Spatial Ecology:

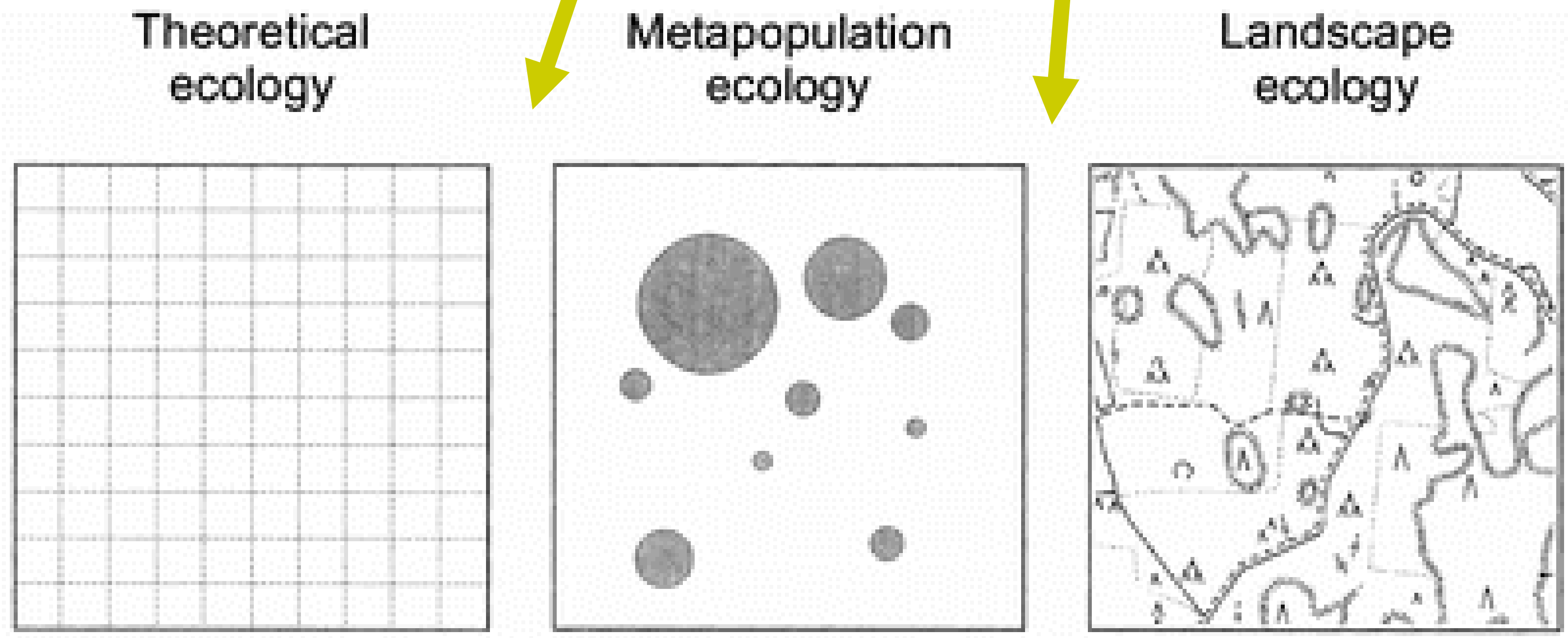
Lecture 2, Reaction-diffusion models: invasion and persistence

II Southern-Summer school on Mathematical Biology

Christina Cobbold (University of Glasgow)

Lecture 2

Lecture 1



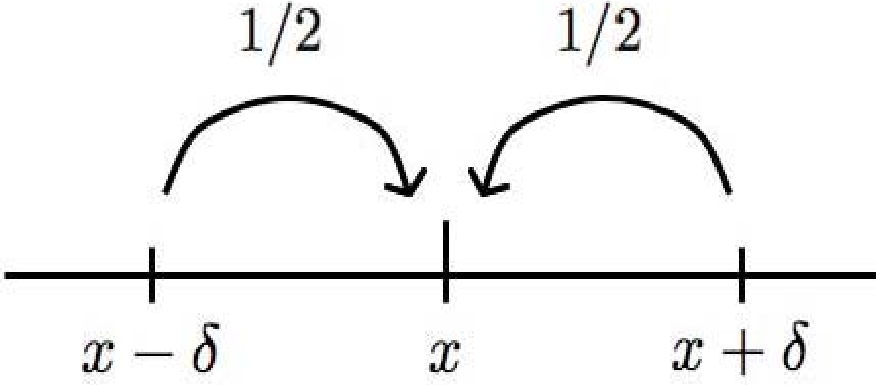
Reaction-diffusion models

- **Partial differential equation models** combine organism movement with population processes
- Answer questions about:
  - Dispersal
  - Ecological invasion
  - Effect of habitat geometry and size
  - Dispersal mediated coexistence
  - Emergence of spatial-temporal patterns
- Derivation of the model
  - ***Lagrangian approach***: Movement of individuals over time
  - ***Eularian approach:*** Fix a point in space and consider flow or flux past the point over time

Fokker-Plank Equation and random walks

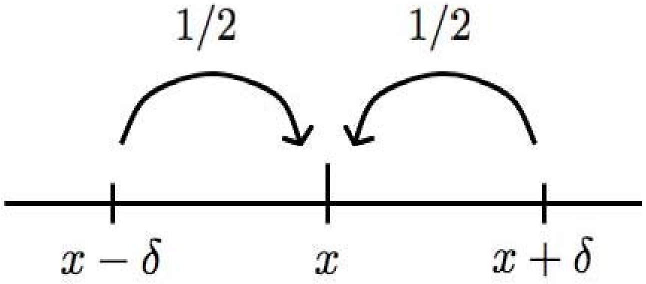
- *Given information about how an organism moves over short time scales can we determine how it moves over long time scales?*
- Answer: Yes, if the movement rules are “fairly” simple.

- Random walk in 1-D:
  - Each time step τ jump left or right a distance δ
  - One step markov process, the precise path taken to get to the current location plays no role in determining the future position



Master equation

- X(t) = stochastic process describing the location of an individual at time t, released at location x=0 at time 0
- p(x,t)δ=probability an individual is between x and x+δ at time t. (So p(x,t) is a probability density function)
- **Unbiased random walk:** probability jump right R=1/2 and probability jump left L=1/2



$$p(x,t+\tau)=\frac{1}{2}p(x-\delta,t)+\frac{1}{2}p(x+\delta,t)$$

Obtaining the PDE

- Expand the RHS of the master equation using Taylor Series:

$$p(x,t)+\tau\frac{\partial p}{\partial t}(x,t)+\tau\frac{\partial^2 p}{\partial t^2}(x,t)+h.o.t=$$

$$\frac{1}{2}\left\{p(x,t)-\delta\frac{\partial p}{\partial x}(x,t)+\frac{\delta^2}{2}\frac{\partial^2 p}{\partial x^2}(x,t)+p(x,t)+\delta\frac{\partial p}{\partial x}(x,t)+\frac{\delta^2}{2}\frac{\partial^2 p}{\partial x^2}(x,t)+h.o.t.\right\}$$

- Simplifying

$$\frac{\partial p}{\partial t}(x,t)+\frac{\tau}{2}\frac{\partial^2 p}{\partial t^2}(x,t)=\frac{\delta^2}{2\tau}\frac{\partial^2 p}{\partial x^2}(x,t)+h.o.t$$

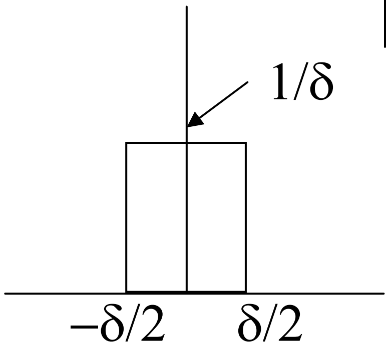
- Ignoring the higher order terms (h.o.t) taking the limit as δ, τ $\to 0$, so that $\delta^2/(2\tau) \to$ D yields the diffusion equation

$$\boxed{\frac{\partial p}{\partial t}= \underbrace{D\frac{\partial^2 p}{\partial x^2}}_{\text{Random movement}}}$$

