3. Turing Space:

$$\partial_t u = f(u,v) + D_u \partial_x^2 u$$
$$\partial_t v = g(u,v) + D_v \partial_x^2 v.$$

→ work in system size L explicitly into dynamics (since change in L commonly encountered in development)

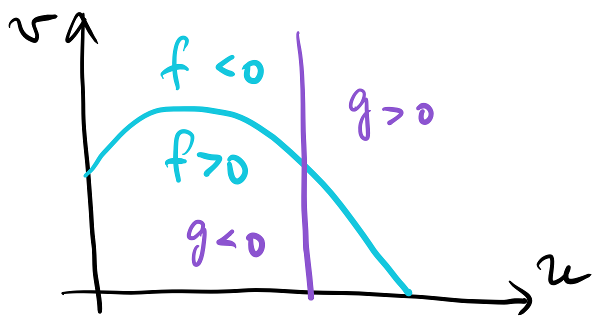
let $\xi = x/L$, $\tau = D_u t/L^2$; $\gamma = \frac{L^2}{D_u}$, $D = \frac{D_v}{D_u}$

then
$$\partial_\tau u = \gamma f(u,v) + \partial_\xi^2 u$$
$$\partial_\tau v = \gamma g(u,v) + D\,\partial_\xi^2 v$$
(will call ξ by x, τ by t)

Specific examples: requirement $f_u > 0 > g_v$

- predator-prey systems insufficient ($g_v = 0$).

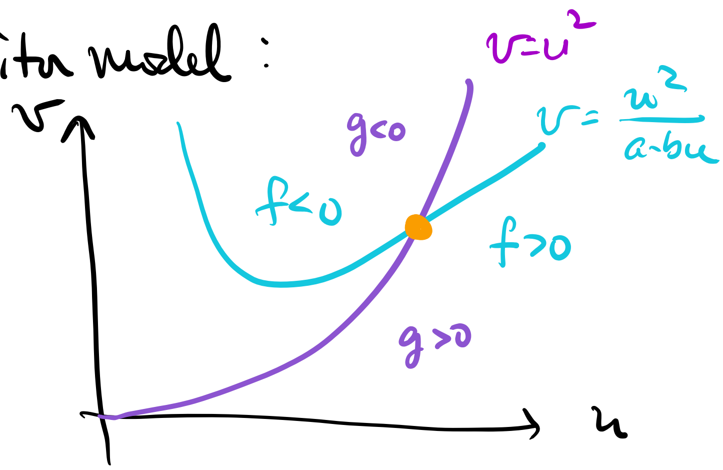
$$f(u,v) = u(1-u) - \frac{uv}{1+u/K}$$
$$g(u,v) = \left(\frac{1}{\eta}\frac{u}{1+u/K} - 1\right)\cdot v$$



- Meinhardt's activator-inhibitor model:

$$f(u,v) = a - bu + u^2/v$$
$$g(u,v) = u^2 - v$$

$f_u > 0$, $f_v < 0$
$g_u > 0$, $g_v < 0$ ok

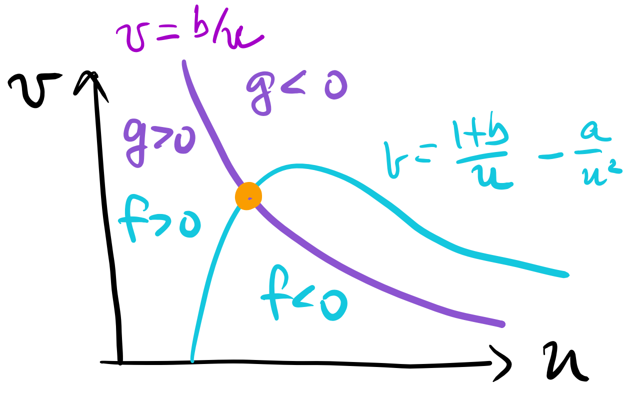


but mathematically cumbersome to analyze.

