Integrodifference equations in spatial ecology

Lectures 2-3: Critical patch size

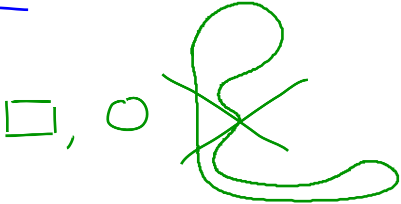
Frithjof Lutscher

Why is there a critical patch size?

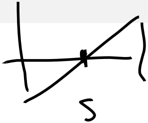
- Loss through perimeter, gain through area
- Perimeter versus area growth
- minimal required area to grow at low density

Here: 1-D

$$\boxed{\Omega = \left[-\frac{L}{2}, \frac{L}{2}\right] \quad \text{length } L}$$



How to calculate a critical patch size?



- Exclude Allee effect ✓ strong
- Trivial solution must be unstable.

Persistence $\longleftrightarrow$ small population can grow. $\Leftarrow$

$\downarrow$

$N = 0$

$N^* = 0$ is unstable

$\Downarrow$

Linearize the IDE at $N^* = 0$ and find eigenvalues.

Linearization

$M_{t+1} = F(M_t) \to M^*$

$$N_{t+1} = \int K(x, y) F(N_t(y)) dy \to N^*\ ?$$

small

Since $F(0) = 0$, $N^* = 0$ is a steady state. Write $N_t = N^* + n_t$.

$N_{t+1} = N^* + n_{t+1}$,

$F(N_t(y)) = F(N^* + n_t(y)) = F(N^*) + F'(N^*) n_t(y) + \text{h.o.t.}$

$N^* + n_{t+1} = \int K(x,y) F(N^*(y)) dy + \int K(x,y) F'(N^*(y)) n_t(y) dy + \ldots$

$\to n_{t+1} = \int K(x,y) F'(N^*(y)) n_t(y) dy + \ldots$

Linear IDE

Linearization

$$n_{t+1}(x) = \underbrace{\int K(x,y)R(y)n_t(y)dy}_{\mathcal{L}[n_t]}$$

Study the eigenvalue problem

$\lambda > 1$

$|\lambda| < 1$

$$\underbrace{\lambda\phi(x) = \int \underbrace{K(x,y)}R\phi(y)dy}_{>0} = \mathcal{L}[\phi]$$

Want to find:

- eigenvalues ✓
- ordered ✓
- positive eigenvector ✓

$R = F'(0) > 0$

BUT: The vectors are functions, the space is infinite dimensional, the theory is more difficult than for matrices in general.

Matrices : Perron – Frobenius Theorem!

Linearization

$\int K(x,y)\,dy \le 1$

Consider

$$\lambda\phi(x) = \int_\Omega K(x-y)R\phi(y)dy, \quad \int_\Omega K(x-y)dx < 1.$$

Then $\lambda < R$.

$$\lambda \int \phi(x)dx = \iint K(x-y) R\, \phi(y)\, dy\, dx$$

$$< \int R\, \phi(y)\, dy$$

$\boxed{\lambda < R}$

$R = F'(0)$

λ: spatially averaged growth rate

R: max. local growth rate.

Laplace kernel and explicit calculations I

$$\underline{\lambda\phi(x)} = \int_{-L/2}^{L/2} \frac{a}{2} e^{-a|x-y|}\phi(y)dy$$

$$= \underbrace{\int_{-L/2}^{x} \frac{a}{2} e^{-a(x-y)} \phi \, dy} - \underbrace{\int_{L/2}^{x} \frac{a}{2} e^{a(x-y)} \phi \, dy}$$

Diff:

$$\lambda \phi'(x) = \frac{a}{2}\cancel{\phi(x)} + \int_{-L/2}^{x} -\frac{a^2}{2} e^{-a(x-y)} \phi \, dy - \frac{a}{2}\cancel{\phi(x)} - \int_{L/2}^{x} \frac{a^2}{2} e^{a(x-y)} \phi \, dy$$

$$\lambda \phi''(x) = \underbrace{-\frac{a^2}{2}\phi(x) + a^2\int_{-L/2}^{x} \frac{a}{2} e^{-a(x-y)} \phi \, dy - \frac{a^2}{2}\phi(x)} - a^2\underbrace{\int_{L/2}^{x} \frac{a}{2} e^{a(x-y)} \phi \, dy} = -a^2\phi + \lambda\phi \, a^2$$

Laplace kernel and explicit calculations II

$$\lambda \phi(x) = R\int_{-L/2}^{L/2} \frac{a}{2} e^{-a|x-y|} \phi(y)dy \Rightarrow \lambda \phi'' = -a^2 \phi R + a^2 \lambda \phi$$

$$\boxed{\phi'' = a^2\left(1 - \frac{R}{\lambda}\right)\phi}$$

Need boundary conditions.