Obtaining the PDE: ICs & BCs

- **Initial conditions:**

$$p(x,0) = \text{Dirac Delta Fucntion}$$



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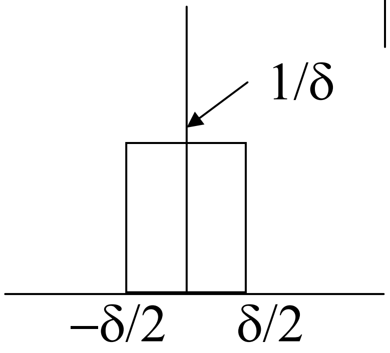

- **Boundaries:** Suppose that
  - Inside region {x>0} individuals move left and right with prob. 1/2
  - At x=0 (the boundary) individuals move right with prob. 1/2, leave with prob. aδ/2 and stay at the boundary with prob. (1-aδ)/2.
  - a is the rate per unit space of leaving the region

Master Equation $p(0,t+\tau) = \frac{1}{2}p(\delta,t) + \frac{1}{2}(1-a\delta)p(0,t)$

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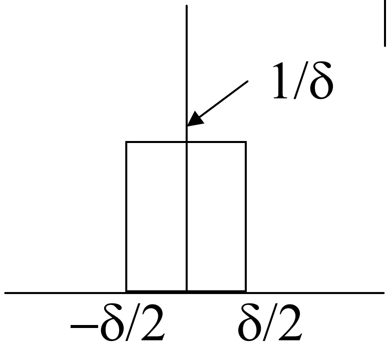

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Robin boundary conditions

$$\frac{\partial p}{\partial t}(0,t) = \frac{\delta}{2\tau}\left(\frac{\partial p}{\partial x}(0,t) - ap(0,t)\right) + \frac{\delta^2}{2\tau}\frac{\partial^2 p}{\partial x^2}(0,t) + h.o.t \Rightarrow \frac{\partial p}{\partial x}(0,t) - ap(0,t) = 0$$

Some slight variations

- **Bias movement:** R=1/2 +γδ, L=1/2 –γδ yields:

Advection-diffusion equation

$$\boxed{\frac{\partial p}{\partial t} = \underbrace{D\frac{\partial^2 p}{\partial x^2}}_{\text{Random movement}} - \underbrace{v\frac{\partial p}{\partial x}}_{\text{Advection}}}$$

where, $\frac{\gamma\delta^2}{2\tau} \rightarrow v,$

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- **Movement probabilities depend on space (current locatoion)**: R(x), L(x), N(x) (prob not moving)

Fokker-Planck equation

$$\frac{\partial p}{\partial t} = \frac{\partial^2}{\partial x^2}\left(\underbrace{\mu(x)}_{\text{Motility}} p\right) - \frac{\partial}{\partial x}\left(\underbrace{\beta(x)}_{\text{Bias}} p\right)$$

$$\text{where, } \mu(x) = D(L(x) + R(x)),$$

$$\beta(x) = \frac{D(L(x) - R(x))}{\delta},$$

Some slight variations

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- **Movement probabilities depend on half way point from current location to next location**

Fickian-diffusion

$$\boxed{\frac{\partial p}{\partial t} = \frac{\partial}{\partial x}\left(\underbrace{D(x)}_{\text{Diffusivity}} \frac{\partial p}{\partial x}\right) - \frac{\partial}{\partial x}\left(\beta(x)\, p\right)}$$

2-D space: Patlak model

$$\frac{\partial p}{\partial t}=\frac{1}{2}\nabla\cdot\left[\frac{1+\psi\left(2\frac{m_1^2}{m_2}\right)}{1-\psi}\nabla\left(\frac{m_2}{2T}p(x,t)\right)-\frac{\psi m_1^3}{Tm_2(1-\psi)}\nabla\left(\frac{m_2}{m_1}\right)p(x,t)\right]$$

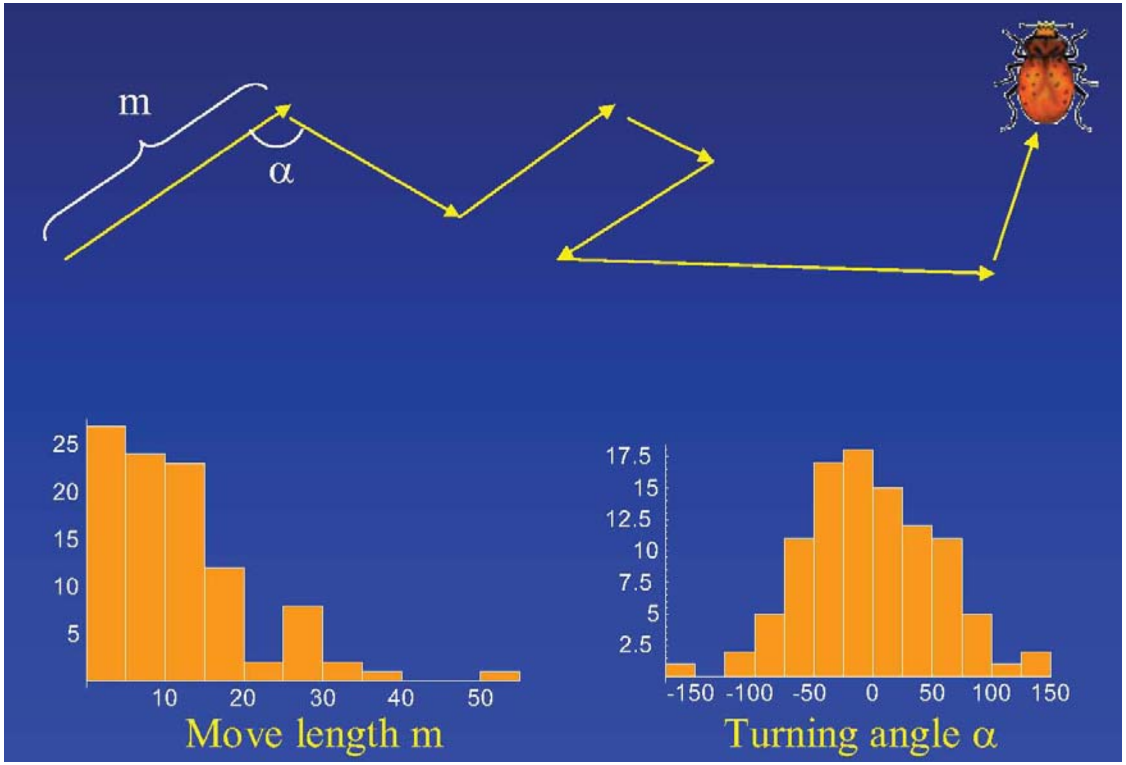
$\nabla=(\partial/\partial x,\partial/\partial y)$

m_1 Average move length

m_2 Average squared move length

T Average move duration

ψ Mean cosine of the turning angle



Probability to density

- p(x,t) ~ probability of finding an indivdual location x at time t
- N=total number of moving organisms
- n(x,t)=Np(x,t)=density of organisms at location x at time t

Equilibrium distributions

Fokker-Planck Equation (no bias)

$$\frac{\partial n}{\partial t} = \frac{\partial^2}{\partial x^2}\left(\underbrace{\mu(x)n}_{\text{Motility}}\right)$$

→

Equilibrium distribution

$$n^*(x) = \frac{\text{constant}}{\mu(x)}$$

Fickian diffusion Equation (no bias)

$$\frac{\partial n}{\partial t} = \frac{\partial}{\partial x}\left(\underbrace{D(x)}_{\text{Diffusivity}}\frac{\partial n}{\partial x}\right)$$

→

Equilibrium distribution

$$n^*(x) = \text{constant}$$

- Fokker-Plank predicts organisms will eventually accumulate in locations where movement rate is low.
- Fickian Diffusion predicts a uniform distribution of individuals even if D varies in space!

