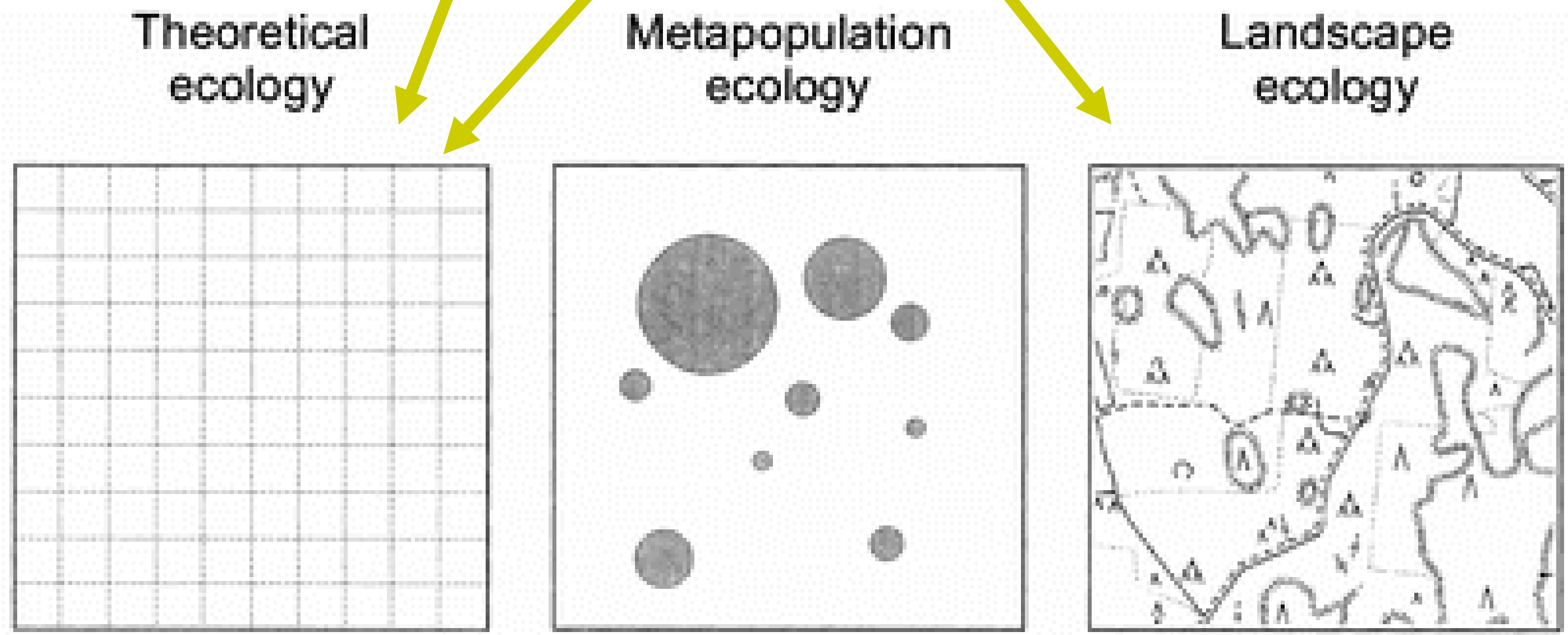
Spatial Ecology:
Lecture 3, Reaction-diffusion models: spatial patterns

II Southern-Summer school on Mathematical Biology

Christina Cobbold (University of Glasgow)

Overview

- Periodic Travelling waves
- Pattern formation



Periodic travelling waves

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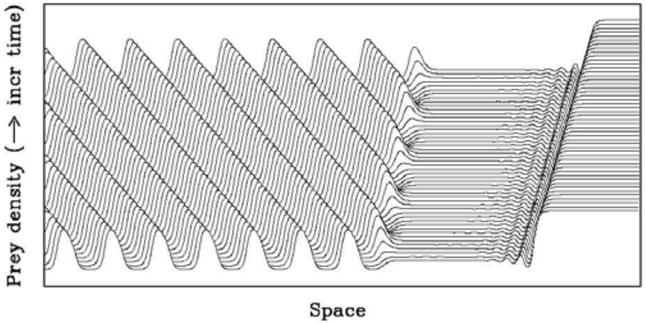
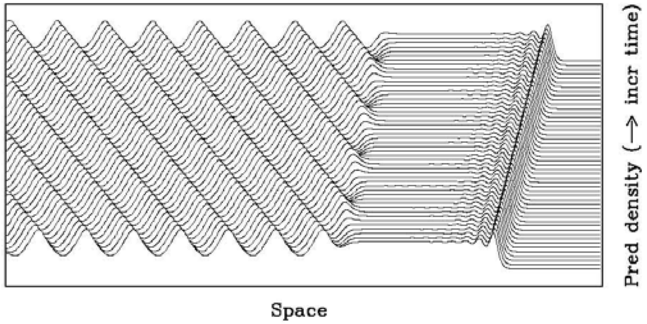
- A: Periodic Travelling Waves (PTW) can form.
- Q: What are periodic travelling waves?
- A: Like the ‘Waves of cheering’ you see in crowds in a soccer stadium.

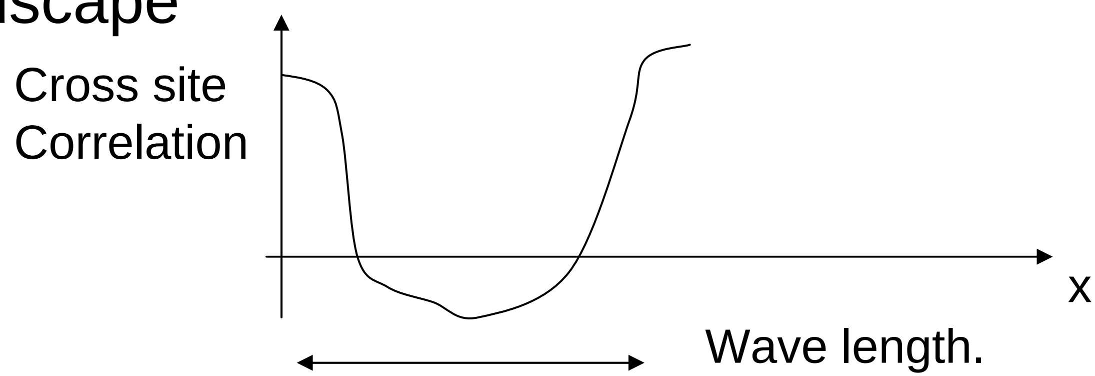




Examples of PTW in nature

- Fennoscandian voles
- Field voles in Kielder forest (UK)
- Larch budmoth in the European Alps
- Autumnal moth in Northern Norway