Laplace kernel and explicit calculations III

$$\phi''(x) + a^2(R/\lambda - 1)\phi(x) = 0$$

Nice ODE, but boundary conditions?

Laplace kernel and explicit calculations IV

$$\lambda\,\phi'\left(\frac{L}{2}\right) = \int_{-L/2}^{L/2} -\frac{a}{2}\cdot a\, e^{-a(x-y)}\phi(y)\,dy = -a\lambda\phi\left(\frac{L}{2}\right)$$

$$\Rightarrow \boxed{\phi'\left(\frac{L}{2}\right) = -a\,\phi\left(\frac{L}{2}\right)}$$

$$\Rightarrow \phi'\left(-\frac{L}{2}\right) = a\,\phi\left(-\frac{L}{2}\right)$$

Laplace kernel and explicit calculations V

$$\phi''(x) + a^2\underbrace{(R/\lambda - 1)}^{>0}\phi(x) = 0$$

$x \to -x$

with boundary $\phi'(\mp l/2) = \pm a\phi(\mp l/2)$
Shown before that $\lambda < R$.
Use symmetry to get $\phi(x) = \cos(Ax)$ with $A = a\sqrt{R/\lambda - 1}$.

$$\phi'\left(\frac{L}{2}\right) = -a\,\phi\left(\frac{L}{2}\right)$$

$$-A\sin\left(A\frac{L}{2}\right) = -a\cos\left(A\frac{L}{2}\right)$$

$$\tan\left(A\frac{L}{2}\right) = \frac{a}{A} = \boxed{\frac{1}{\sqrt{R/\lambda - 1}} = \tan\left(\frac{aL}{2}\sqrt{R/\lambda - 1}\right)}$$

Laplace kernel and explicit calculations VI

$$\phi''(x) + a^2(R/\lambda - 1)\phi(x) = 0$$

with boundary $\phi'(\mp l/2) = \pm a\phi(\mp l/2)$
Substitute $\phi(x) = \cos(Ax)$ with $A = a\sqrt{R/\lambda - 1}$.

Laplace kernel and explicit calculations VII

$$\lambda\phi = \int_{-L/2}^{L/2} \frac{a}{2} e^{-a|x-y|} R\phi \, dy$$

Transcendental relation

$$\tan\left(\frac{aL\sqrt{R/\lambda - 1}}{2}\right) = \frac{1}{\sqrt{R/\lambda - 1}}.$$

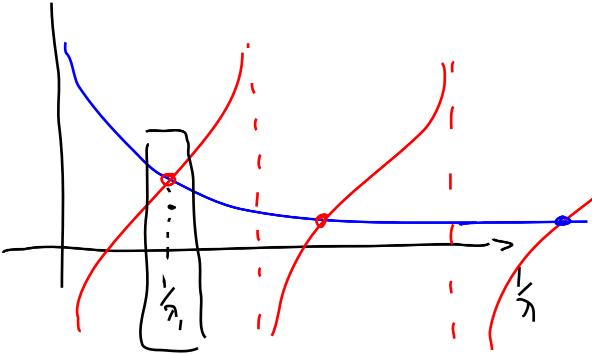
Or: $\lambda = 1$

$\Downarrow$

$$\tan\left(\frac{aL\sqrt{R-1}}{2}\right) = \frac{1}{\sqrt{R-1}}$$

$\Downarrow$

$L^* = \ldots$

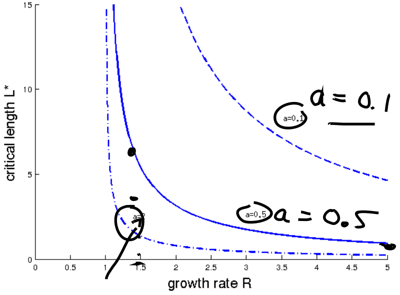


Laplace kernel and explicit calculations VIII

$$aL = \frac{2}{\sqrt{R-1}} \arctan\left(\frac{1}{\sqrt{R-1}}\right)$$

Critical domain size

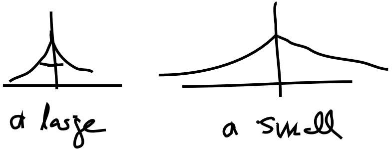
$$\boxed{L^* = \frac{2}{a\sqrt{R-1}} \arctan\left(\frac{1}{\sqrt{R-1}}\right).}$$



a = 2

a small ⇒ requires L large.

