p}\right)\cos\left(\frac{n\pi y}{q}\right)$$

where,

$$k^2 = a^2 + b^2 = \pi^2\left(\frac{m^2}{p^2} + \frac{n^2}{q^2}\right).$$

Our solution is then of the form,

$$w(x,y,t) = \sum_{m,n} c_{mn} e^{\lambda_{mn} t} \cos\left(\frac{m\pi x}{p}\right) \cos\left(\frac{n\pi y}{q}\right)$$

We now recall the stability discussion. Any m, n that satisfy our stability condition will grow in time, these develop into different states that are dependent on the eigenfunctions.

Suppose the only unstable wave numbers are $m = 1$ $n = 0$. The only unstable mode is then,

$$w(x,y,t) = Ae^{\lambda t} \cos\left(\frac{\pi x}{p}\right) \qquad \text{for } \operatorname{Re}\lambda > 0$$

Thus,

$$u(x,y,t) = u_0 + \varepsilon e^{\lambda t} \cos\left(\frac{\pi x}{p}\right)$$

where we have a steady state and perturbation terms. Similarly for v. Typically a patter will be laid down where the morphogen u is about it's steady state. So we get some halved pattern,

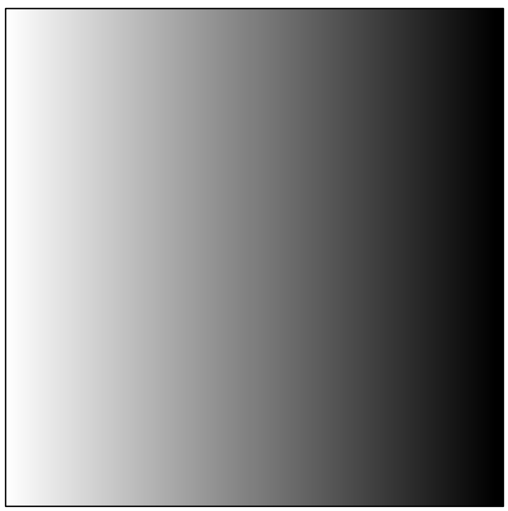

Figure 26: Pattern Formation from $m = 1$, $n = 0$ unstable.

We can generalise this. If we have some pairing (m, n) corresponds to an unstable solution then,

$$w(x,y,t) = Ae^{\lambda t} \cos\left(\frac{m\pi x}{p}\right) \cos\left(\frac{n\pi y}{q}\right) \qquad \text{for } \operatorname{Re}\lambda > 0$$

Thus,

$$u(x,y,t) = u_0 + \varepsilon e^{\lambda t} \cos\left(\frac{m\pi x}{p}\right) \cos\left(\frac{n\pi y}{q}\right)$$

and similarly for v. We therefore expect $u > u_0$ in an $(m+1) \times (n+1)$ chessboard pattern. We get spots.

More complex geometries and reaction kinetics lead to more complex patterns. Murray has a detailed discussion. We know that the wave numbers satisfy of our problem (a Helmhotlz Problem) satisfy,

$$k^2 = \pi \left(\frac{m^2}{p^2} + \frac{n^2}{q^2}\right).$$

Typically, the chemistry, rather than the geometry will force unstable wave numbers k to satisfy the condition $k_1^2 < k^2 < k_2^2$.

For a tail, length >>> width and so $p >>> q$. Then we might allow only $n = 0$ and $m = M >>> 1$ say, giving a striped tail and if $n = 2$ we might get a spotted tail.