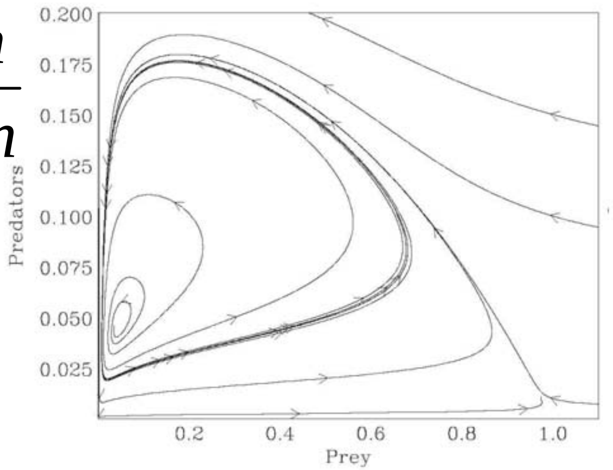
- Spatial-temporal patterns in cyclic populations are characterised by the way synchrony in population dynamics change cross a landscape



Predator-prey model

$$\frac{dh}{dt} = rh\left(1 - \frac{h}{h_0}\right) - \frac{ckph}{1+kh}$$

$$\frac{dp}{dt} = \frac{akp}{1+kh} - bp$$



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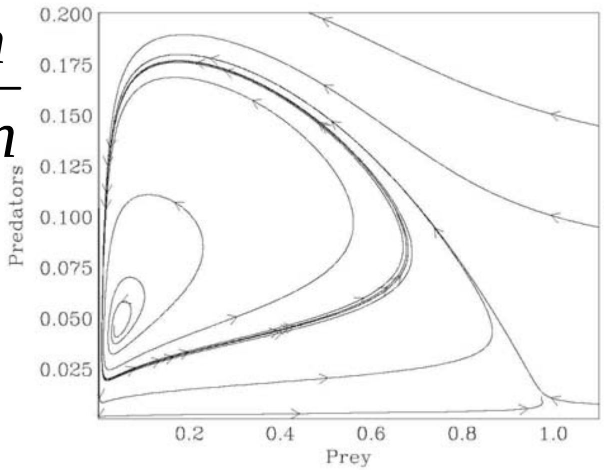

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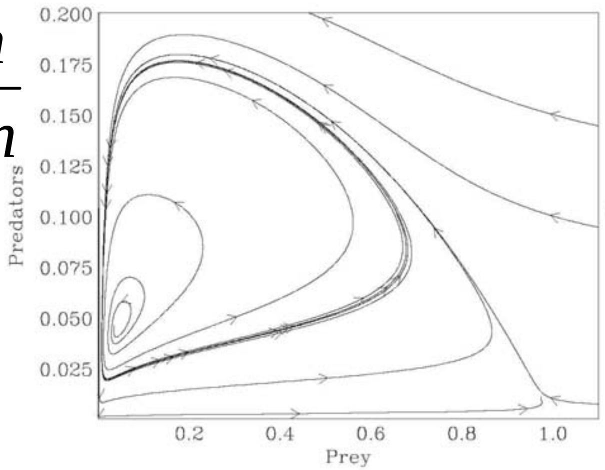

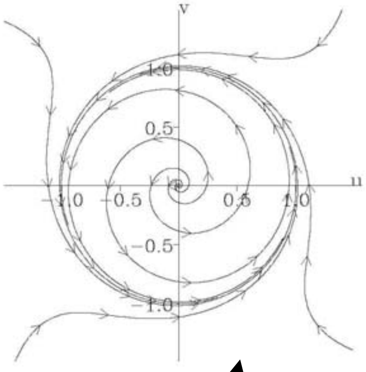

- Linearise about coexistence equilibrium and examine the behaviour close to the hopf bifurcation.
- Change variables so that the cycle is a circle in the transformed phase space – convert to Normal Form.

Lambda-Omega system

$$\frac{du}{dt} = \lambda(r)u - \omega(r)v$$

$$\frac{dv}{dt} = \omega(r)u + \lambda(r)v$$

where, $\lambda(r) = 1 - r^2, \quad \omega(r) = \omega_0 + \omega_1 r^2$

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- Change to polar coordinates $r = \sqrt{u^2 + v^2}, \quad \theta = \tan^{-1}(v/u)$

$$\frac{dr}{dt} = r\lambda(r), \qquad \frac{d\theta}{dt} = \omega(r)$$

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- One solution of this equation is the limit cycle: $r = R, \quad \theta = \theta_0 + \omega(R)t$
- Limit cycle has radius R=1, frequency ω(R)

Adding space: random movement

- We require diffusion constants $D_h = D_p$ for the analysis close to the limit cycle to work. Scale space such that $D_h = D_p = 1$.

$$\frac{\partial u}{\partial t} = \lambda(r)u - \omega(r)v + \frac{\partial^2 u}{\partial x^2}, \qquad \frac{\partial v}{\partial t} = \omega(r)u + \lambda(r)v + \frac{\partial^2 v}{\partial x^2}$$