$$a \sim \frac{1}{\sqrt{\sigma^2}}$$



More general theory on linearization

- Analogy with matrices: Perron–Frobenius
- Choose function space, depending on properties of K.
- Krein–Rutman theorem

$C([-\frac{L}{2}, \frac{L}{2}])$ $\mathcal{L}^2[\Omega]$

Theorem:
Assume that Ω is bounded and connected and that K and R are continuous and positive. Then the integral operator

$$\phi \mapsto \int_\Omega K(x,y)R(y)\phi(y)dy$$

has a dominant eigenvalue, i.e., a real, positive eigenvalue that is larger in modulus than all other eigenvalues. The population can persist if the dominant eigenvalue is larger than one.

Scaling

$[a] = \frac{1}{\text{space}}$

Notice that aL is the quantity of interest. Can scale the equation.

$$\lambda \phi(x) = \int_{-L/2}^{L/2} K(x-y) R \phi(y)\, dy$$

$y = Lz \quad z \in [-\tfrac{1}{2}, \tfrac{1}{2}]$

$x = Lw \quad w \in$

$$\lambda \phi(Lw) = \int_{-1/2}^{1/2} L K(L(w-z)) R \phi(Lz)\, dz$$

$$K(x-y) = \frac{a}{2} e^{-a|x-y|}$$

$$\tilde{K}(w-z) = \frac{La}{2} e^{-aL|w-z|}$$

$$\tilde{\phi}(w) = \phi(Lw)$$

$$\hat{L} = La$$

$$\tilde{K}(w-z) = LK(L(w-z))$$

$[\hat{L}] = 1$

$$\boxed{\lambda \tilde{\phi} = \int_{-1/2}^{1/2} \tilde{K}(w-z) R \tilde{\phi}(z)\, dz}$$

$[L] = \text{space}$

What is the effect of different dispersal kernels

- Gaussian
- Laplace
- others

Need numerics: Discretize and use eigenvalue routines.

Example: Different kernels I

Variance = 1

name	formula	constraint
Gaussian	$\frac{1}{\sqrt{2\pi\sigma^2}} \exp\left(-\frac{x^2}{2\sigma^2}\right)$	$\sigma^2 = 1$
Laplace	$\frac{a}{2} \exp(-a\|x\|)$	$a = \sqrt{2}$ $\rightarrow \sigma^2 = 1$
Top-hat	$\frac{1}{2\beta}, \quad x \in [-\beta, \beta]$	$\beta = \sqrt{3}$
Tent	$\frac{1}{\eta} - \frac{\|x\|}{\eta^2}, \quad x \in [-\eta, \eta]$	$\eta = \sqrt{6}$
Double Gamma	$\frac{1}{2\Gamma(k)\theta}\left\|\frac{x}{\theta}\right\|^{k-1} \exp\left(-\left\|\frac{x}{\theta}\right\|\right)$	$k(k+1)\theta^2 = 1$
Double Weibull	$\frac{k}{2\theta}\left\|\frac{x}{\theta}\right\|^{k-1} \exp\left(-\left\|\frac{x}{\theta}\right\|^{k}\right)$	$\theta^2\Gamma(1+2/k) = 1$