Residence Index

- *Residence index* connects individual movement to population level redistribution patterns

$$\rho(x) = \frac{1}{\mu(x)}$$

- Residence index is proportional to density and is for comparative purposes, e.g. “the density of organisms in patch i is three times that in patch j”)
- E.g. Random walk, fixed move length

$$\rho(x) = \frac{2\tau}{\delta^2 \left(R(x) + L(x)\right)}$$

Example: Flea beetles in collard patches

- Patch distance 2 metres=δ
- Movement of beetles recorded 1 hour (=τ) after release
- Data:
  - proportion moved Pm
  - proportion stayed Ps
  - 1-(Ps+Pm) not captured
- (R+L)=Pm/(Pm+Ps)

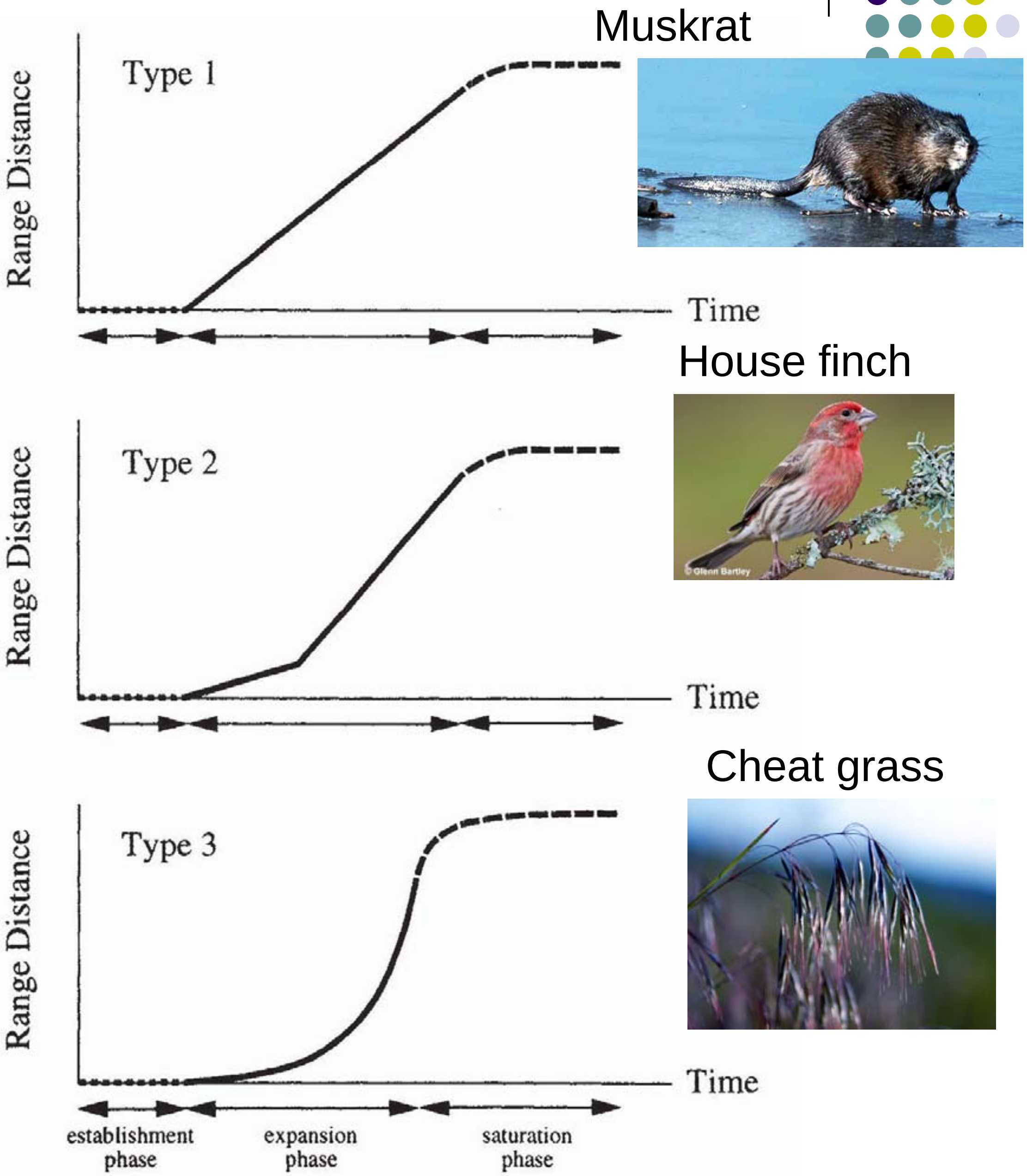
$$\mu_{\text{Lush}} = 0.61\,\text{m}^2/\text{h} \quad \mu_{\text{Stunted}} = 1.63\,\text{m}^2/\text{h}$$

$$\frac{\rho_{\text{Lush}}}{\rho_{\text{Stunted}}} = \frac{\mu_{\text{Stunted}}}{\mu_{\text{Lush}}} = 2.67$$

Density in lush is 2.67 times density in stunted patches

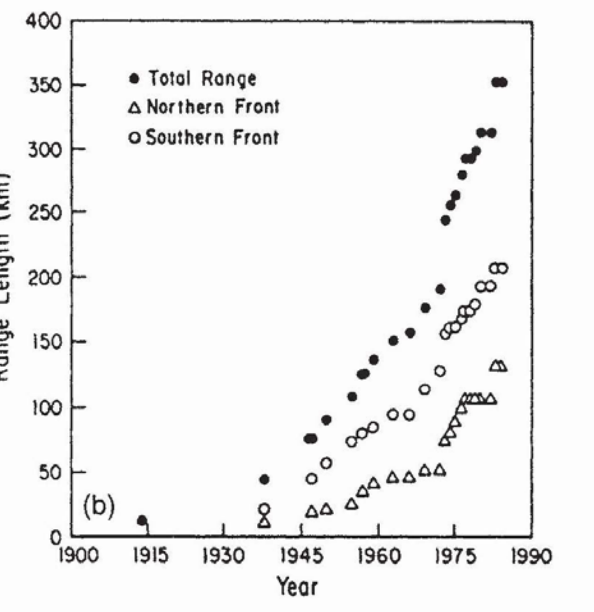
Population spread and invasion

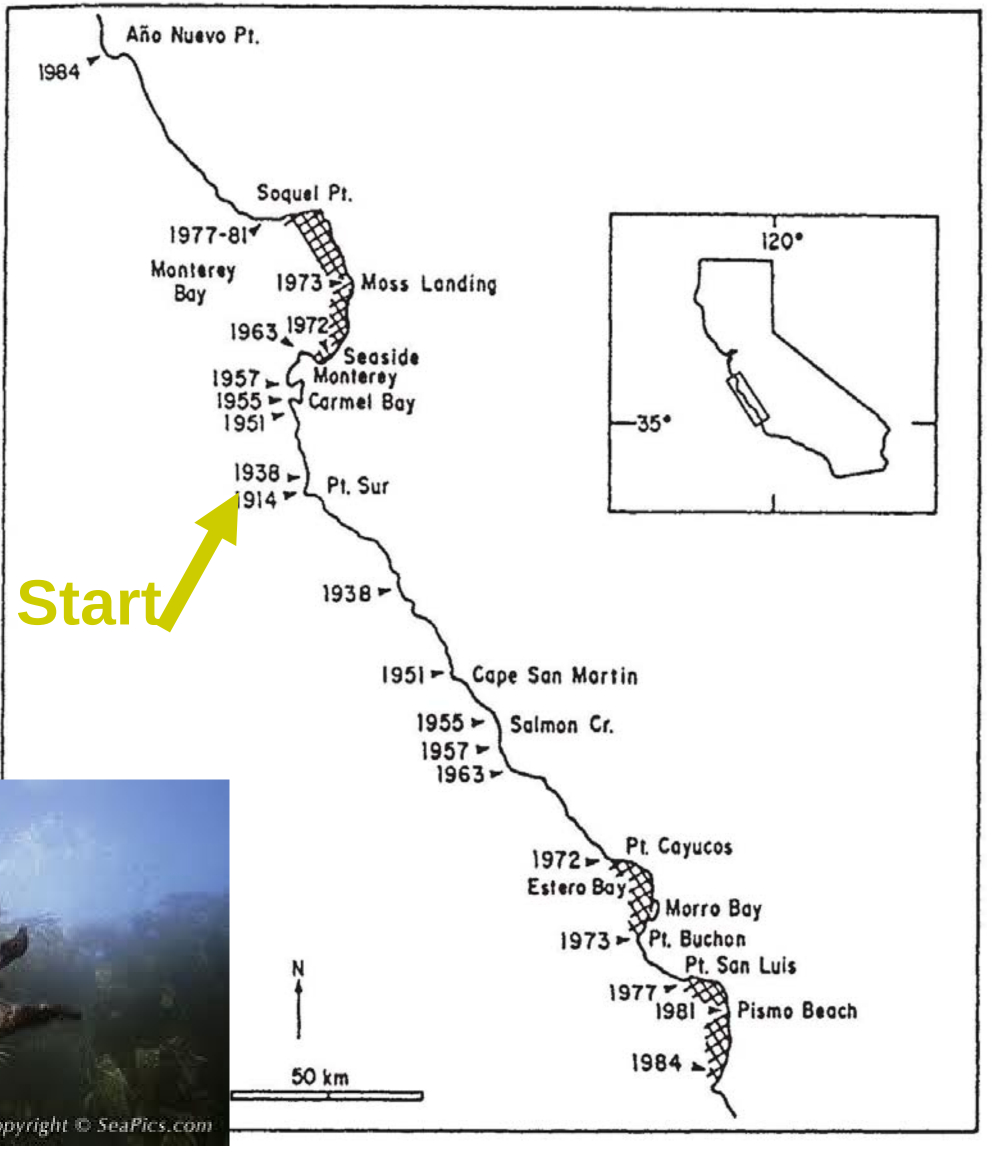
- Linear expansion with time
- Slow initial spread followed be linear expansion *(e.g.Allee effects)*
- Spread rate continually increases with time *(e.g long distance dispersal)*