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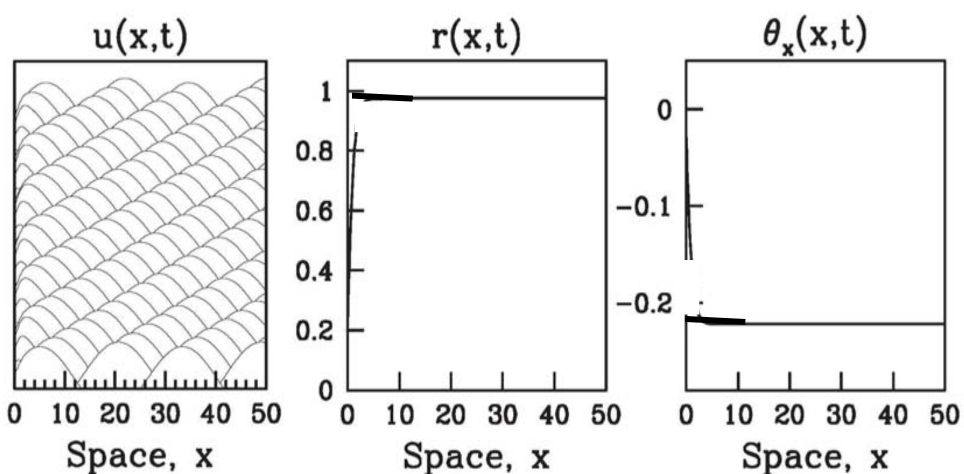
- Change to polar coordinates:

$$\begin{aligned} r_t &= r_{xx} - r\theta_x^2 + r(1-r^2) \\ \theta_t &= \theta_{xx} + 2r_x\theta_x/r + \omega_0 - \omega_1 r^2. \end{aligned}$$



Looking for PTW solutions

- In polar form the PTW is: $r = R, \quad \theta = \sigma t - kx$
- Substituting into the PDE gives: $\sigma = \omega(R), \quad k^2 = \lambda(R)$

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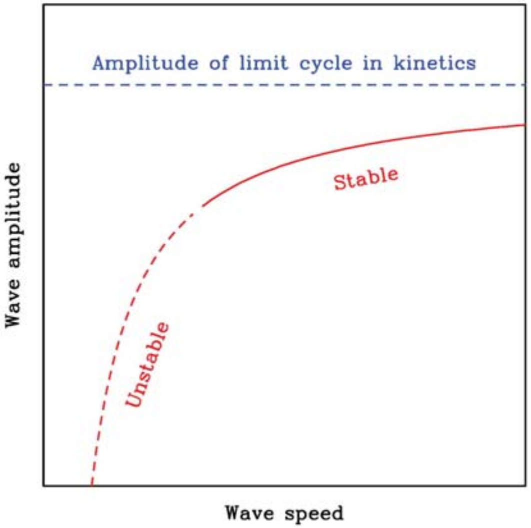
- So the 1-parameter (R) family of solutions is :

$$u = R\cos\left[\omega(R)t \pm \sqrt{\lambda(R)}x\right], \qquad v = R\sin\left[\omega(R)t \pm \sqrt{\lambda(R)}x\right]$$

  - Wave speed $c = \dfrac{\sigma}{k} = \dfrac{\omega(R)}{\sqrt{\lambda(R)}}$
  - Period in time $\dfrac{2\pi}{\sigma}$
  - Period in space $\dfrac{2\pi}{k}$

PTW stability and wave selection

- **Infinite domain:** Koppel & Howard (1973)



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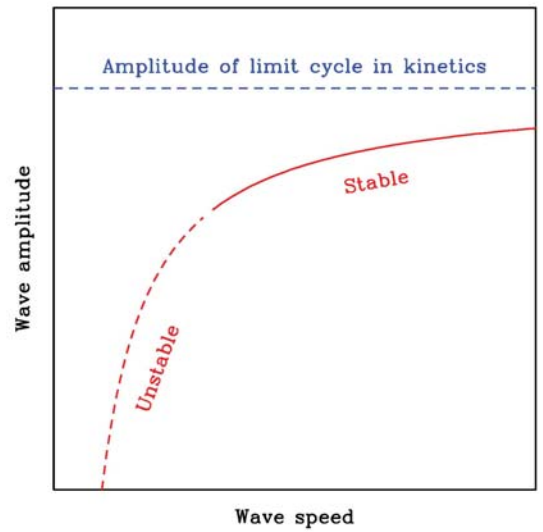
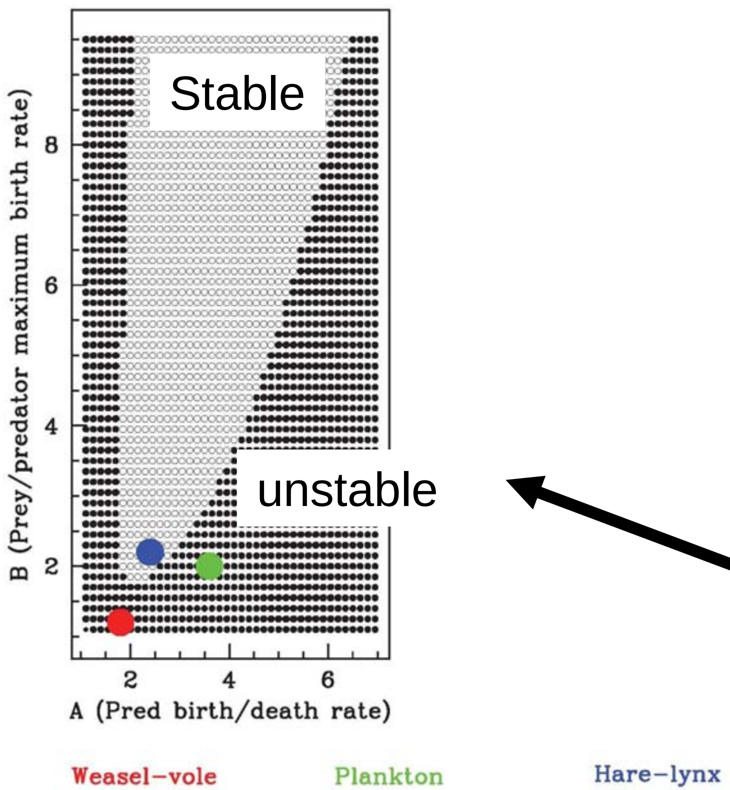