→ will use the "Brusselator" model: $\begin{cases} A \to B \\ 2A + B \to 3A \end{cases}$

$f(u,v) = a - (1+b)u + u^2 v$

$g(u,v) = bu - u^2 v$

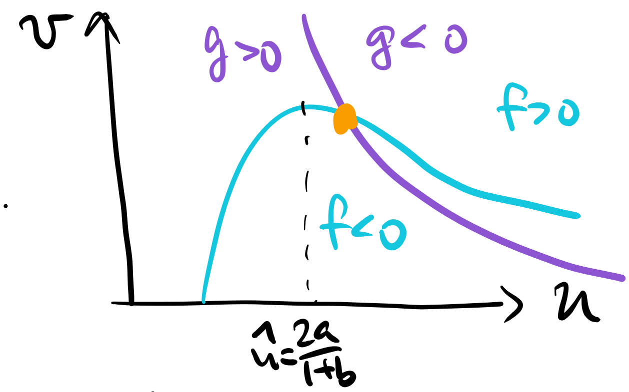


$f_u < 0 \quad f_v > 0$ no Turing

$g_u < 0 \quad g_v < 0$ Instability

$f_u > 0, \quad f_v > 0$ → Turing

$g_u < 0, \quad g_v < 0$ Instab.



(requires $u^* > \hat{u}$)

Explicitly compute:

$g = 0 \to v^* = b/u^* = b/a$

$f = 0 \to u^* = a$

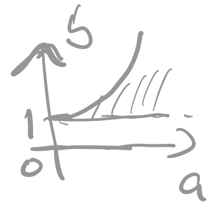
$f_u^* = -(1+b) + 2u^* v^* = b-1 \qquad f_v^* = (u^*)^2 = a^2$

$g_u^* = b - 2uv = -b, \qquad g_v^* = -u^2 = -a^2$

Note: Turing instability requires $f_u > 0 > g_v$
or $b - 1 > 0$

also, $\mathrm{Tr}\,M < 0$: $f_u + g_v < 0 \to b - 1 - a^2 < 0$

$\Rightarrow 1 < b < 1 + a^2$



* Search for parameter space where Turing instability occurs (= Turing space)

look at spatio temporal perturbation:

$$u(x,t) = u^* + \delta u\, e^{\lambda t} e^{ikx}$$

$$v(x,t) = v^* + \delta u\, e^{\lambda t} e^{ikx}$$

$$\lambda \begin{pmatrix} \delta u \\ \delta v \end{pmatrix} = \gamma \cdot \begin{pmatrix} b-1 & a^2 \\ -b & -a^2 \end{pmatrix} \begin{pmatrix} \delta u \\ \delta v \end{pmatrix} + \begin{pmatrix} -k^2 \delta u \\ -Dk^2 \delta v \end{pmatrix}$$

$$\left[\gamma(b-1) - k^2 - \lambda\right] \cdot \left[-\gamma a^2 - Dk^2 - \lambda\right] + \gamma^2 a^2 b = 0$$

$$\lambda^2 + \lambda\left((D+1)k^2 + \gamma a^2 - \gamma(b-1)\right)$$

$$+ Dk^4 - \gamma\left(D(b-1-a^2)\right)k^2 + \gamma^2 a^2 = 0 .$$

$$\lambda = -\frac{1}{2}\left[(D+1)k^2 + \gamma(a^2+1-b)\right] \cdot \left(1 \pm \sqrt{1-X}\right)$$

$$X = \frac{Dk^4 - \gamma\left(D(b-1) - a^2\right)k^2 + \gamma^2 a^2}{\frac{1}{4}\left[(D+1)k^2 + \gamma(a^2+1-b)\right]^2}$$

Turing instability: $X(k \neq 0) < 0$ (Small X)

