Integrodifference equations in spatial ecology

Lecture 13: Dispersal patterns

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Aspects of dispersal

1. Dispersal is risky: mortality during dispersal
2. Dispersal in rivers is biased
3. Dispersal can have different mechanisms

Mortality during dispersal

So far $\int_{-\infty}^{\infty} k(x,y)\,dx = 1$ every individual settles somewhere.

Dispersal is risky:

$$\int_{-\infty}^{\infty} k(x,y)\,dx = S(y) \leq 1$$

Scale : $\hat{k}(x,y) = \dfrac{k(x,y)}{S(y)}$.

Q: Trade-off ?

Mechanistic derivation

Random walk with settling and mortality

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} - \alpha u - \beta u \qquad , u(0,x) = \delta(x)$$

Kernel? $\quad K(x) = \int_0^\infty \alpha u \, dt \quad$ only settling, not death.

Case: $\cdot\ \underline{\alpha = \alpha(t) = \delta(t-\tau)} \quad \rightarrow \quad$ Gaussian

$\cdot\ \alpha = \text{const} \quad \rightarrow \quad$ Laplace

The Gaussian case

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} - \beta u \quad \text{for} \quad 0 < t < \tau \qquad u(0,x) = \delta(x)$$

$$K(x) = u(\tau, x) = \frac{e^{-\beta\tau}}{\sqrt{2\pi D\tau}}\, e^{-\frac{x^2}{2D\tau}} = e^{-\beta t} \cdot \text{Gauss}(x; 2D\tau)$$

Put this into a linear IDE

$$\boxed{N_{t+1}(x)} = R\int_{-\infty}^{\infty} K(x-y) N_t(y)\,dy = \underbrace{\overset{\tilde{R}}{R e^{-\beta\tau}} \int_{-\infty}^{\infty} \text{Gauss}(x-y, \sigma^2) N_t(y)\,dy}$$

Hence speed

$$\hat{c} = \sqrt{2\sigma^2 \ln(R e^{-\beta\tau})} = \sqrt{2\sigma^2(\ln R - \beta\tau)}$$

$$= \sqrt{2D\tau(\ln R - \beta\tau)} = \hat{c}(\tau) \quad \text{has a max at } \tau = \frac{\ln R}{2\beta}$$

Observe: Require $\underline{R e^{-\beta\tau} > 1}$: growth rate must make up for dispersal loss

The Laplace case

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} - (\alpha+\beta)u$$

$$\int_0^\infty (\alpha+\beta)u \, dt = \frac{a}{2} e^{-a|x|} \qquad a = \sqrt{\frac{\alpha+\beta}{D}}$$

$$\int_0^\infty \alpha u \, dt = \frac{\alpha}{2(\alpha+\beta)}\sqrt{\frac{\alpha+\beta}{D}}\, e^{-\sqrt{\frac{\alpha+\beta}{D}}|x|}$$

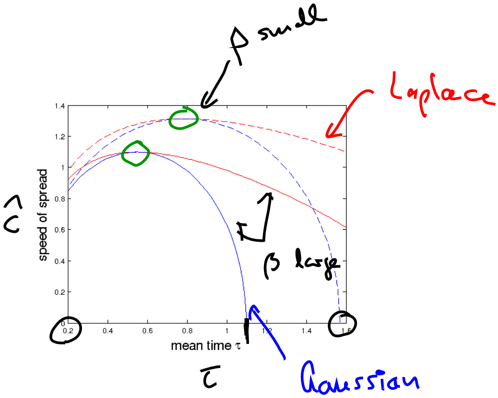
$\hat{c}$ is not explicitly available: $\hat{c} = \min_{s>0} \frac{1}{s} \ln(R\,M(s))$

Here: to compare: $\alpha = \frac{1}{\tau}$: mean dispersal time

is the same for Case 1, 2

$$= \boxed{\min_{s>0}} \frac{1}{s} \ln\left(\frac{R}{1+\beta\tau - D\tau s^2}\right)$$

The comparison



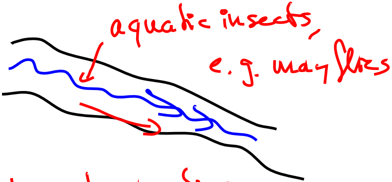
Open question?