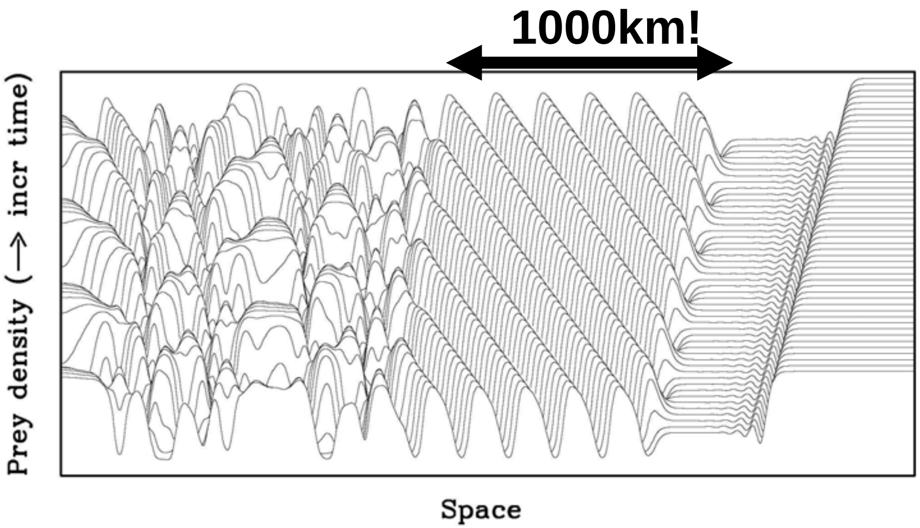
Mechanisms of wave generation and selection

- Invasion
- Boundary conditions

Jonathan Sherratt (Herriot-Watt)

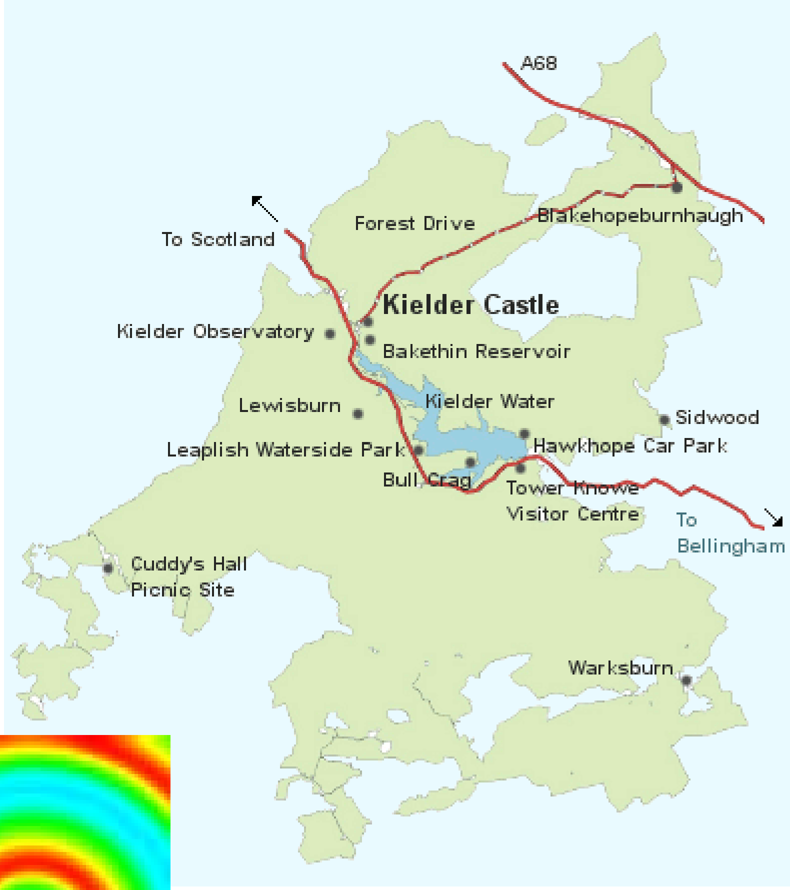
Field voles

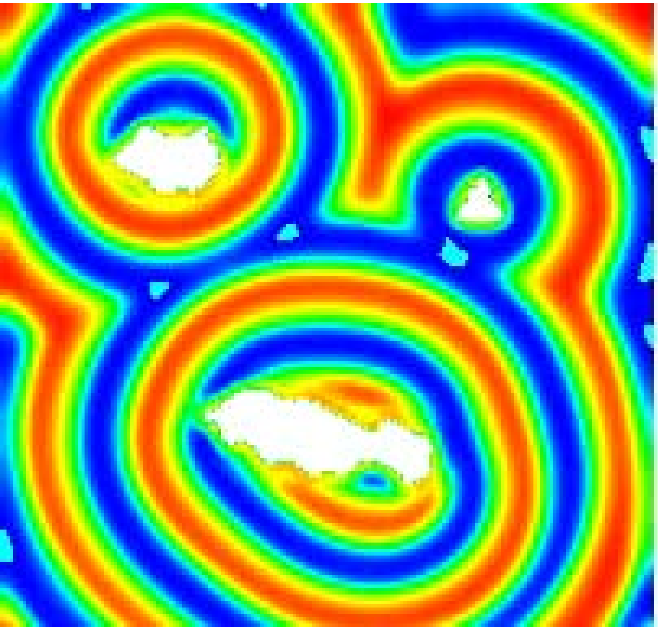
- Experiments: Wave length in Keilder Forest 56-76km; Wave speed 14-19 km/year
- Size of Keilder forest = 30km. So wavelength larger than forest
- Bandwidth of unstable PTW is also a lot larger than Keilder forest, so we could observe PTWs