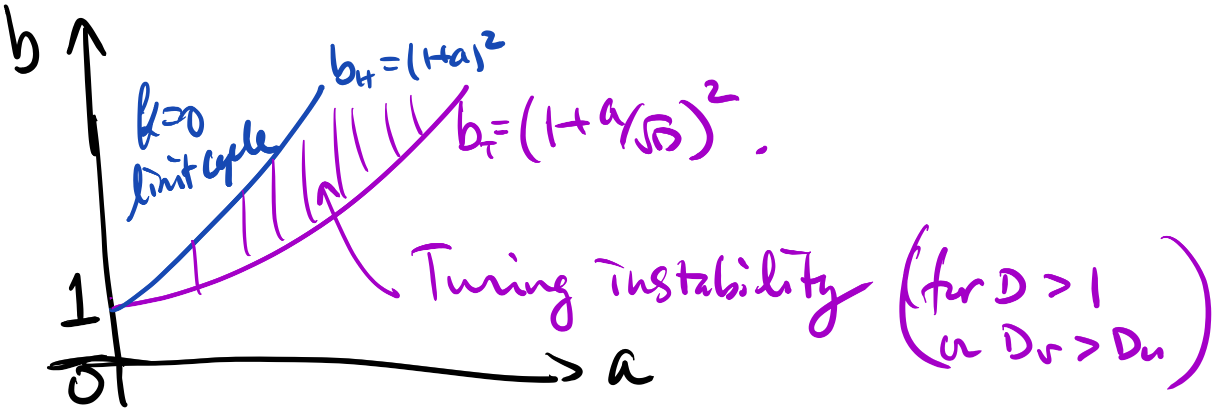
$$\left.\frac{dX}{dk}\right|_{k_T} = 0 \rightarrow 4Dk_T^3 - 2k_T\gamma\left[D(b-1) - a^2\right] = 0$$

$$k_T^2 = \frac{\gamma\left[D(b-1) - a^2\right]}{2D} ; \quad k_T^2 > 0 \rightarrow b > 1 + a^2/D$$

$$X(k_T) \leq 0 \rightarrow \frac{\cancel{\gamma^2}\left[D(b-1) - a^2\right]^2}{4D} \geq \cancel{\gamma^2} a^2$$

$$b-1 - a^2/D \geq 2a/\sqrt{D} . \rightarrow b \geq \left(1 + a/\sqrt{D}\right)^2 > 1 + \frac{a^2}{D}$$

or $$b-1 - a^2/D \leq -2a/\sqrt{D} \rightarrow b \leq \left(1 - a/\sqrt{D}\right)^2 < 1$$



[condition of Hopf bifurcation:
$f_u + g_v \geq 0$ or $b_H \geq 1 + a^2$]

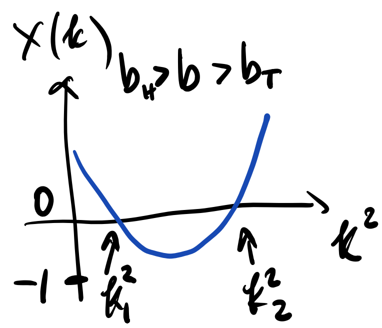
4. Mode Selection:

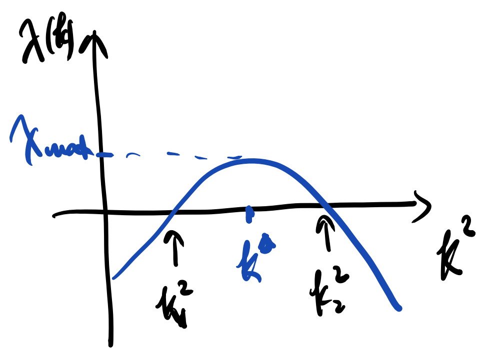
At the threshold of Turing instability,

$$k_T^2 = -\frac{\gamma}{2}\left[b_T - 1 - a^2/D\right] = \gamma a \sqrt{D}$$

- for $b_H > b > b_T$, $\lambda(k) > 0$ for a range $k_{T_1} < k < k_{T2}$

from $\lambda = -\frac{1}{2}\left[(D+1)k^2 + \gamma(a^2+1-b)\right]\cdot\left(1 \pm \sqrt{1 - X(k)}\right)$