California Sea Otter expansion

1-D invasion: Hunted for fur until near extinction. A surviving population of 50 slowly recovered & spread

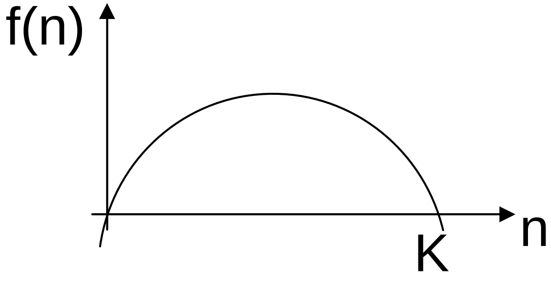




Population spread: model

- n(x,t)=density of individuals

$$\frac{\partial n}{\partial t} = \underbrace{D\frac{\partial^2 n}{\partial x^2}}_{\text{Random movement}} + \underbrace{f(n)}_{\text{Growth}}$$

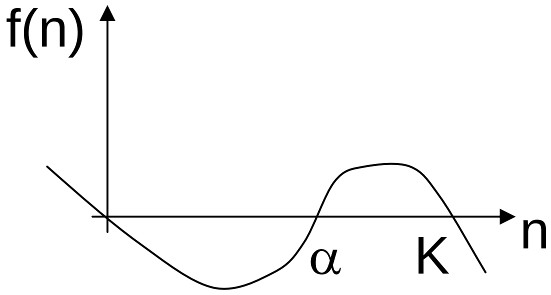


- f(n)=rn(1-n/K) *Logistic growth*

- f(n)=rn(1-n/k)(n-α) *Bistable (Allee effect)*

Difficulty reproducing at low density due to

e.g. mate finding, low genetic diversity



Scale (non-dimensionalise) the model

$$u = n / K, \quad t^{*} = rt, \quad x^{*} = \sqrt{\frac{r}{D}}x$$

Scale density by carry capacity

Scale time by Growth rate

Scale space by average dispersal distance

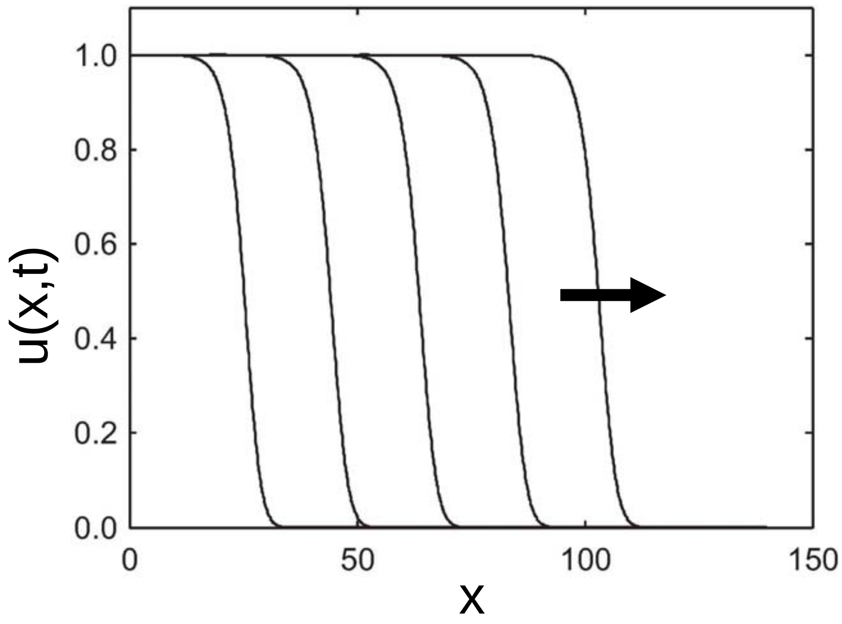
- Scaled model is

$$\frac{\partial u}{\partial t} = \underbrace{\frac{\partial^2 u}{\partial x^2}}_{\text{Random movement}} + \underbrace{g(u)}_{\text{Growth}}$$

- g(u)=u(1-u) logistic
- g(u)=u(1-u)(u-a)

Travelling wave solutions

- Look for travelling wave solutions
  - Constant speed, c
  - Constant shape ⟶ $u(x,t) = U(x-ct) = U(z)$

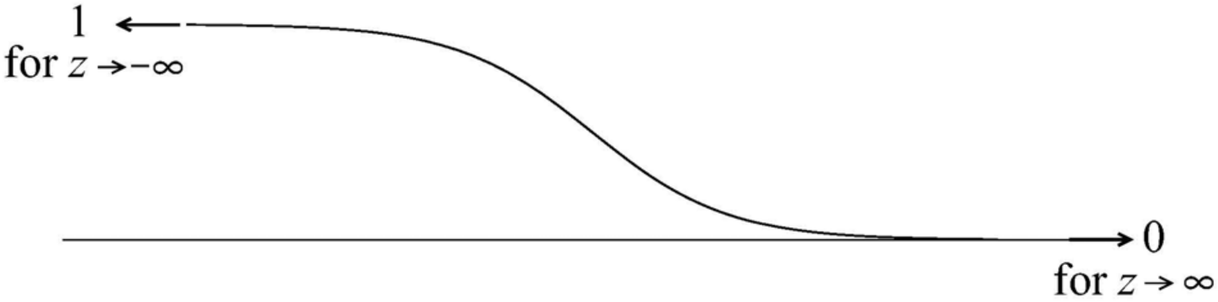


z=x-ct is the *wave variable* (moving coordinate)

***Analogy:** Watching a metro train go by you see the people on the train move.*
If you are on the train then the people on the train are not moving this is the moving frame of reference

PDE to ODEs

- Travelling wave profile



- Behind the wave the population is at carry carrying capacity, in front of the wave there is no population
- So in the new variables: $\frac{\partial u}{\partial t} = -c\frac{dU}{dz}, \quad \frac{\partial^2 u}{\partial x^2} = \frac{d^2U}{dz^2}$
- The PDE becomes $U'' = -cU' - g(U)$
- Introduce the new variable V=U’=dU/dz:

$$U' = V$$
$$V' = -cV - g(U)$$

Phew!!! A system of ODEs we know how to work with these.

Case 1: logistic growth g(u)=u(1-u)

- The steady states are (U,V)= (0,0) or (1,0)

