Diffusion Driven Instability

Imagine a stable steady state of a well-mixed prey predator system. If, by a perturbation, the prey population exceeds the steady state value, it will trigger the rise of the predator population which will then bring the prey level down again. And, since we assumed stability of the steady state, this will not lead to oscillatory overshoot instability, but to restoration of the steady situation.

Now leave out "well-mixed" in the description above and imagine the same scenario in a spatial domain Ω where, at the start, prey- and predator levels are uniform, i.e., constant over space. The perturbation is now a very localized one. At the position of the perturbation the predator population density will rise. If predators are "stupid", in the sense that their motion is undirected and random, the local rise will be spread out over a larger region. This has two effects: i) the subsequent suppression of the prey at the position of the perturbation is less strong, since the predators moved away from where they were produced and ii) the prey population at nearby positions is reduced to below the steady state level by the predators that arrive from the site of the perturbation.

The aim of this section is to show that the interplay of dynamics/kinetics on the one hand, and undirected motion on the other, can lead to instability of a uniform steady state that is stable with respect to uniform perturbations. The implicit implication is that, by exchange of stability, stable patterns arise. To make this explicit one has to embark on a calculation of the direction of bifurcation, as in Lecture 7:8. Also see: Zhen Mei, Numerical Bifurcation Analysis for Reaction-Diffusion Equations, Springer, 2000

13.2 and Junping Shi's website : jxshix.people.wm.edu

13.1 Proof of concept : a general two dimensional system with the whole real line as the spatial domain

Consider

$$(13.1)\quad \begin{aligned} \frac{\partial u_1}{\partial t} &= d_1 \frac{\partial^2 u_1}{\partial x^2} + f_1(u_1, u_2) \\ \frac{\partial u_2}{\partial t} &= d_2 \frac{\partial^2 u}{\partial x^2} + f_2(u_1, u_2) \end{aligned} \qquad -\infty < x < \infty$$

and assume that

$$(13.2)\quad f_1(0,0) = 0 = f_2(0,0)$$

Let M denote the Jacobi matrix of f in $(0,0)$

$$(13.3)\quad m_{ij} := \frac{\partial f_i}{\partial x_j}(0,0) \qquad i,j = 1,2$$

Assume that $(0,0)$ is a stable steady state of the kinetic system $\dot{u} = f(u)$, i.e., assume that

$$(13.4)\quad \begin{aligned} \text{Trace } M &= m_{11} + m_{22} < 0 \\ \text{Det } M &= m_{11} m_{22} - m_{12} m_{21} > 0 \end{aligned}$$

Our key question is : how does the stability of the uniform steady state $(\bar{u}_1(x), \bar{u}_2(x)) = (0,0)$ of (13.1) depend on the two diffusion constants d_1 and d_2 ?

To find the answer, we first of all linearize (13.1) to

$$(13.5)\quad \frac{\partial v}{\partial t} = d \frac{\partial^2 v}{\partial x^2} + Mv$$

and next make the separation of variables Ansatz

$$v(t,x) = \psi(t)\,\phi(x)\,\bar{v} \tag{13.6}$$

where ψ and ϕ take values in $\mathbb{R}$ and $\bar{v} \in \mathbb{R}^2$. We find that we should focus on

$$\psi(t) = e^{\lambda t}$$

and on ϕ such that

$$-\phi'' = \mu\,\phi$$

resulting in the eigenvalue problem

$$(M - \mu d)\,\bar{v} = \lambda\,\bar{v} \tag{13.7}$$

NB μ here corresponds to μ^2 in Section 6.6 of syllabus_ch6.pdf

where μ is a positive parameter and λ the eigenvalue that has to be determined. The underlying idea is the following. Since, for the time being, we do not consider a bounded domain with no-flux boundary conditions, there is a continuum of μ-possibilities rather than a countable discrete set. But we require ϕ to be bounded on all of $\mathbb{R}$, so the solutions of the form

$$\phi(x) = c_+\, e^{\sqrt{-\mu}\,x} + c_-\, e^{-\sqrt{-\mu}\,x}$$

should be bounded, leading to the condition $\mu \geq 0$.

We are now able to give a sharper formulation of the key question: is it possible that (13.7) has a nontrivial solution $\bar{v}$ for some λ with $\mathrm{Re}\,\lambda > 0$ if we choose $\mu > 0$ suitably, given our assumption (13.4) that for $\mu = 0$ this is impossible? And more in particular: what are the conditions on d_1, d_2 for this to be possible? And on $m_{11}, m_{12}, m_{21}, m_{22}$?