$$X(k) = 0 \rightarrow Dk^4 + \gamma\left(D(1-b) + a^2\right)k^2 + \gamma^2 a^2 = 0$$

$$k^2 = \frac{\gamma}{2}\left[b - 1 - a^2/D\right] \pm \sqrt{\left(\frac{\gamma}{2}\left(b - 1 - a^2/D\right)\right)^2 - \gamma^2 a^2/D}$$

$$\sqrt{\cdots} = \sqrt{\left[\frac{\gamma}{2}\left(b-b_T+2\frac{a}{\sqrt{D}}\right)\right]^2-\gamma^2 a^2/D}$$

$$= \frac{\gamma}{2}\sqrt{(b-b_T)^2+4\frac{a}{\sqrt{D}}(b-b_T)}$$

$$k^2 = \frac{\gamma}{2}\left(\left(b-b_T+2a/\sqrt{D}\right)\pm\sqrt{4\frac{a}{\sqrt{D}}(b-b_T)+(b-b_T)^2}\right)$$

$$\simeq \gamma a/\sqrt{D} \pm \gamma\sqrt{(b-b_T)a/\sqrt{D}} \quad \text{for } b \gtrsim b_T.$$

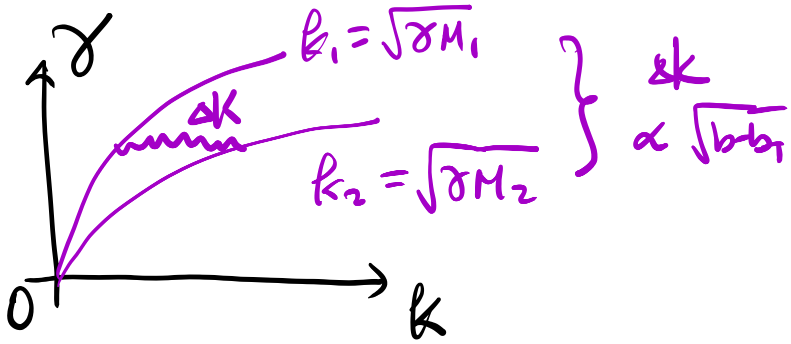
→ find range of unstable k for different $\gamma(L)$

let $k_1^2 = \gamma\cdot M_1$; $M_1 = \frac{1}{2}\left[\left(b-b_T+2a/\sqrt{D}\right)-\sqrt{\frac{4a}{\sqrt{D}}(b-b_T)+(b-b_T)^2}\right]$

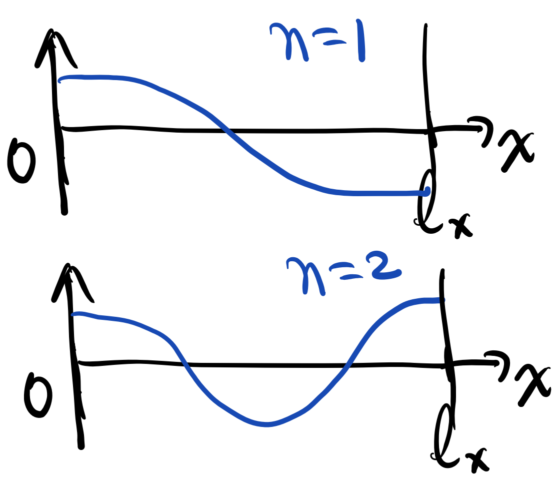
$k_2^2 = \gamma\cdot M_2$; $M_2 = \frac{1}{2}\left[\left(b-b_T+2a/\sqrt{D}\right)+\sqrt{\frac{4a}{\sqrt{D}}(b-b_T)+(b-b_T)^2}\right]$