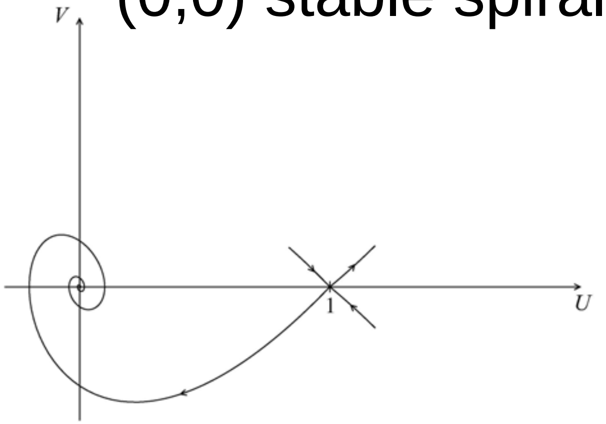
$$U' = V$$

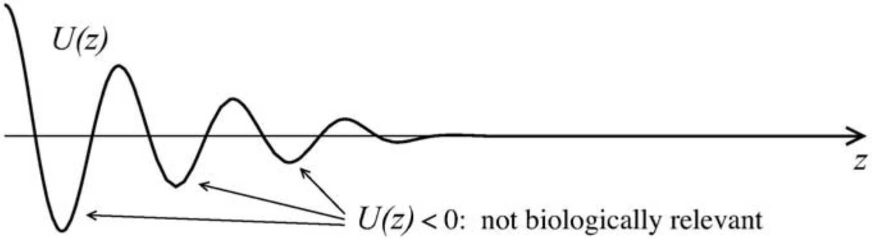
$$V' = -cV - g(U)$$

Stable for c>0

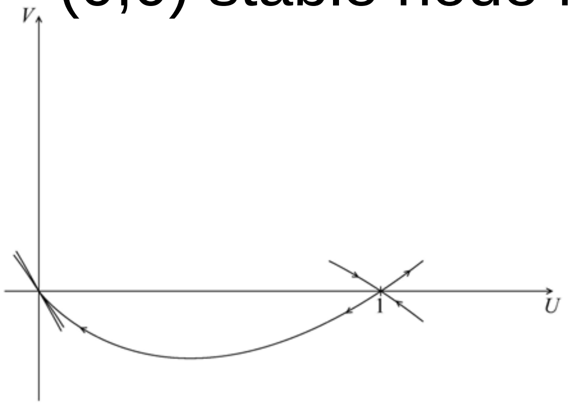
Always saddle point

(0,0) stable spiral for c<2

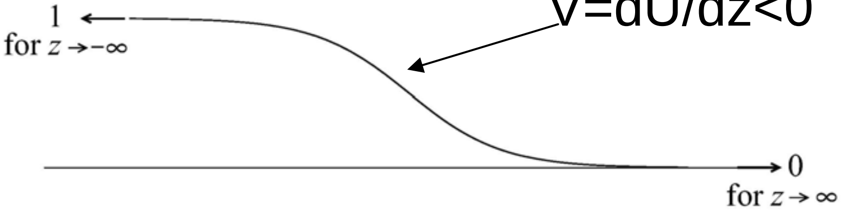




(0,0) stable node for c>=2



V=dU/dz<0

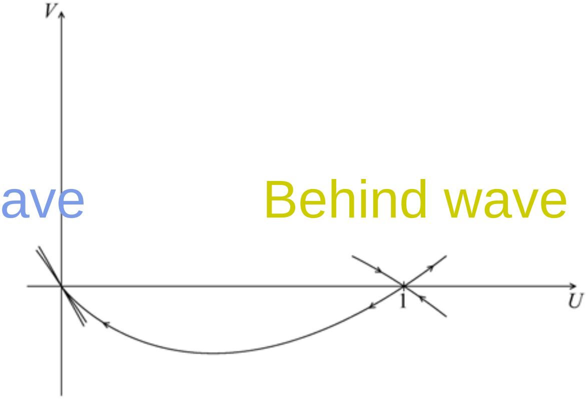


Spread rate for logistic growth

- c>=2 is a necessary condition for a travelling wave solution

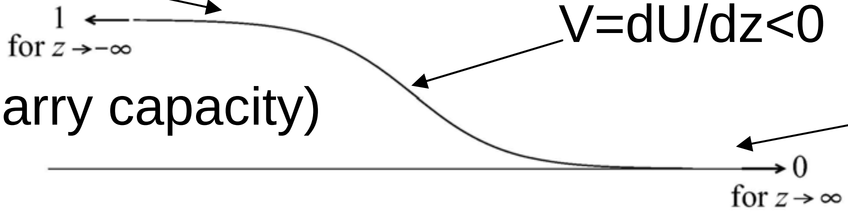
Ahead of wave

Behind wave



Travelling wave solution in our ODE phase plane.

Behind wave:
V=dU/dz=0
U=1 (scaled carry capacity)



V=dU/dz<0

Ahead of wave:
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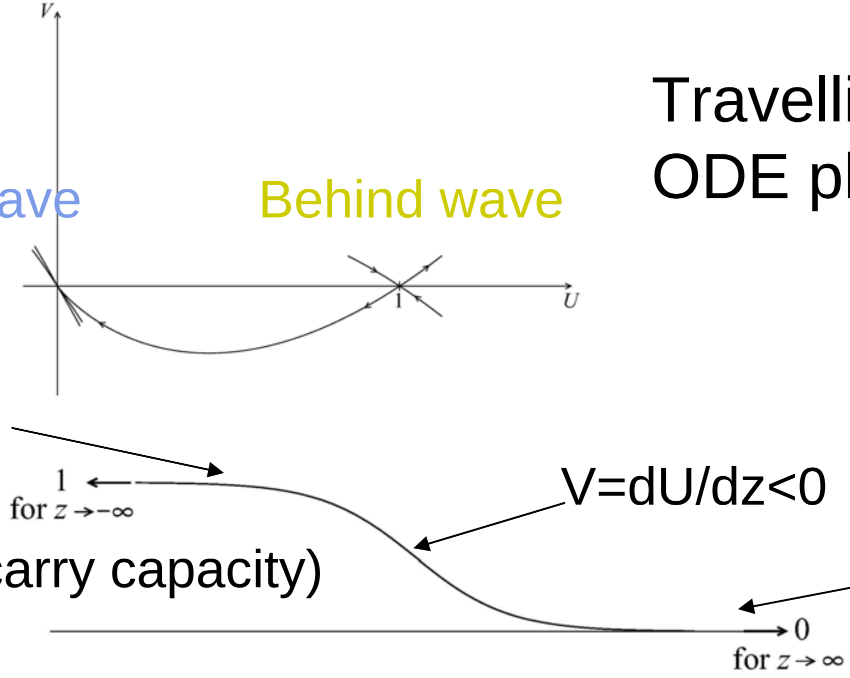

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V=dU/dz<0

Ahead of wave:
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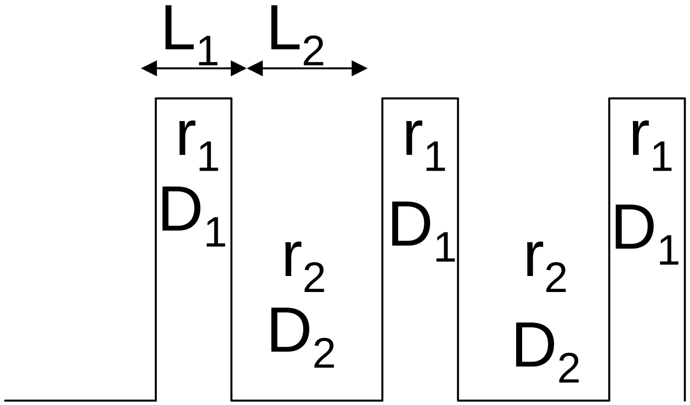
U=0

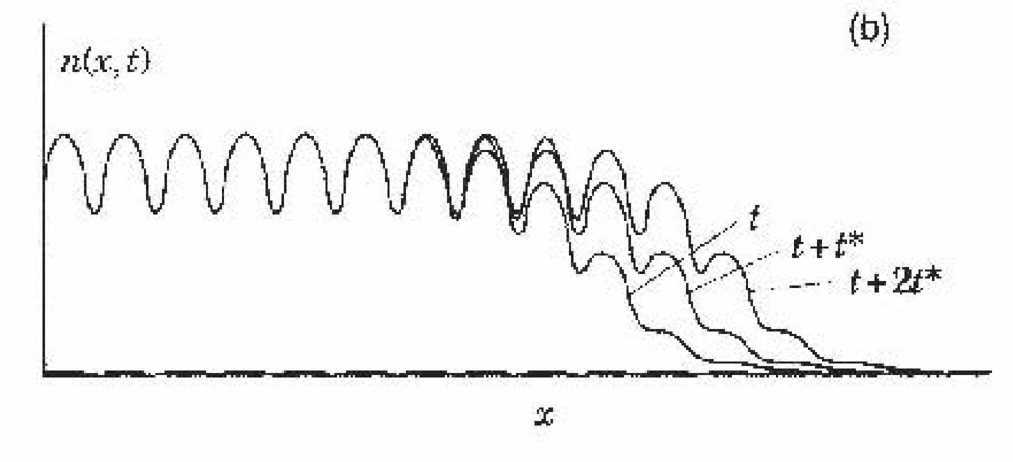
- Aronson & Weinberger(1975) show the spread rate for the logistic case is exactly the minimum speed

$$c^* = 2\sqrt{rD}$$

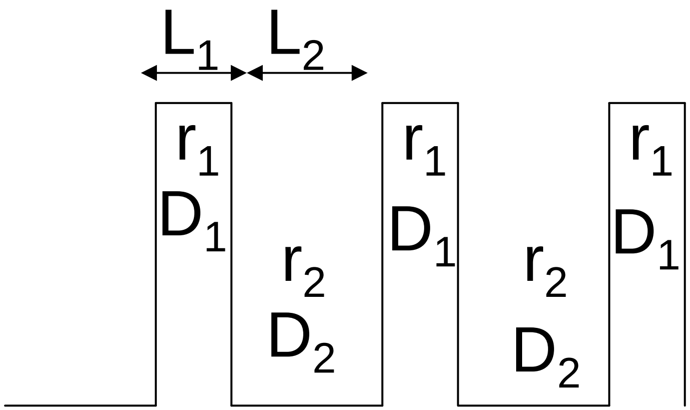
(dimensional value)