Can you show that

$$\max_{\tau} \hat c_{\text{Laplace}}(\tau) = \max_{\tau} \hat c_{\text{Gauss}}(\tau)$$

$$= \hat c\left(\frac{\ln R}{2\beta}\right)$$

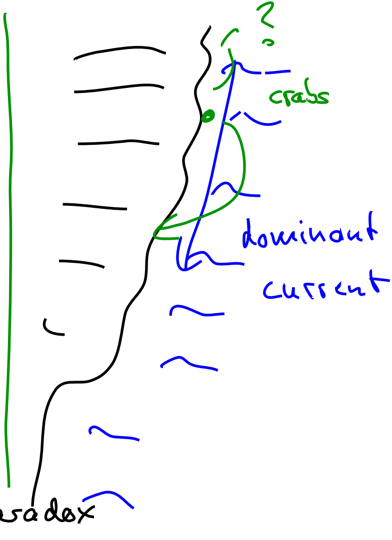
Biased dispersal



downstream bias

Why/how can populations persist at a certain location in the river?

Müller (1954)



Drift paradox

Mechanistic derivation

Biased random walk with settling

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} - q\frac{\partial u}{\partial x} - \alpha u$$

Gaussian

$$\frac{1}{\sqrt{2\pi D\tau}} e^{-\frac{(x-q\tau)^2}{2D\tau}}$$

asymmetric Laplace $\quad a_1, a_2 > 0$

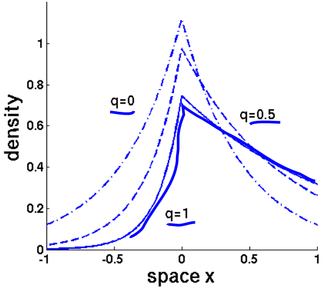
$$K(x) = \begin{cases} A \cdot e^{-a_1 x} & x > 0 \\ A \cdot e^{a_2 x} & x < 0 \end{cases}$$

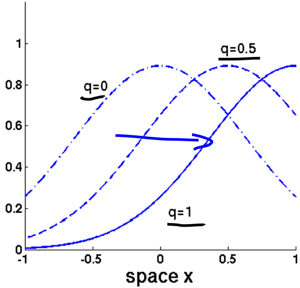
$$A = \frac{a_1 a_2}{a_1 ?}$$

Biased dispersal

Gaussian

Biased random walk with settling





Laplace

Definitions of persistence

$$N_{t+1}(x) = R\int_{-\infty}^{\infty} K(x-y)N_t(y)\,dy \qquad \int_{-\infty}^{\infty} K(x)\,dx = 1$$

$\mu = q\tau$
$\sigma^2 = D\tau$
$R > e^{\frac{q^2\tau}{2D}}$

$$\bar N_t = \int N_t(x)\,dx \qquad \bar N_{t+1} = R\bar N_t \quad \text{if } R>1 \text{ then } \bar N_t \sim R^t \to \infty$$

Persistence at a given point. e.g. $x=0$

as $t\to\infty$:
$$\left(R e^{-\frac{q^2\tau}{2D}}\right)^t$$
need $\cdots > 1$

Gaussian:

$$N_{t+1}(x) = R\int_{-\infty}^{\infty} \text{Gauss}(x-y;\mu=q\tau,\sigma^2=2D\tau)\,N_t(y)\,dy.$$