range of unstable k:

$$\gamma\cdot M_1(a,b,D)\le k^2\le \gamma\cdot M_2(a,b,D)$$



allowed k over interval l_x:



suppose $\frac{\partial \rho}{\partial x}=0$ at both boundary

then $u(x,t)=\delta u\, e^{\lambda t}\cdot\cos\frac{n\pi x}{l_x}$

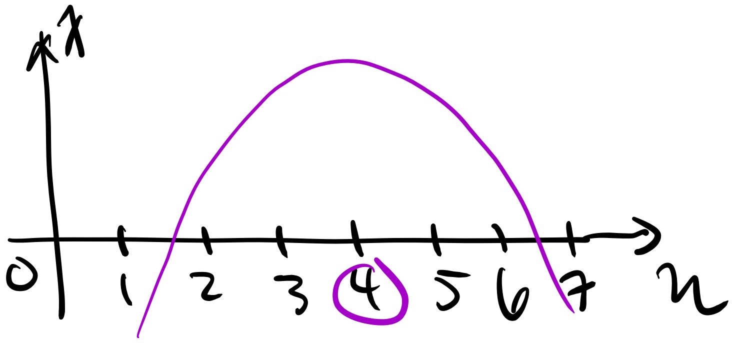
$$k=\frac{n\pi}{l_x},\quad n=\pm1,\pm2,\ldots$$

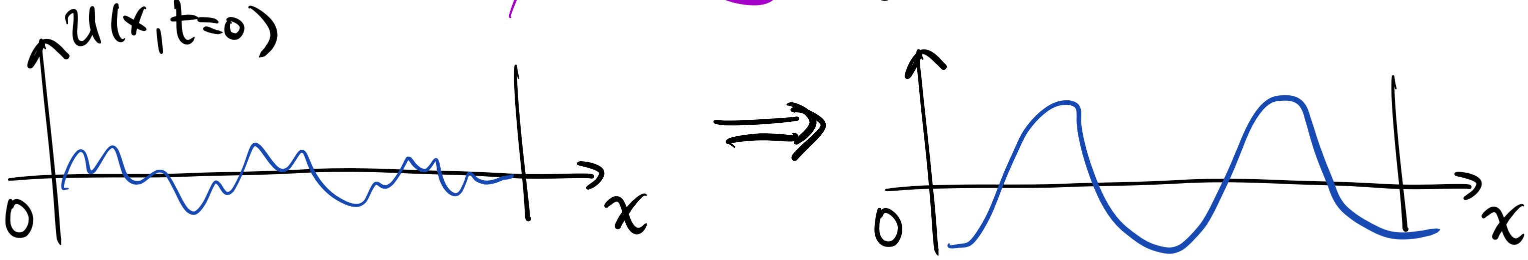
$$\gamma M_1 \le \left(\frac{n\pi}{l_x}\right)^2 \le \gamma M_2$$

unstable mode: $\frac{l_x}{\pi}k_1 \le n \le \frac{l_x}{\pi}k_2$

⇒ for large δk, large L (discreteness effect negligible)
most unstable mode k^* where $\lambda(k^*)$ is maximum
dominates if starting from random init cond.