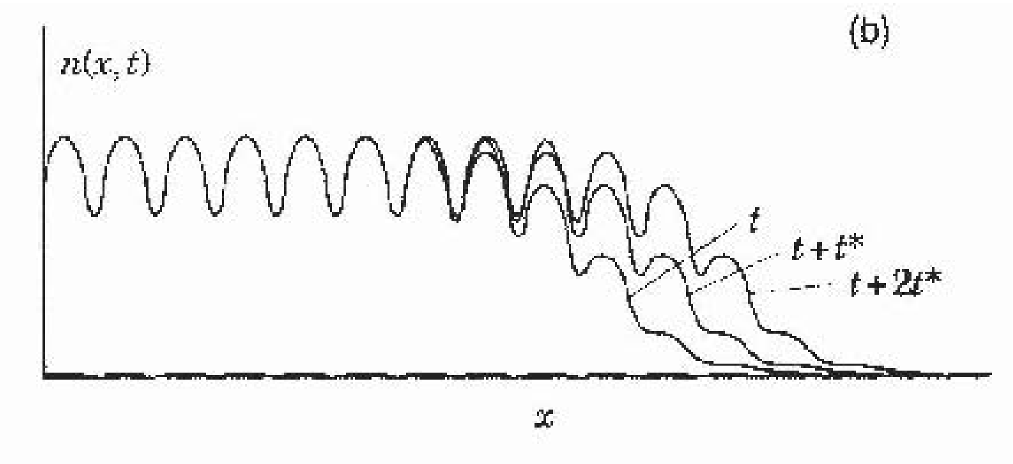
Spread rate in a heterogeneous environment





Spread rate in a heterogeneous environment





$$c^* = 2\sqrt{r_a D_h}$$

$$r_a = \frac{r_1 L_1 + r_2 L_2}{L_1 + L_2} \qquad D_h = \frac{L_1 + L_2}{L_1 / D_1 + L_2 / D_2}$$

- Invasion is determined by growth and diffusion
- Spatial variation in dispersal can deter spread because harmonic means are much lower than arithmetic means when there is lots of variation.

River problem: Drift paradox

- Drift paradox: Why can population persist in streams when they are being constantly washed down stream?

$$\frac{\partial n}{\partial t} = \underbrace{D\frac{\partial^2 n}{\partial x^2}}_{\text{Random movement}} - \underbrace{v\frac{\partial n}{\partial x}}_{\text{Advection}} + rn(1-n/K)$$

- v=speed of the stream.

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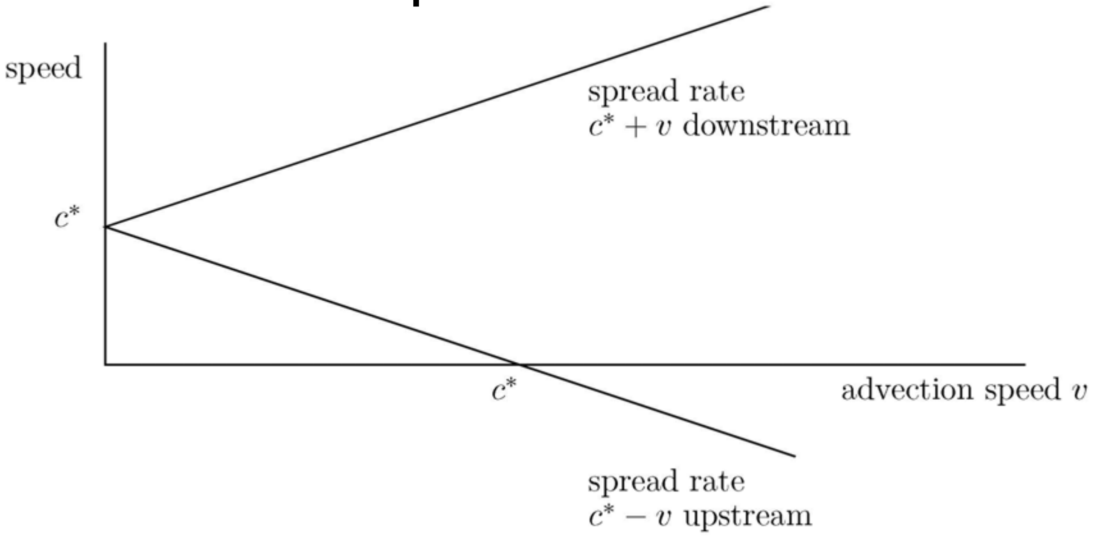
- v=speed of the stream.
- Change coordinates to move at the speed to the river. Let X=x-vt, T=t

$$\frac{\partial n}{\partial T} = \underbrace{D\frac{\partial^2 n}{\partial X^2}}_{\text{Random movement}} + rn(1-n/K)$$



Case 2: Allee effect g(u)=u(1-u)(u-a)

$$\frac{\partial u}{\partial t} = \underbrace{\frac{\partial^2 u}{\partial x^2}}_{\text{Random movement}} + \underbrace{g(u)}_{\text{Growth}} \xrightarrow{\text{Travelling wave coordinates}} U'' = -cU' - g(U)$$

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- Multiply by U’ and integrate over z

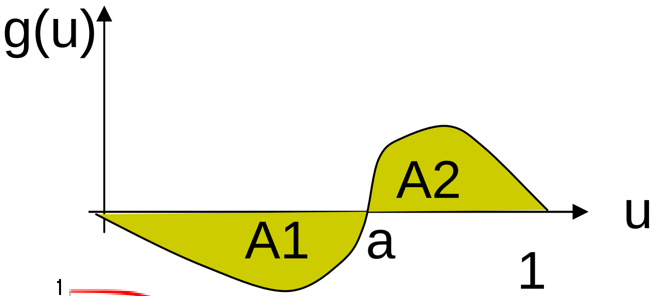
$$0 = \underbrace{\int_{-\infty}^{\infty} U''U'dz}_{\text{zero}} + \int_{-\infty}^{\infty} (U')^2\, dz + c\int_{-\infty}^{\infty} g(U)U'dz$$

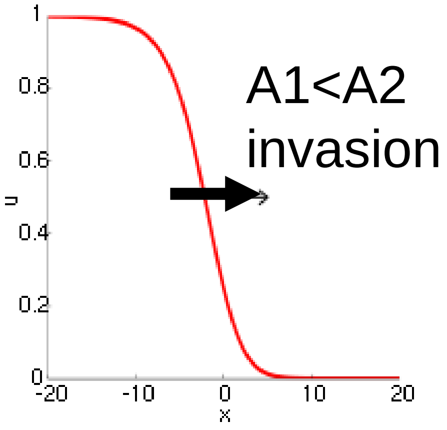
$$c = \frac{\int_0^1 g(U)dU}{\int_{-\infty}^{\infty} (U')^2\, dz} \longleftarrow \text{positive}$$

Case 2: Allee effect - conclusions

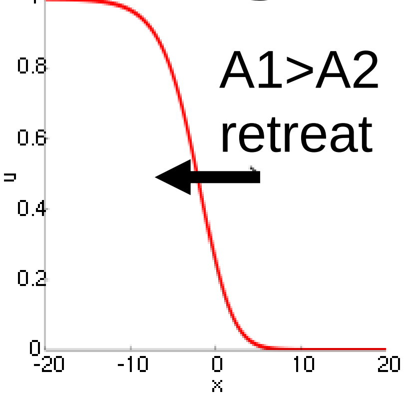
- If the travelling wave exists it has a unique speed.

$$c = \frac{\int_0^1 g(U)dU}{\int^{\infty} (U')^2 dz}$$





'Pushed Waves'



- We can show (using another method) that $c^* = \sqrt{2}\left(\frac{1}{2} - a\right)$

Key differences that arise from an Allee effect

- A threshold density must be exceeded for invasion to take hold.
- Initial spatial arrangement of invades effects the fate of an invasion.
- Velocity of spread is reduced in proportion to the Allee effect.