Assume $N_0(x) = \delta(x)$

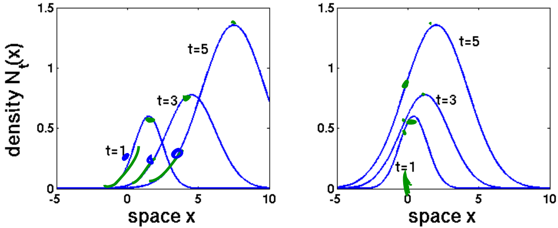
$$N_t(x) = R^t\,\text{Gauss}(x;\mu=q\tau\cdot t,\sigma^2=2D\tau t) = \frac{R^t}{\sqrt{2\pi D\tau t}}\,e^{-\frac{(x-q\tau t)^2}{2D\tau t}}$$

at 0: $\dfrac{R^t e^{-\frac{q^2\tau t}{2D}}}{\sqrt{2\pi D\tau t}}$

Illustration of persistence

Persistence of a point
$\neq$
persistence overall.

bias →



R small

R large

retreat with the bias

← spread upstream (against the bias)

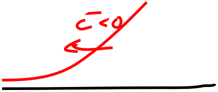
Upstream and downstream speed

$\Longrightarrow$ bias

Recall:

$$N_t(x) \sim e^{-s(x-ct)}$$

Spread to the right when $c^+, s > 0$



$$N_t(x) \sim e^{-s(x-ct)}$$

$s < 0$, $c^- < 0 \Rightarrow$ spread against the bias

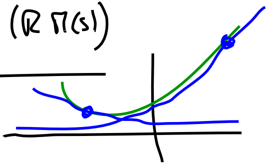
$c^- > 0 \Rightarrow$ retreat with the bias

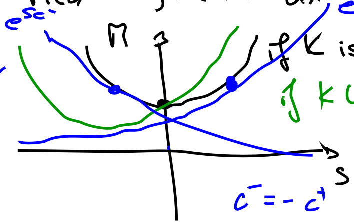
Same as before:

$$e^{sc} = R\,M(s)$$

$$c = \frac{1}{s}\ln\left(R\,M(s)\right)$$

$$M(s) = \int K(x)\,e^{sx}\,dx$$





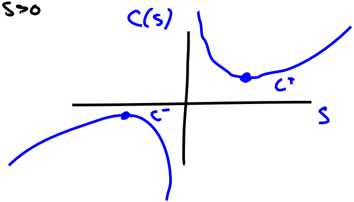
if K is even

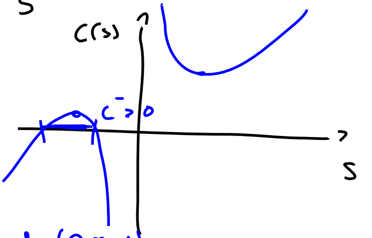
if K has bias

$c^- = -c^+$

Upstream speed and persistence: Gauss

$$c^+ = \inf_{s>0} \frac{1}{s} \ln\big(R\Gamma(s)\big) \qquad c^- = \sup_{s<0} \frac{1}{s} \ln\big(R\Gamma(s)\big)$$





Threshold condition:

$$c^- = 0 \iff R = \frac{1}{\min \Gamma(s)}$$

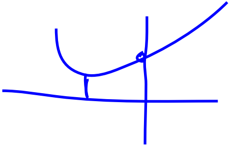
if $\ln\big(R\Gamma(s)\big) < 0$

$\Updownarrow$

$R\Gamma(s) < 1$ for some s

Upstream speed and persistence: ~~Laplace~~ Gauss

$$\text{Gauss}(x;\mu>0,\sigma^2>0) \to M(s) = e^{\frac{\sigma^2 s^2}{2}+\mu s}$$



$$M'(s) = (\sigma^2 s + \mu)\, M(s)$$

$$M'(s) = 0 \iff s^* = -\frac{\mu}{\sigma^2}$$

$$M(s^*) = \exp\left(\frac{\sigma^2}{2}\frac{\mu^2}{\sigma^4} - \frac{\mu^2}{\sigma^2}\right) = \exp\left(-\frac{\mu^2}{2\sigma^2}\right) < 1$$

for upstream spread, $c^- < 0$

$$R > R_{min} = \exp\left(\frac{\mu^2}{2\sigma^2}\right)$$

For Laplace:

Can calculate $M(s) = \frac{a_1 a_2}{(a_1 - s)(a_2 - s)}$, $M'(s)$ ...., M_{min}

Critical patch size

$M(s^*) = \min_s M(s)$

if $RM(s^*) > 1 \Rightarrow L^* < \infty$

if $RM(s^*) < 1 \Rightarrow L^*$ does not exist.

$$\boxed{L^* = \frac{4\arctan\left(1\Big/\sqrt{\frac{4Ra_1|a_2|}{(a_1-a_2)^2}-1}\right)}{(a_1-a_2)/\sqrt{\frac{4Ra_1|a_2|}{(a_1-a_2)^2}-1}}} = \frac{4\arctan\left(1\Big/\sqrt{RM(s^*)-1}\right)}{(a_1-a_2)/\sqrt{RM(s^*)-1}}.$$

$N_{t+1}(x) = \int_0^L k(x-y)\, R N_t(y)\, dy$ find L^* s.t. $N=0$ is unstable

Explicit for Laplace kernel, also for asymmetric Laplace.

as $RM(s^*) \to 1^+$ $L^* \to \infty$

$\Rightarrow$ (Persistence on a finite patch $\Leftrightarrow c^- < 0$)

Multiple dispersal modes

Examples: seeds by wind and/or trucks/cars

$\downarrow$ large % $\qquad\qquad$ $\downarrow$ small %

How much of a difference in invasion speed can a small % make?

Two dispersal modes

1. seeds: wind dispersed vs animal vectored
2. insects: flight vs human transport vs wind
3. scale difference

% %

$$N_{t+1}(x) = R \int (gK_1(x-y) + (1-g)K_2(x-y)N_t(y)dy$$

Scale difference: $\underbrace{K_1(x) = \delta(x)}_{\text{no dispersal}}$, $\underbrace{K_2 = K}_{\text{e.g. Gauss, Laplace}}$

We want: $\hat{c} = \hat{c}(g)$

what is the curve?

$$\hat{K}(x-y) = gK_1 + (1-g)K_2$$

Speed of spread

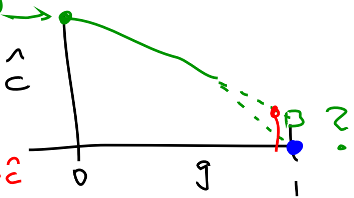
Weinberger 1982

Asymptotic spreading speed exists and is determined by

$$\hat{c}(g) = \inf_{s>0} \frac{1}{s} \ln \left(R[\underbrace{(1-g)}_{=0 \text{ if } g=1} M(s) + \overset{1}{g}] \right) = \inf_{s>0} \frac{\ln R}{s}$$

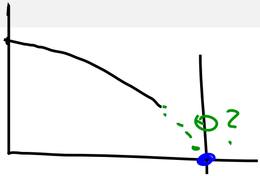
- $\hat{c}(1) = 0$ no dispersal
- If K is even, then $M \geq 1$ and hence $\hat{c}(g)$ is decreasing in g. $g<1$
- $\lim_{g\to 1} \hat{c}(g) = ?$

$\inf_{s>0} \frac{\ln R M(s)}{s}$



If $\lim_{g\to 1} \hat{c}(g) = 0$ then small % dispersing does not have sig impact on $\hat{c}$