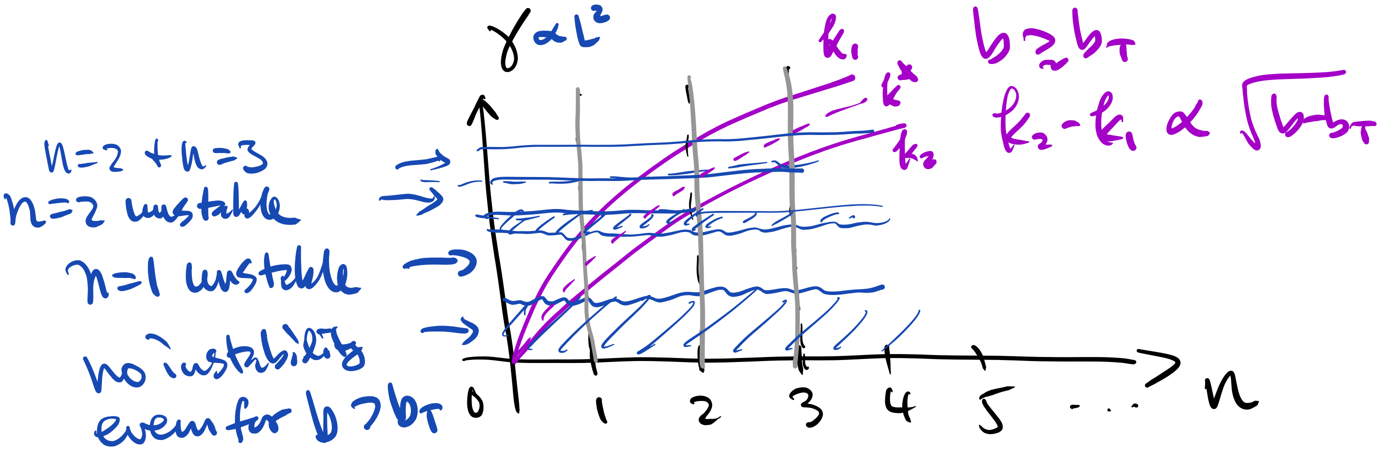
since $u(x,t) = e^{\lambda(k)t} \cos kx$





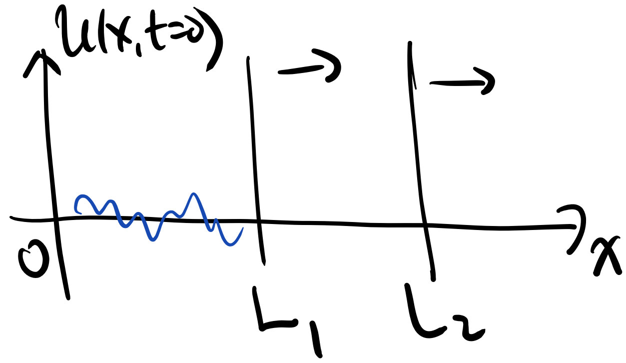
→ stabilized by higher order nonlinearity (later)

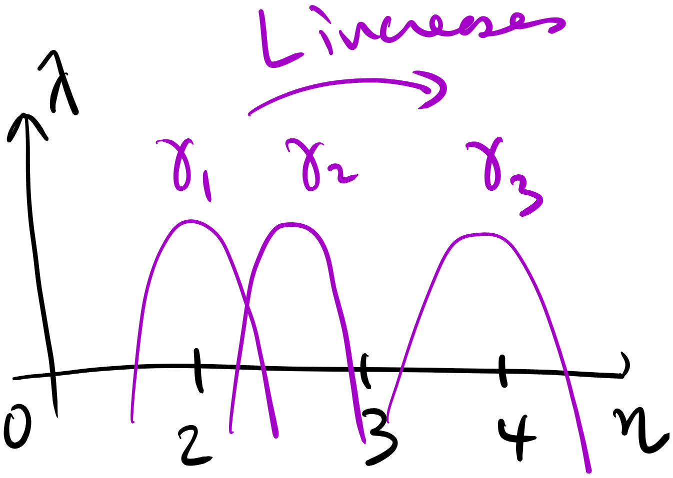
⇒ discreteness important for small systems w/ $b \gtrsim b_T$