PTW generation by boundaries

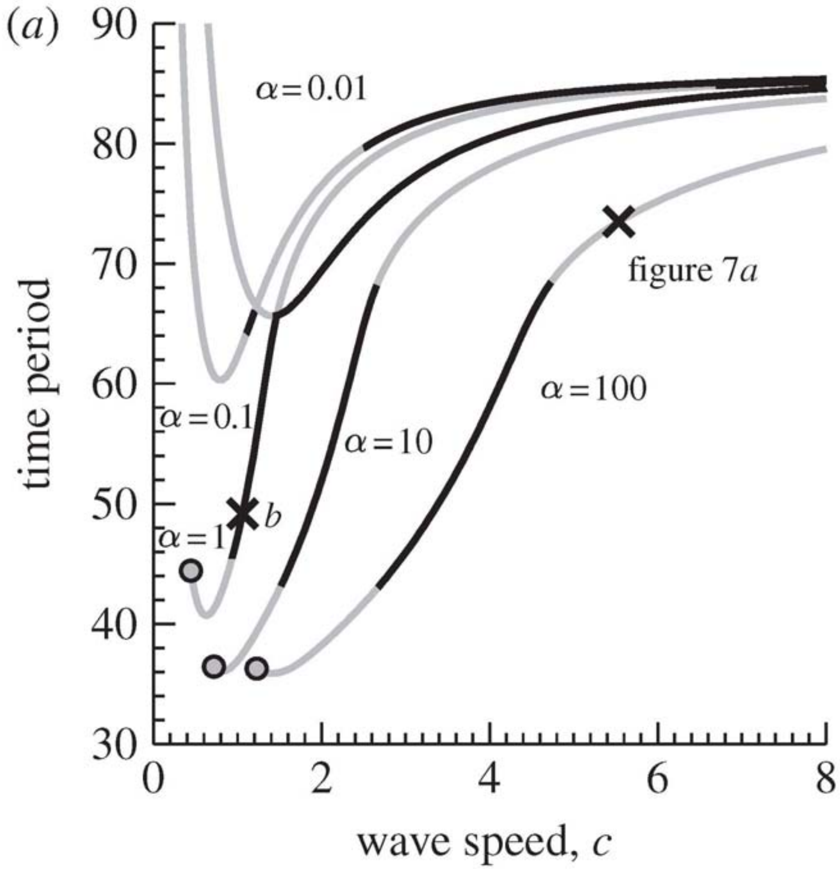
- Each obstacle generates waves, but those from the largest dominate.





BCs:
•Hostile at lake edges
•Zero flux at the Domain edges

Unequal diffusion coefficients

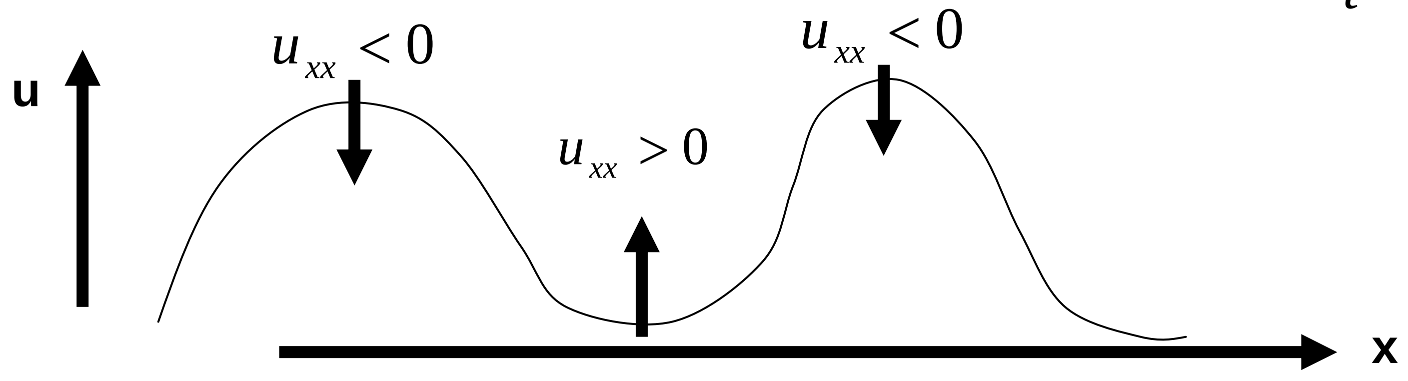


- Diffusion coefficients can significantly change the properties the periodic travelling wave.

- $\alpha = D_u / D_v$
- Grey lines: Stable waves
- Black lines: Unstable waves

Pattern formation

- Generally diffusion plays a role of increasing stability $u_t = u_{xx}$



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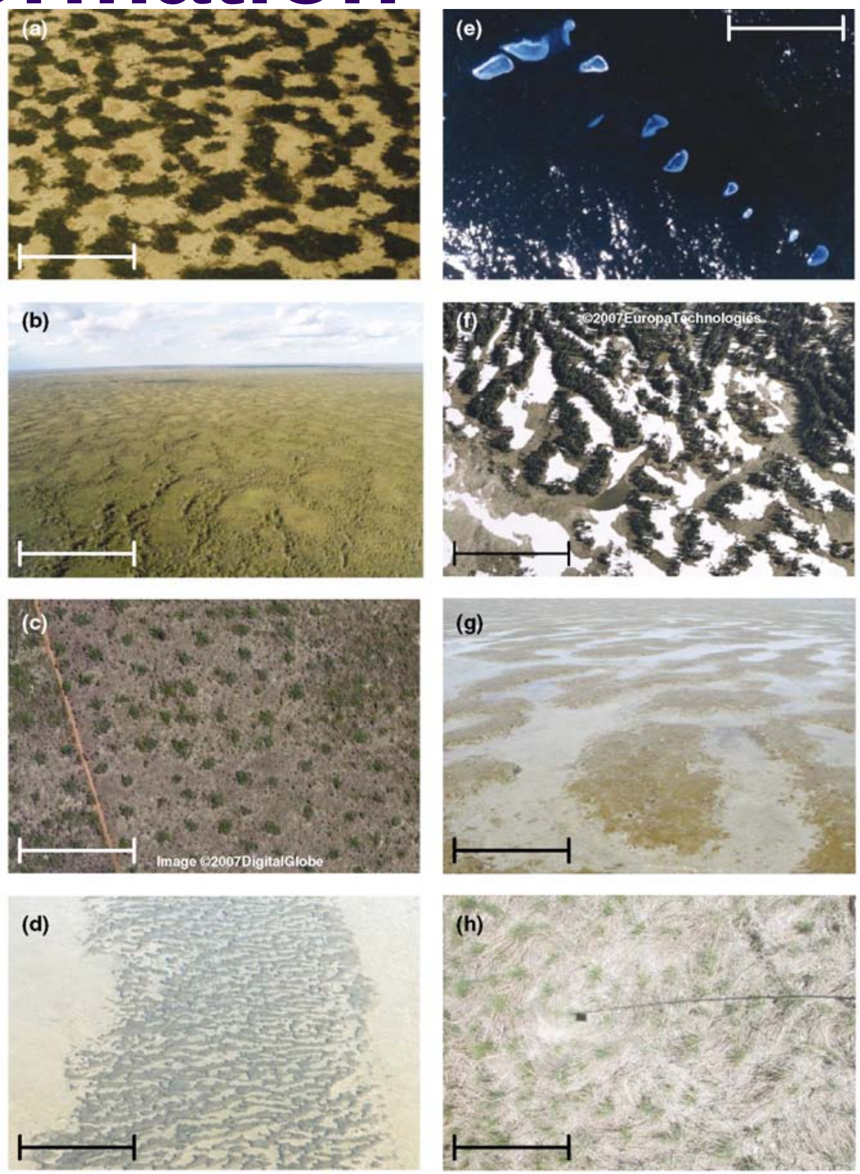