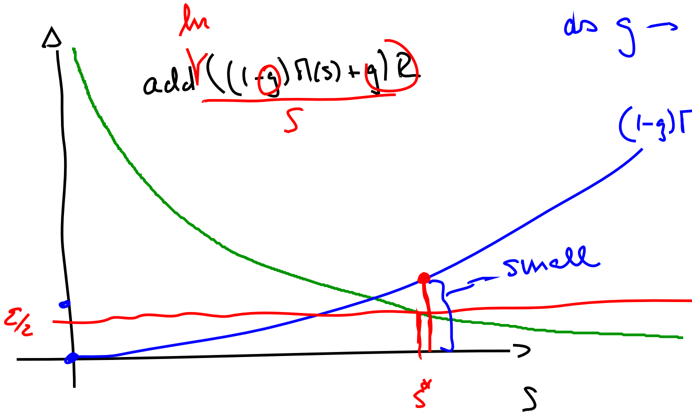
A Lemma



The spreading speed $\hat{c}$ is monotonically decreasing in g, and $\hat{c}(1) = 0$. 1) If $M(s)$ is defined on all of $\mathbb{R}$ (e.g. the Gaussian kernel) then $\hat{c}$ is continuous at $g = 1$. 2) If $\lim_{s \to a} M(s) = \infty$ for some $a < \infty$ (e.g. the Laplace kernel), then $\boxed{\lim_{g \to 1} \hat{c}(g) = \ln(R)/a} > 0$. In particular, $\hat{c}$ is not continuous at $g = 1$.

Proof: 1) $\Pi(s)$ exist for all $s \in \mathbb{R}^+$

$\hat{c}(g) \to 0$ as $g \to 1$



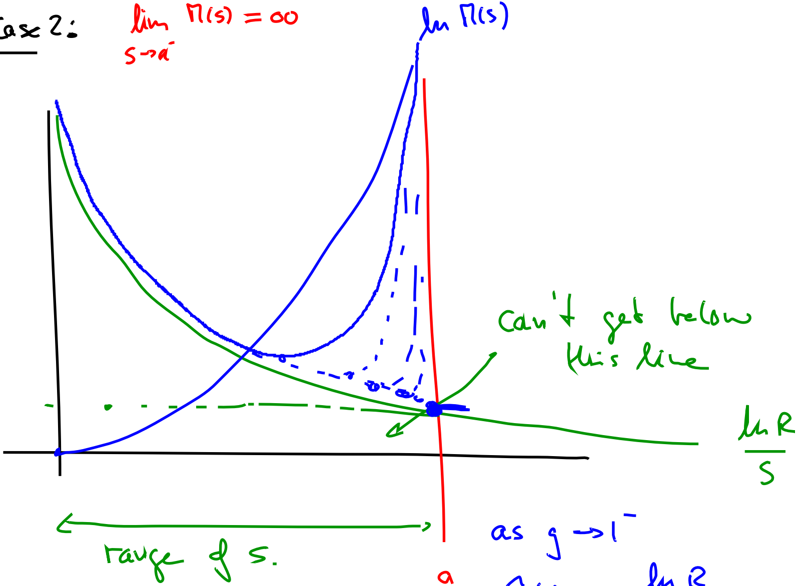
$\frac{\ln(R)}{s} < \frac{\varepsilon}{2}$ for $s > s^*$

Choose $\varepsilon > 0$

Choose g close enough to 1 s.t. $(1-g)\Pi(s^*)$ is small

$$\Rightarrow \hat{c}(g) = \min_{s>0} \ldots < \varepsilon$$

Proof Case 2: $\lim_{s \to a^-} M(s) = \infty$



as $g \to 1^-$

$\hat{c}(g) \to \frac{\ln R}{a} > 0$

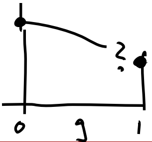
Reid's paradox (1899) Tree populations in UK

- Oaks moved from south to north after ice-age   1000km
- have generation time of ~ 60 years
- ice age 18.000 years (10.000) $\Rightarrow < 300$ generation

$\Rightarrow c \approx 3.3$ km/generation. $c = \sqrt{2\sigma^2 \ln R} \Rightarrow \sigma^2 \approx 0.3 km^2$

$\rightarrow$ animals must move them!

What percentage of long-distance dispersal is necessary for these speeds?



$$N_{t+1}(x) = R\int \big(g K_1(x-y) + (1-g) K_2(x-y)\big) N_t(y)\,dy$$

Homework || Read on Reid's paradox

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