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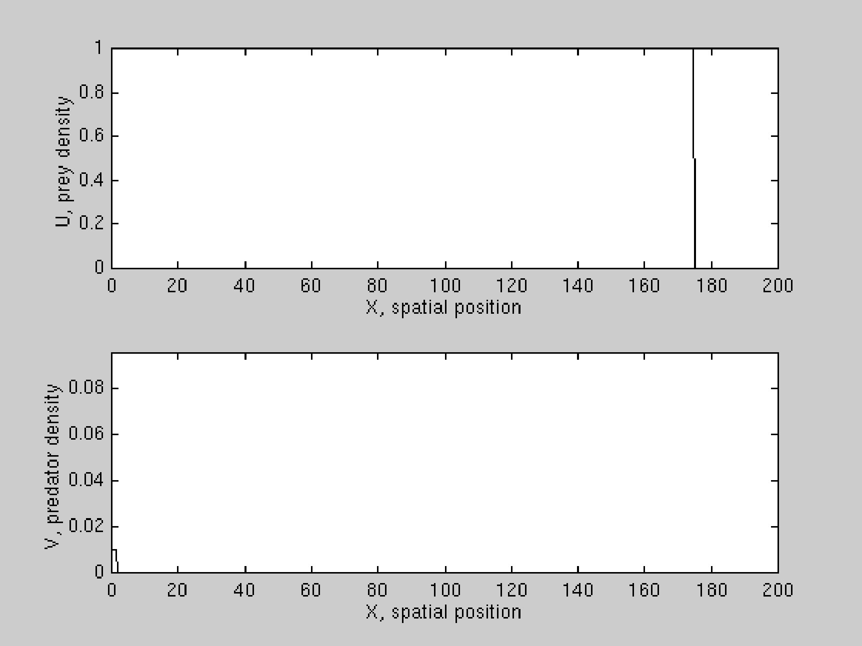
- A threshold density must be exceeded for invasion to take hold.
- Initial spatial arrangement of invades effects the fate of an invasion.
- Velocity of spread is reduced in proportion to the Allee effect.
- In a predator-prey system with Allee effect in the prey, predators can reverse the wave of invading prey.



Critical domain size

- Q: Will a population grow when rare?
- A: Assume the population is at low density so we linearise about n=0. If this *steady state* is *stable* with have *extinction* if it is *unstable* with have *persistence*.

Hostile exterior

$$\frac{\partial n}{\partial t} = D\frac{\partial^2 n}{\partial x^2} + rn$$

$$n(0,t) = n(L,t) = 0, \qquad n(x,0) = n_0(x)$$

Critical domain size

- Q: Will a population grow when rare?
- A: Assume the population is at low density so we linearise about n=0. If this *steady state* is *stable* with have *extinction* if it is *unstable* with have *persistence*.

Hostile exterior

$$\frac{\partial n}{\partial t} = D\frac{\partial^2 n}{\partial x^2} + rn$$

$$n(0,t) = n(L,t) = 0, \qquad n(x,0) = n_0(x)$$

- Ansatz: Solutions have the form

$$n(x,t) \propto e^{\lambda t} f(x) \qquad \text{Hence}: \underbrace{f'' + \frac{r-\lambda}{D} f = 0,}_{\text{ODE}} \;\; f(0) = f(L) = 0$$

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$$\text{Solution}: \; f(x) = A\cos\left(\sqrt{\frac{r-\lambda}{D}}x\right) + B\sin\left(\sqrt{\frac{r-\lambda}{D}}x\right)$$

$$\text{BCs } f(0) = 0 \Rightarrow A = 0, \; f(L) = 0 \Rightarrow \sqrt{\frac{r-\lambda}{D}} = \frac{k\pi}{L}$$

Critical domain size

$$n(x,t) = \sum_{k=1}^{\infty} B_k \exp\left(\left(r - D\left(k\pi / L^2\right)\right)t\right)\sin\left(k\pi x / L\right)$$

- We have $\lambda_1 > \lambda_2 > \lambda_3 > \lambda_4 > \ldots.$ So if the largest eigenvalue is positive then the population persists.

$$L > L_c = \pi\sqrt{\frac{D}{r}}$$

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- What about non-hostile boundary conditions?

$$\frac{\partial n}{\partial t} = D\frac{\partial^2 n}{\partial x^2} + rn \qquad Dn_x(0,t) = an(0,t) \qquad nD_x(L,t) = an(L,t)$$

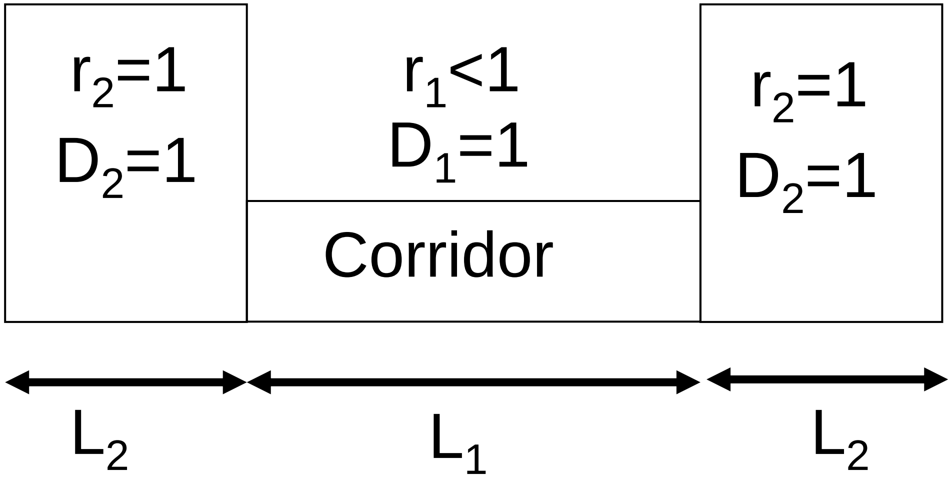
$$L > L_c = 2\sqrt{\frac{D}{r}}\tan^{-1}\left(\frac{a}{\sqrt{Dr}}\right)$$