So we should study how the position in the complex plane of the roots of the equation for λ

(13.8) $0 = \det(M - \mu d - \lambda I) = \lambda^2 + c_1(\mu)\lambda + c_2(\mu)$

depends on the parameter μ. Here

$$(13.9)\quad \begin{aligned} c_1(\mu) &= (d_1 + d_2)\mu - m_{11} - m_{22} \\ c_2(\mu) &= d_1 d_2 \mu^2 - (d_1 m_{22} + d_2 m_{11})\mu + m_{11}m_{22} - m_{12}m_{21} \end{aligned}$$

and already now we point out that, because of (13.4)

$$c_1(\mu) > 0$$

so destabilization by way of a Hopf bifurcation, i.e., a pair of complex roots moving from left half $\mathbb{C}$ plane to right half $\mathbb{C}$ plane when μ is increased, is not possible. As a function of real λ, the right hand side of (13.8) has a minimum in $\lambda = -\frac{1}{2}c_1(\mu) < 0$, so (13.8) has at most one real root that is positive and it does indeed have such a positive root iff the value of the right hand side for $\lambda = 0$ is negative. We conclude that

$$(13.10)\quad c_2(\mu) < 0$$

is both necessary and sufficient for (13.8) ~~having~~ to have a root in the right half plane. So the question boils down to: what are the conditions on d_1, d_2 for (13.10) to hold for an interval of positive μ values? Or, more precisely, the conditions on $d_1, d_2, m_{11}, m_{12}, m_{21}, m_{22}$ given the constraint (13.4)?

c_2 is a quadratic function of μ with minimum

$$(13.11)\quad c_2^{min} = m_{11}m_{22} - m_{12}m_{21} - \frac{1}{4}\frac{(d_1 m_{22} + d_2 m_{11})^2}{d_1 d_2}$$

for $\mu = \mu_{min}$ with

$$\mu_{min} = \frac{1}{2}\left(\frac{m_{11}}{d_1} + \frac{m_{22}}{d_2}\right) \tag{13.12}$$

By (13.4) we know that $c_2(0) > 0$. So, in order to be able to satisfy (13.10) for positive μ, we should have

$$\mu_{min} > 0 \quad \text{and} \quad c_2^{min} < 0 \tag{13.13}$$

Now recall the first condition in (13.4). Clearly we have that $\mu_{min} < 0$ if $d_1 = d_2 > 0$. Likewise $\mu_{min} < 0$ if m_{11} and m_{22} are both negative, so we should have $m_{11} m_{22} < 0$. But if $m_{11} m_{22} < 0$ and we want to satisfy the second condition of (13.4), we need to have that $m_{12} m_{21} < 0$ as well. So for the sign pattern of the matrix M we do have the following 4 possibilities:

$$\underset{(1)}{\begin{pmatrix} + & - \\ + & - \end{pmatrix}} \qquad \underset{(2)}{\begin{pmatrix} + & + \\ - & - \end{pmatrix}} \qquad \underset{(3)}{\begin{pmatrix} - & + \\ - & + \end{pmatrix}} \qquad \underset{(4)}{\begin{pmatrix} - & - \\ + & + \end{pmatrix}}$$

Exercise 1. Verify that (1) relates to (3) and (2) relates to (4) by a renumbering of the two "species", i.e., by the transformation $\begin{pmatrix} v_1 \\ v_2 \end{pmatrix} \mapsto \begin{pmatrix} v_2 \\ v_1 \end{pmatrix}$

Exercise 2. Verify that (1) relates to (2) and (3) to (4) by the transformation $\begin{pmatrix} v_1 \\ v_2 \end{pmatrix} \mapsto \begin{pmatrix} v_1 \\ -v_2 \end{pmatrix}$

<u>Exercise 3</u> Consider sign pattern (1). Show that the local phase portrait for the kinetic system is

meaning more precisely that, given (13.4) and the sign pattern:

– both isoclines are described by u_2 as an increasing function of u_1

– the 2-isocline defined by $f_2 = 0$ increases more steeply than the 1-isocline defined by $f_1 = 0$

– rotation is counter clockwise

<u>Exercise 4</u> Interpret the local phase portrait of the preceding exercise as telling us that peaks of $u_1 - \bar{u}_1$ are not far from peaks of $u_2 - \bar{u}_2$ and likewise valleys of the two deviations from steady state are "in-phase".