Labyrinth pattern in busy vegetation in Niger

Coral reef islands in Australia

Regular maze patterns of shrubs and trees in Siberia

Striped pattern of tree lines and snow deposition USA

Spotted pattern Of isolated trees in Niger

Labyrinth pattern of marine benthic diatomes

Patterned mussel bank in the Netherlands

Regular spaced Tussocks of the Sedge *Carex stricta*

Pattern formation

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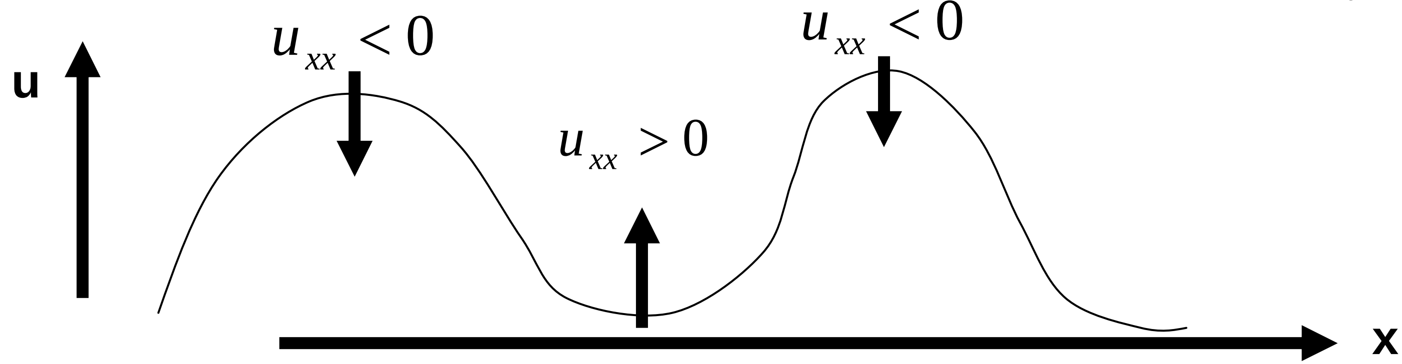
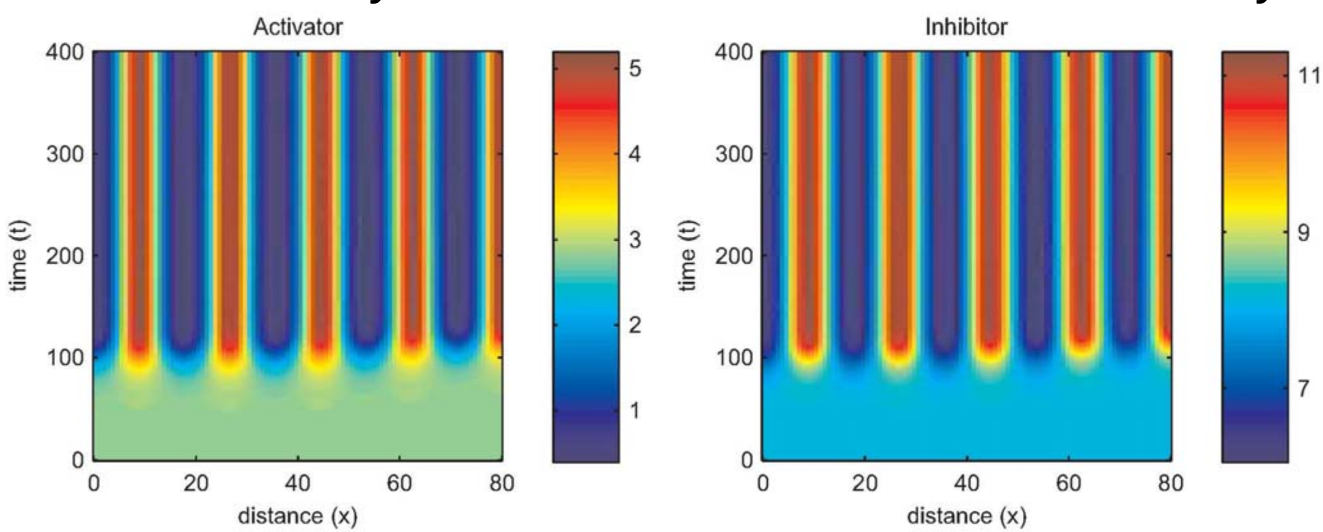


- BUT, this is not always the case: ‘Diffusion driven instability’



General idea in 1-D

$$\frac{\partial u}{\partial t} = D_1 \frac{\partial^2 u}{\partial x^2} + F(u,v), \qquad \frac{\partial v}{\partial t} = D_2 \frac{\partial^2 u}{\partial x^2} + G(u,v)$$

- Assume there exists a spatially uniform positive equilibrium (u*,v*). i.e. F(u*,v*)=G(u*,v*)=0, which stable in the absence of diffusion.
- The Jacobian associated to the linearisation about this equilibrium is

$$J = \begin{bmatrix} F_u & F_v \\ G_u & G_v \end{bmatrix}$$

- So stability means $F_u + G_v < 0$ and $F_u G_v - F_v G_u > 0$

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- So stability means $F_u+G_v<0$ and $F_u G_v - F_v G_u>0$
- A stable ecosystem that is perfectly homogeneous would continue indefinitely to be homogeneous.
- In practice irregular and stochastic fluctuations in population size and the environment continuously introduce small local perturbations.