$$\text{as} \quad a \to \infty, \ \tan^{-1}(a/\sqrt{Dr}) \to \pi/2$$

$$\text{as} \quad a \to 0, \ \tan^{-1}(a/\sqrt{Dr}) \to 0$$

Corridors and persistence

p, probability of staying in the corridor when reaching the corridor boundary



$r_2=1$
$D_2=1$

$r_1<1$
$D_1=1$

Corridor

$r_2=1$
$D_2=1$

L_2 L_1 L_2

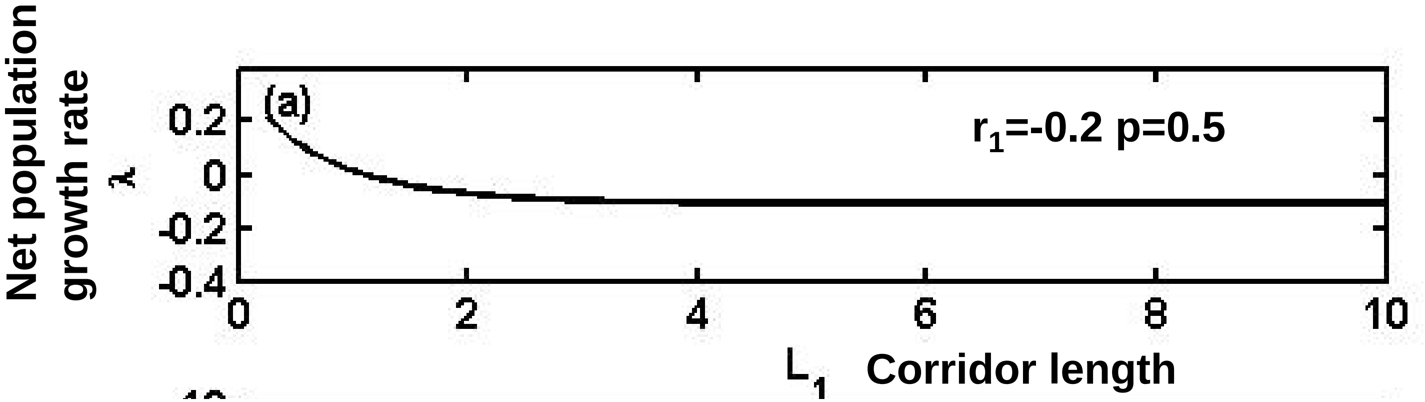
Patches are too small to persist on

$$L_2 < L_c = \pi\sqrt{\frac{D_2}{r_2}}$$

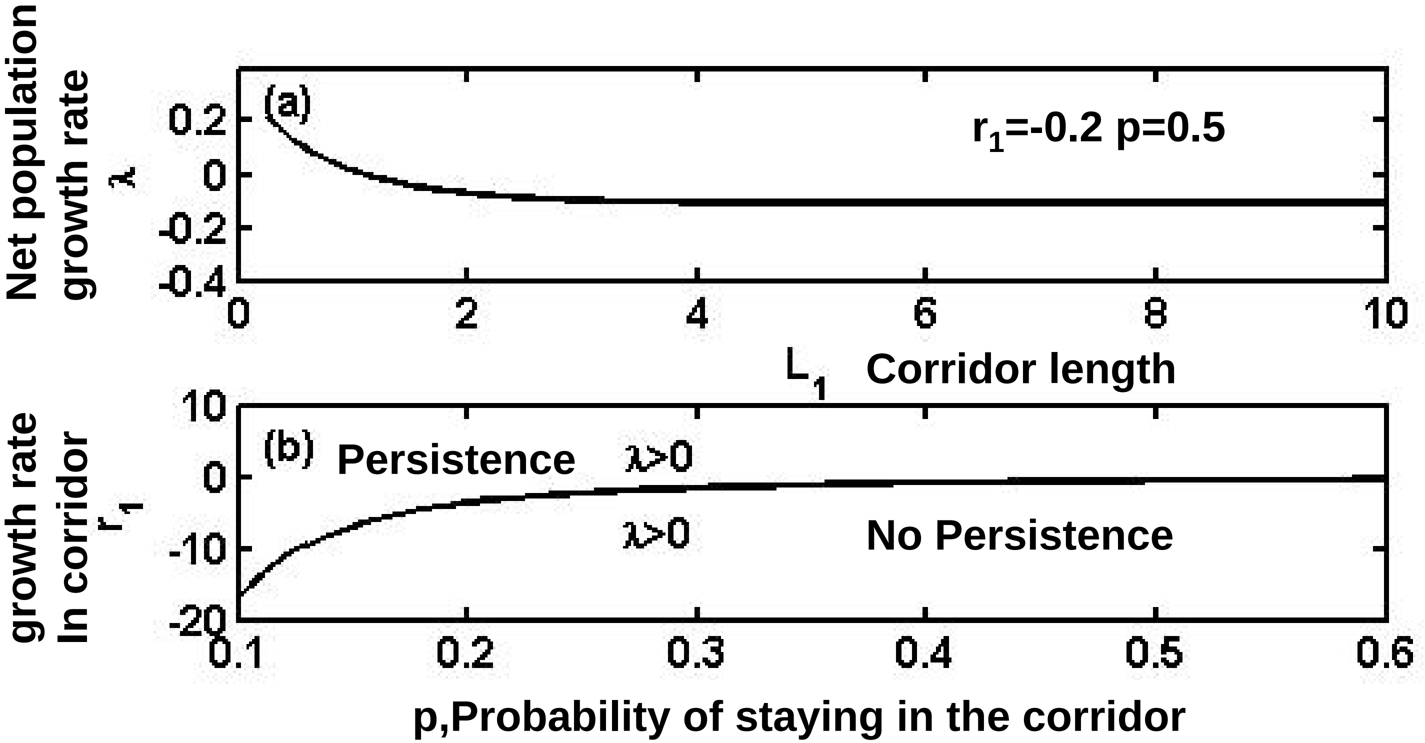
But, combined persistence is possible

$$2L_2 > L_c = \pi\sqrt{\frac{D_2}{r_2}}$$

Corridor results



Corridor results



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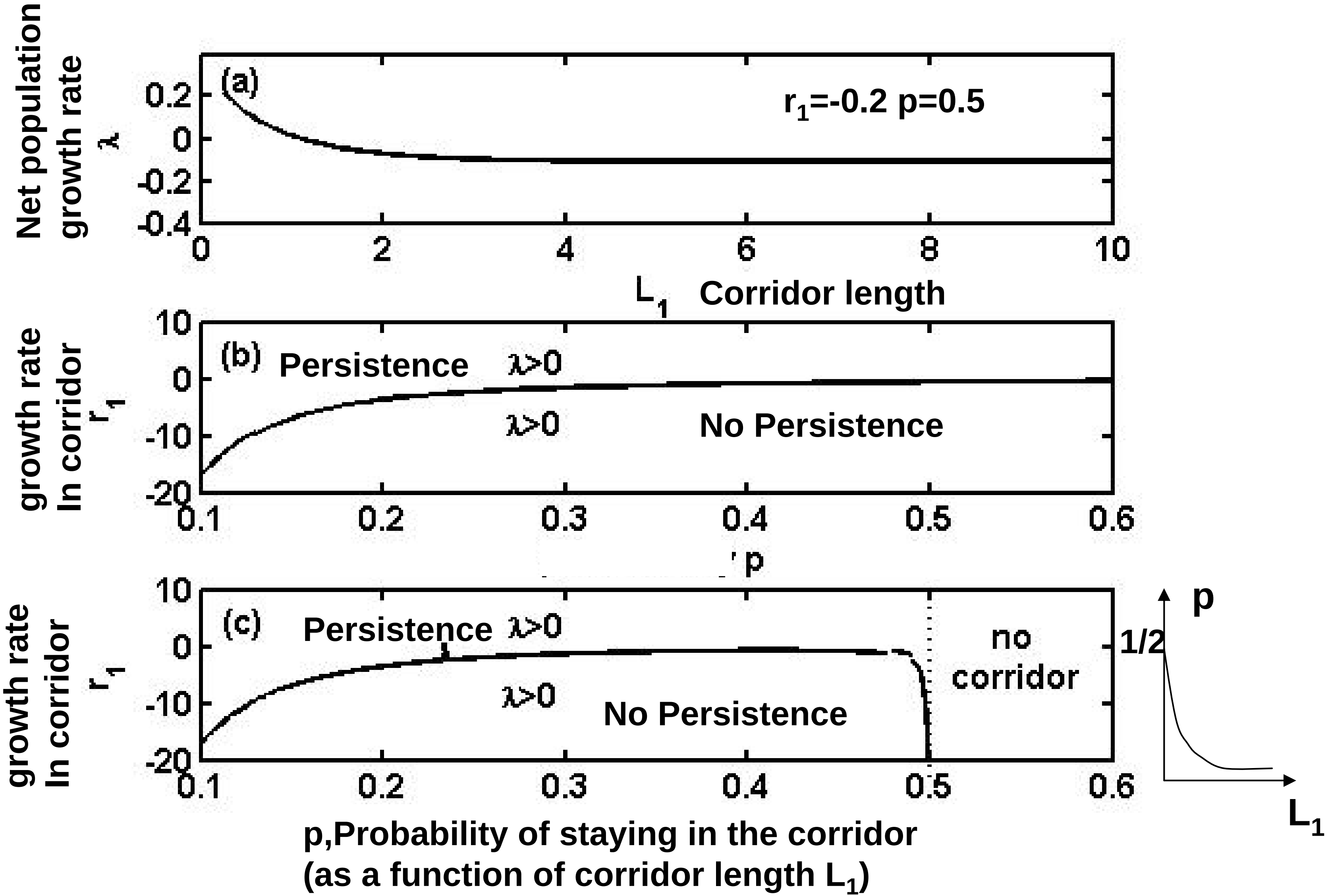

Critical Domain Size summary

- Factors that increase movement out of a patch (drift or repulsion) lead to larger Critical Domain Sizes
- Factors that decrease movement out of a patch (attraction to the patch, or density dependent dispersal) lead to smaller Critical Domain Sizes
- Density-dependent growth regulates population size in a patch, BUT it does not effect Critical Domain Size unless there are Allee growth dynamics.

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