<u>Exercise 5</u> Show that for sign pattern (2) the local phase portrait looks like

and conclude that now both peaks as well as valleys are out-of-phase.
Next convince yourself that the transformation of Exercise 2 turns relative peaks into relative valleys and that, accordingly, the results of this exercise can also be derived from the results of the preceding exercise by way of this transformation.

<u>Terminology</u> We call $\begin{pmatrix} + & - \\ + & - \end{pmatrix}$ a pure activator-inhibitor system and $\begin{pmatrix} + & + \\ - & - \end{pmatrix}$ a cross activator-inhibitor system. In the pure case species 1 activates/promotes the growth of both ~~its~~ itself and species 2. In the cross case, species 1 activates itself and inhibits species 2, while species 2 inhibits itself but activates species 1. In the pure case species 2 inhibits both itself and species 1.

<u>Exercise 6</u> Assume that $\lambda = 0$ for a pure activator-inhibitor system. Show that the two components of the corresponding eigenvector have the same sign. Interpret this as a spatial variant of the result from Exercise 4. Next, do the same for a cross activator-inhibitor system and relate the result to Exercise 5. Explain how these observations can be used when trying to make inferences from an observed spatial pattern of two interacting variables.

<u>Remark</u> One often encounters statements like "Diffusive instability requires long range inhibition and short range activation". This reflects a rewriting of the condition $\mu_{min} > 0$ (recall (13.13) and (13.12)) in the form

$$\tau_1 d_1 < \tau_2 d_2$$

where d_i is the mean square displacement of species i and $\tau_1 = m_{11}^{-1}$, $\tau_2 = |m_{22}|^{-1}$ are the relaxation times of the two species when we ignore the interaction. So as already suggested in the introduction of this lecture, the inhibitor cannot locally control the activator, because it is too rapidly dispersed over too large a distance.

So far we focussed on the condition $\mu_{min} > 0$ in (13.13), but let us now take the condition $\varsigma_2^{min} < 0$ into account as well, so consider

$$\left(d_1 m_{22} + d_2 m_{11}\right)^2 > 4 d_1 d_2 \left(m_{11} m_{22} - m_{12} m_{21}\right)$$

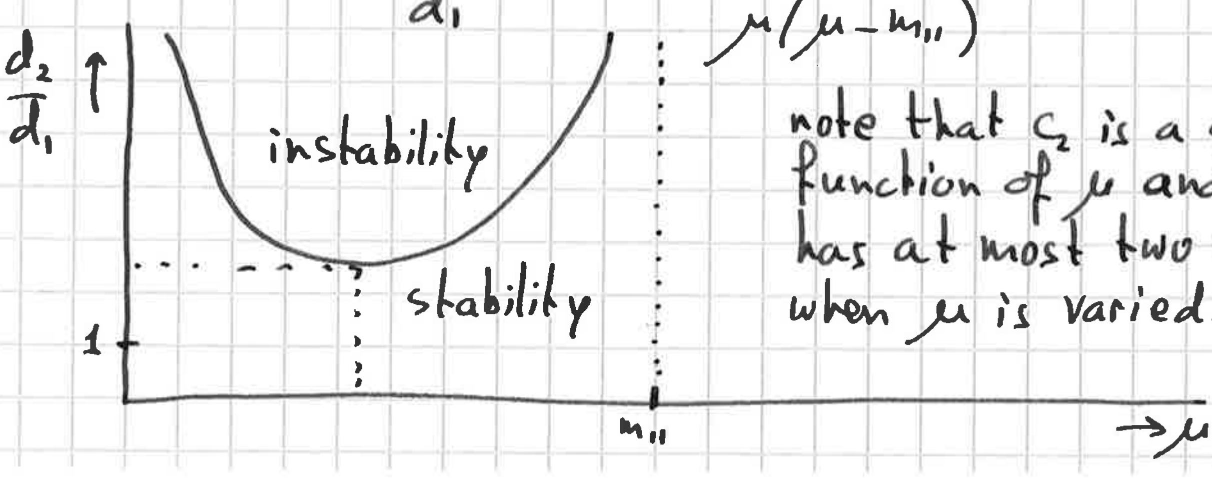
Note that, because of (13.4), the right hand side is positive, so we can take its square root and still have a real number. If $\mu_{min} > 0$ then $d_1 m_{22} + d_2 m_{11} > 0$ and we can rewrite the inequality as

$$(13.14) \qquad d_1 m_{22} + d_2 m_{11} > 2\sqrt{d_1 d_2 (m_{11} m_{22} - m_{12} m_{21})}$$

But if (13.14) holds then automatically $\mu_{min} > 0$ is satisfied. We conclude that (13.13) is equivalent to (13.14). Thus we answered the key question: if d and M are such that (13.14) holds, there exists an interval of positive μ values for which (13.7) has a nontrivial solution $\bar{v}$ for some $\lambda > 0$, while if (13.14) does not hold, we have $\operatorname{Re} \lambda \leq 0$ for every λ for which (13.7) has a nontrivial solution.