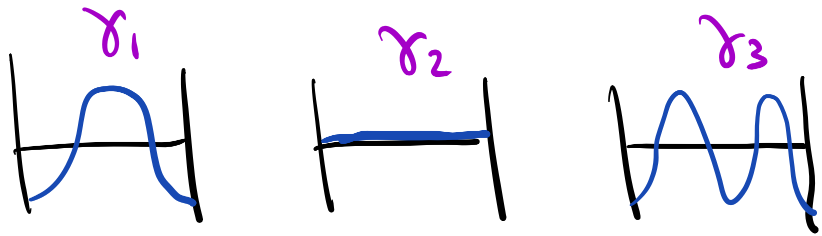


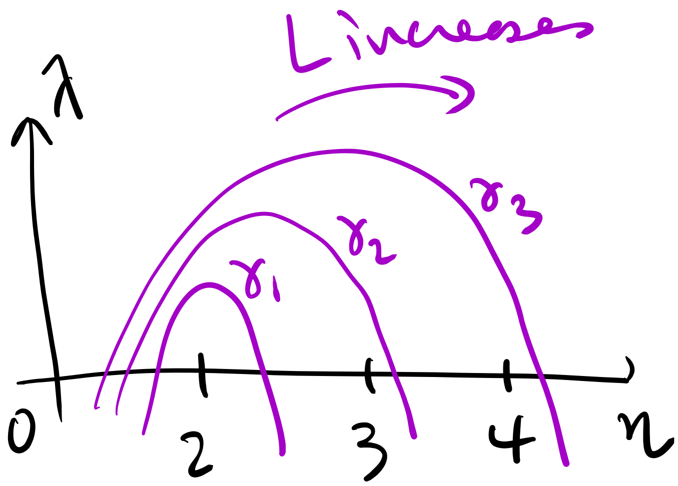
⇒ as length scale ($\gamma \sim L^2$) is increased,
more and more modes become unstable

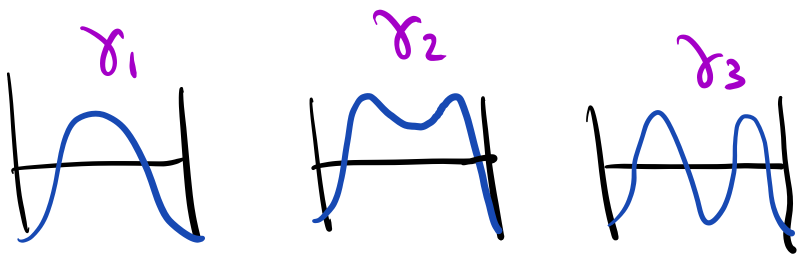
Domain growth:











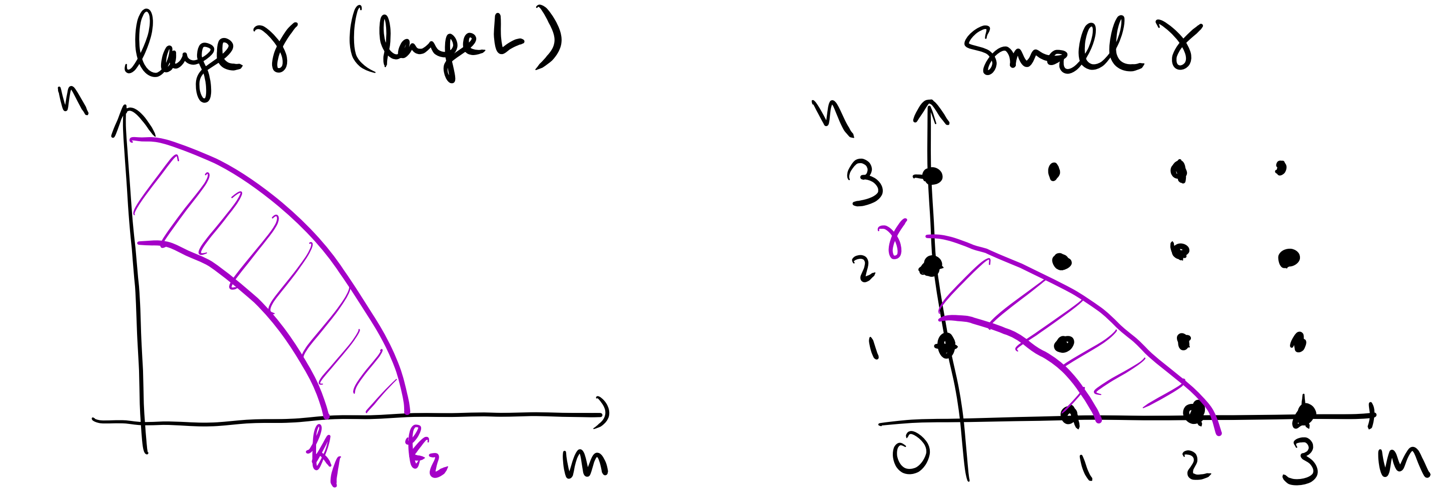
Many biological applications

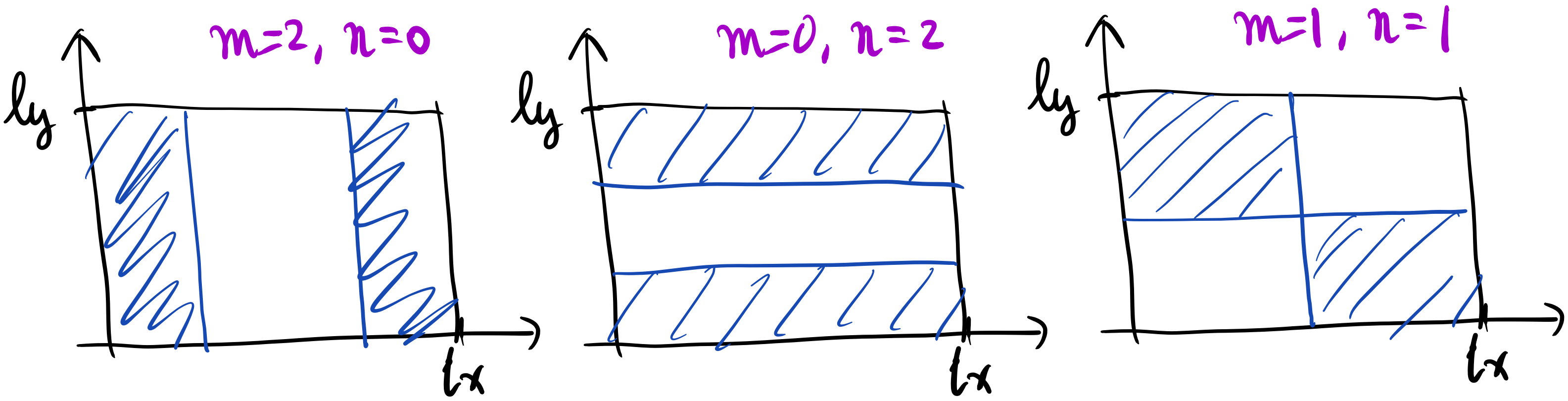
* 2d patterns:

Same condition for instability: $\gamma M_1 < k^2 < \gamma M_2$

but for $u(x,y) \sim \cos\frac{m\pi x}{l_x} \cdot \cos\frac{n\pi y}{l_y}$

$$k^2 = \left(\frac{m\pi}{l_x}\right)^2 + \left(\frac{n\pi}{l_y}\right)^2$$





other tesselation pattern, e.g. hexagonal.

$$u(x,y) \sim \cos kx + \cos k\left(\frac{x}{2} + \frac{\sqrt{3}}{2}y\right) + \cos k\left(\frac{\sqrt{3}}{2}y - \frac{x}{2}\right)$$

$\Rightarrow$ regular array of spots

(e.g. hair follicles, spot coating, ...)

or combinations of stripes and spots.

$\Rightarrow$ pattern selection depends on nonlinear terms which stabilizes linear instability