Stability of the local perturbations

- Linearise the PDE about the equilibrium

$$\frac{\partial}{\partial t}\begin{bmatrix} u \\ v \end{bmatrix} = \frac{\partial}{\partial x^2}\begin{bmatrix} D_1 u \\ D_2 v \end{bmatrix} + \begin{bmatrix} F_u & F_v \\ G_u & G_v \end{bmatrix}\begin{bmatrix} u \\ v \end{bmatrix}$$

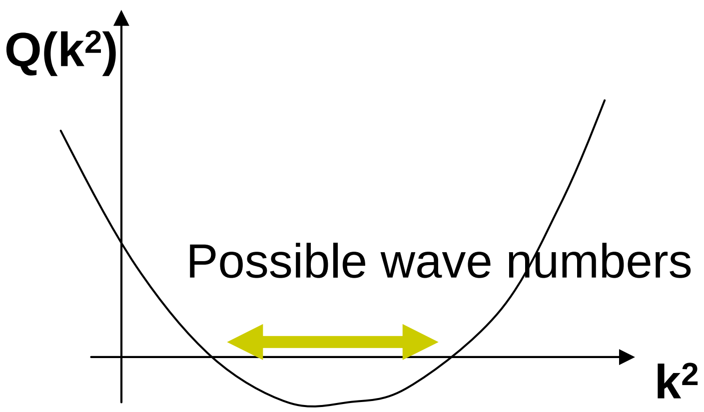
- Look for solutions of the form $\begin{bmatrix} u(x,t) \\ v(x,t) \end{bmatrix} = \begin{bmatrix} u_0 \\ v_0 \end{bmatrix}\cos(kx)\exp(\lambda t)$

$$\begin{bmatrix} 0 \\ 0 \end{bmatrix} = \begin{bmatrix} F_u - k^2 D_1 - \lambda & F_v \\ G_u & G_v - k^2 D_2 - \lambda \end{bmatrix}\begin{bmatrix} u_0 \\ v_0 \end{bmatrix}$$

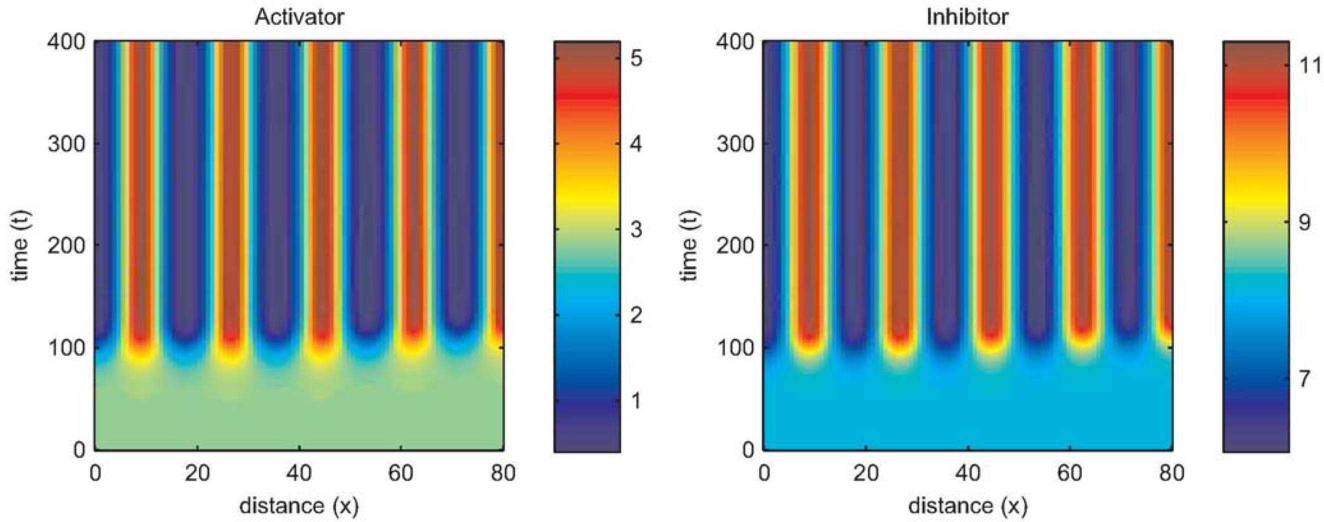
- Q: What is the frequency of growing perturbations?
- We want non-zero solutions (u_0,v_0). So we have an eigenvalue problem. Perturbation growth means $\lambda>0$. This occurs if

$$Q(k^2) = \det\begin{bmatrix} F_u - k^2 D_1 & F_v \\ G_u & G_v - k^2 D_2 \end{bmatrix} < 0$$

Observed patterns

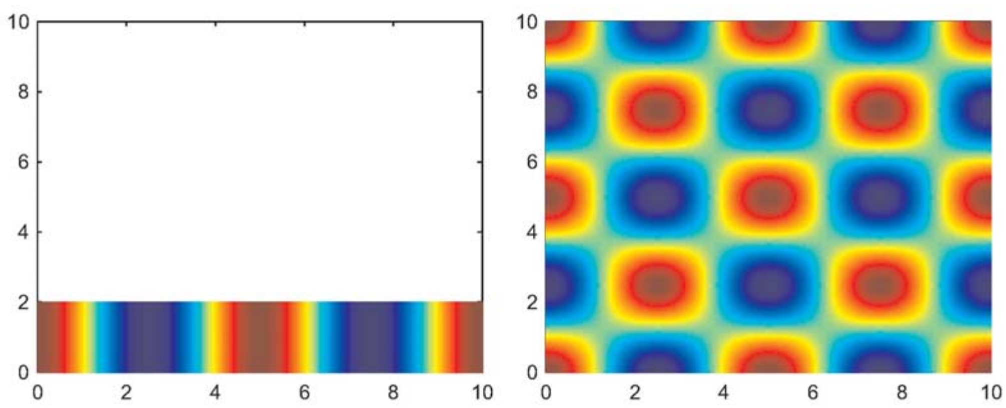


- k_c satisfies $Q((k_c)^2)=0$ are the first perturbations to grow in an infinite spatial domain, and this is what we observe.



2-D bounded domain

- In a finite domain, boundary conditions select the wavelength of the pattern that is observed.
- In 2-D domain geometry also determines the wavelength of the observed patterns.