Much more insight can be obtained by depicting the μ-intervals for which ~~$\lambda > 0$ exists~~ (13.7) has an eigenvalue $\lambda > 0$ as a function of the ratio $\frac{d_2}{d_1}$ of the two diffusion coefficients. To do so, we first replace μ by μ/d_1, which amounts to a scaling of the spatial variable x such that the diffusion coefficient of the first species becomes 1 and that of the second d_2/d_1. Next recall (13.8) and (13.9): $\lambda = 0$ is an eigenvalue iff $c_2(\mu) = 0$. After the scaling of μ, we solve this equation for d_2/d_1, which is straightforward because d_2/d_1 occurs linearly. The result is

$$(13.15) \qquad \frac{d_2}{d_1} = \frac{m_{22}\mu - m_{11} m_{22} + m_{12} m_{21}}{\mu(\mu - m_{11})}$$



note that c_2 is a quadratic function of μ and therefore has at most two sign changes when μ is varied.

If we restrict to a <u>bounded</u> domain

$$0 \leq x \leq L$$

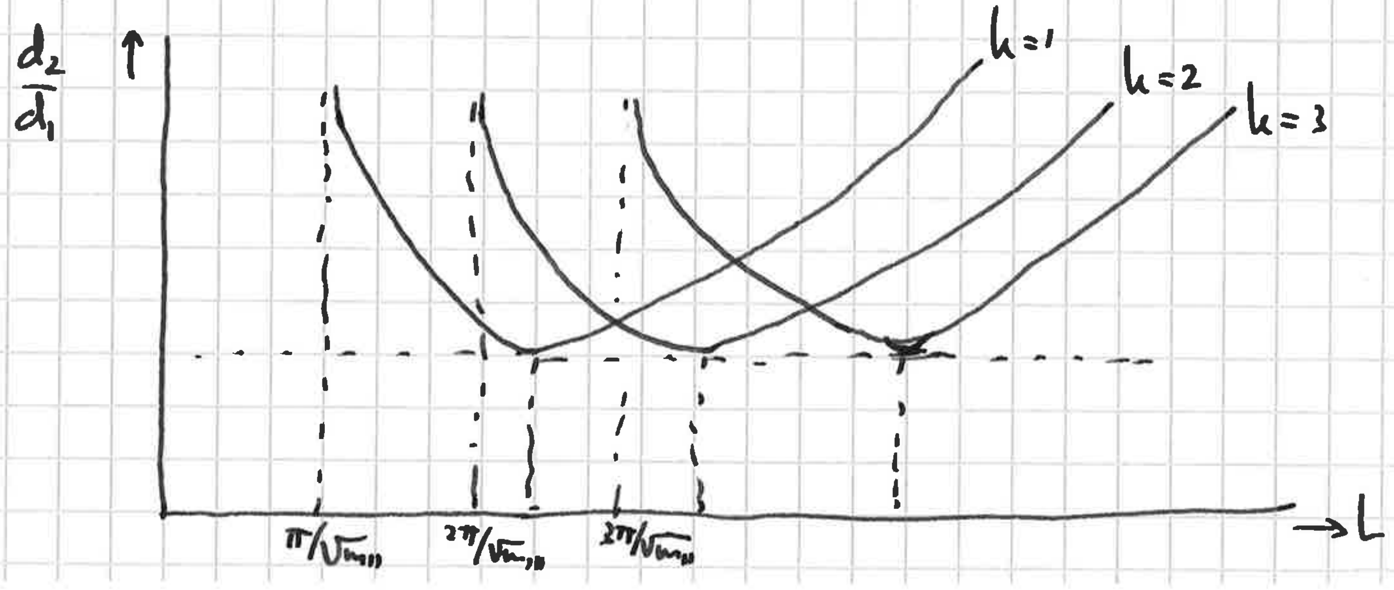
while imposing, for both components, no-flux boundary conditions

$$\frac{\partial u}{\partial x}(0) = 0 = \frac{\partial u}{\partial x}(L)$$

we find (since the function ϕ from page 13.3 should satisfy these boundary conditions), that μ is restricted to the countable discrete set

$$\mu = \mu_k = \frac{k\pi}{L} \qquad k = 1, 2, 3, \dots$$

(we ignore $k=0$ since (13.4) guarantees that the corresponding two-dimensional mode is stable). By viewing L as a parameter, ranging from 0 to ∞, we restore the continuous character. This allows us to "translate" the picture of the preceding page into a picture of the instability domain in the $(L, d_2/d_1)$ plane. Note that $\mu=0$ corresponds to $L=\infty$ and that the upperbound m_{II} on μ sets a lower bound on L. But more importantly: note that now each value of k yields a curve



and that these curves are identical if we scale L with a factor k.