Interpreting the pattern formation conditions

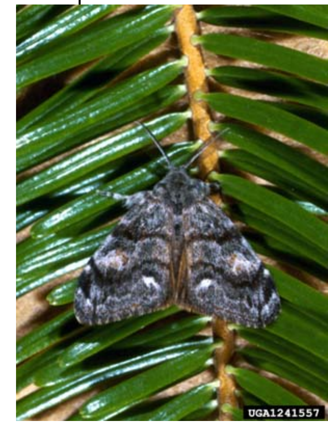
- The sign structure of the Jacobian of the non-spatial model much have the following sign structure

$$\boldsymbol{J} = \begin{pmatrix} + & + \\ - & - \end{pmatrix} \text{ or } \begin{pmatrix} + & - \\ + & - \end{pmatrix} \text{ or } \begin{pmatrix} - & - \\ + & + \end{pmatrix} \text{ or } \begin{pmatrix} - & + \\ - & + \end{pmatrix}.$$

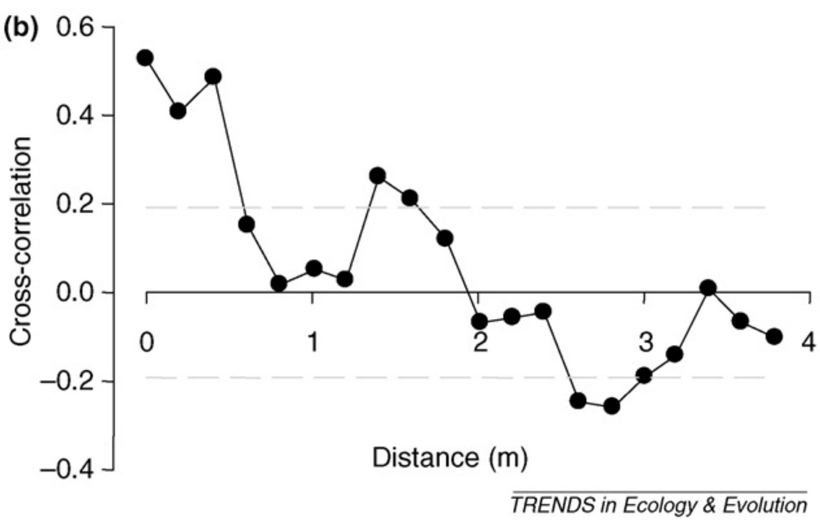
Positive feedback Activator-Inhibitor Positive feedback Activator-Inhibitor

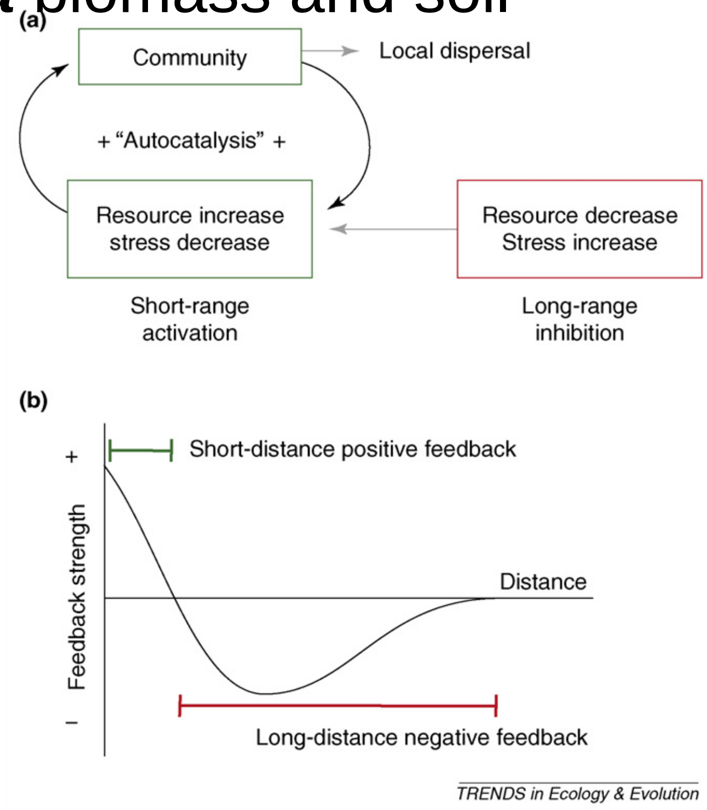
- Without loss of generality let $F_u>0$ then for pattern formation we require $D_2> D_1$, v disperses further than v.
- We **cannot** get pattern formation in a **competition model**, as the off diagonal entries of J have the same sign.

Examples in nature



- Outbreaks of ***Douglas fir tussock moths*** remain spatially restricted despite the widespread and continuous availability of their abundant host plant
- Cross correlation of ***Carex stricta*** biomass and soil moisture





A general predator-prey model

$$\frac{\partial}{\partial t}\begin{bmatrix} u \\ v \end{bmatrix} = \frac{\partial}{\partial x^2}\begin{bmatrix} D_1 u \\ D_2 v \end{bmatrix} + \begin{bmatrix} f(u)u & -r(u)uv \\ \kappa r(u)uv & -g(v)v \end{bmatrix}$$

$$J = \begin{bmatrix} f'(u)u - r'(u)uv & -r(u)u \\ \kappa r'(u)uv + \kappa r(u)v & -g'(v)v \end{bmatrix}$$

- If g(v)=constant then G_u=0 so no patterns, so g(v) must depend on v and g'(v)>0 *(density dependent mortality of the predator)*
- If r(u)=constant then we also require f'(u)>0 (e.g. an Allee effect in the prey)
- If f'(u)<0 (e.g. logistic) then we need r'(u)<0 (saturation predation rate)

Key ingredients for pattern formation

1. Predator disperses faster than the prey
2. At low densities, an increase in prey leads to an increase in net rate of prey population growth
   - Prey population growth is autocatalytic (e.g. Allee effect)
   - Increase in prey leads to a decrease in per capita predation risk (e.g. Type II functional response and density-dependent predator mortality)
3. Increase in predator density leads to a decrease in prey and predator growth (e.g. Generally holds for predator-prey systems)

Other types of movement

- Predator aggregation toward prey can either *promote* (aggregation increase predator response to prey) or *prevent* (predator rapidly aggregates to control prey) pattern formation
- Pattern formation in competitive systems requires two competitors to avoid each other
- In a single species system non-local aggregation is needed.

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