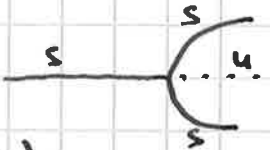
Note that if, for fixed d_2/d_1, we increase L, each mode will regain stability. If d_2/d_1 is slightly above the critical lower value that allows for instability, the constant steady state will in fact regain stability. And then, when L is further increased, lose it again. Etcetera. It is unclear what exactly this means for the (non)existence of nontrivial (i.e., non-uniform = not constant in space) solutions? But one can anyhow interpret the phenomenon as a kind of "resonance" of the natural wave length associated with the instability on the one hand, and the size of the domain on the other.

<u>Exercise 7</u> Recall Exercise 3 from 14novexercises.pdf as well as the exercise on pages 3.5 & 3.6 of lectures3:4.pdf (beware: k here corresponds to $k-1$ in that exercise). Do you agree that

i) branches of nontrivial solutions bifurcating from the trivial solution for various values of k are related to each other by a simple scaling of the spatial variable x, once we extend them from $[0,L]$ to $(-\infty,\infty)$ by a combination of reflection and periodic continuation?

ii) all bifurcations are of pitchfork type, with for (the present) k odd one branch providing the other by $x \mapsto L-x$ and for k even one branch providing the other by a shift over $L/2$

iii) <u>assuming</u> that the pitchfork bifurcation is

13.11/ supercritical 

it is unclear how in a "real" system one or the other of the two stable branches  versus  will be selected? (just random noise?)

<u>Exercise 8</u> Recall Exercise 1 from 14novexercises.pdf = Exercise 5.2.6 on page 47 of syllabus_chs.pdf. Consider a two-dimensional rectangular domain and enlarge it while keeping its shape, i.e., the <u>ratio</u> of the two lengths, fixed. How does the pattern that you expect to see depend on this ratio? Keep your answer in mind till your next visit to a zoo and then look for spotted bodies and striped tails!

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side remark

For interesting work on landscape patterns visit the web pages of

Ehud Meron bgu.ac.il

Max Rietkerk www.uu.nl/staff/MGRietkerk

The critical value of $\frac{d_2}{d_1}$, for which the interval of μ-values shrinks to a point, is determined by $c_2^{min} = 0$, with c_2^{min} given by (13.11). As this is a quadratic equation for d_2/d_1, there are two roots. Only one of these, viz.

$$(13.16) \quad \left(\frac{d_2}{d_1}\right)_{crit} = \frac{\det M - m_{12}m_{21} + 2\sqrt{-m_{12}m_{21}\det M}}{m_{11}^2}$$

satisfies the additional requirement that μ_{min}

defined by (13.12) is positive.

If we put $\quad \text{Trace } M = -\varepsilon_1 \quad , \text{Det } M = \varepsilon_2$

with $\varepsilon_1, \varepsilon_2 > 0$ and then let both ε_1 and ε_2 tend to zero, the corresponding critical ratio d_2/d_1 defined by (13.16) tends to one. This shows that the constraint on the ratio of the two diffusion coefficients is intimately related to the "size" of the eigenvalues of the Jacobi matrix for the kinetic system.

By rewriting the formula (13.12) for μ_{min} we obtain

$$(13.17) \qquad \mu_{crit} = \frac{1}{d_1} \; \frac{m_{11} (d_2/d_1)_{crit} + m_{22}}{2 \, (d_2/d_1)_{crit}}$$

and, recalling the formula for $\phi(x)$ on page 13.3, the mode $\sin(\sqrt{\mu}\, x)$ has <u>wavelength</u> (= spatial period)

$2\pi / \sqrt{\mu_{crit}}$ which Turing called the <u>chemical wavelength</u>

in A.M. Turing, The chemical basis of morphogenesis, Phil. Trans. Roy. Soc. Lond. B (1952) <u>237</u> : 37-72