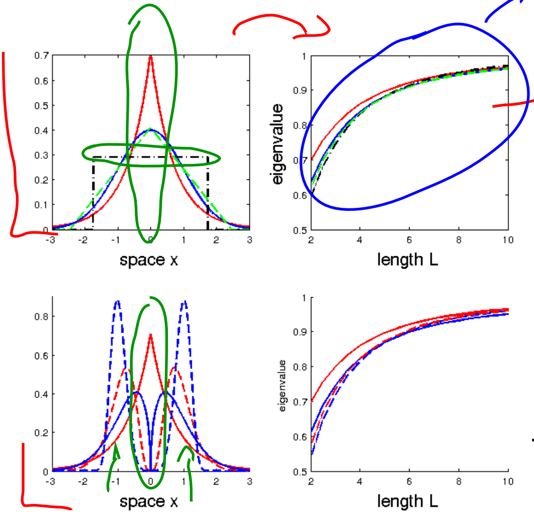
$-\beta \quad 0 \quad \beta$

$0 \quad \eta$

0

Example: Different kernels II

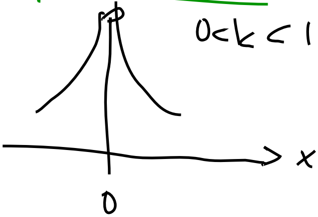
Chap 9 approx.



L is insensitive to dispersal behaviour

Laplace concentrates near zero.

$0<k<1$



Separable kernels: reduction to finite dimension

allow $R = R(y)$

Simple example: $K(x,y) = K_1(x)K_2(y)$.

$$\lambda \phi(x) = \int K_1(x) K_2(y) R \phi(y)\, dy = K_1(x) \int K_2 R \phi\, dy$$

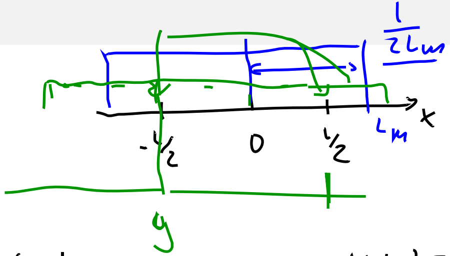
$$\Rightarrow \phi(x) = K_1(x)$$

$$\lambda = \int K_2(y) R(y) K_1(y)\, dy$$

Separable: $K(x,y) = \sum_{j=1}^{m} K_1^{(j)}(x) K_2^{(j)}(y)$

Uniform dispersal

$K(x,y) = \frac{1}{2L_m}$ and $L_m > L$.



$$\lambda \phi(x) = \frac{1}{2L_m} \int_{-L/2}^{L/2} R(y)\phi(y)\,dy$$

$K_1(x) = \frac{1}{2L_m}$, $K_2(y) = 1$

$\phi(x) = 1$

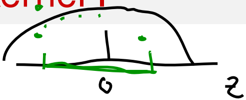
$$\lambda = \frac{1}{2L_m} \int_{-L/2}^{L/2} R(y)\,dy = \left(\frac{L}{2L_m}\right) \underbrace{\frac{1}{L}\int_{-L/2}^{L/2} R(y)\,dy}_{\text{average growth}}$$

prob of staying in Ω

domain length / dispersal area

The cosine kernel I

We can write



$$K(w,z) = \begin{cases} \frac{\pi}{2}\cos\left(\pi(w-z)\right), & z - 0.5 \le w \le z + 0.5 \\ 0 & \text{otherwise}, \end{cases}$$

as

$\cos(w-z) = \cos(w)\cos(z) + \sin(w)\sin(z)$

$$K(w,z) = \sum_{j=1}^{2} K_1^{(j)}(w) K_2^{(j)}(z)$$

with $K_1^{(j)} = K_2^{(j)}$ and

$$K_1^{(1)}(w) = \sqrt{\frac{\pi}{2}}\cos(\pi w) \quad \text{and} \quad K_1^{(2)}(w) = \sqrt{\frac{\pi}{2}}\sin(\pi w).$$

Note: scaled max dispersal distance to 0.5. Choose domain length $l < 0.5$. $[-l/2, l/2]$

The cosine kernel II

Substitute $\phi(w) = c_1 K_1^{(1)}(w) + c_2 K_1^{(2)}(w)$ into the IDE.

$$\lambda \phi(\omega) = \int \underbrace{K_1^{(1)}(\omega) K_2^{(1)}(z) R(z) \phi(z)}_{} + \underbrace{K_1^{(2)}(\omega) K_2^{(2)}(z) R(z) \phi(z)\, dz}_{}$$

$$\to \lambda c_1 K_1^{(1)} + c_2 K_1^{(2)}$$

$$\to K_1^{(1)}(\omega) \int K_2^{(1)} R (c_1 K_1^{(1)} + c_2 K_1^{(2)}) dz = c_1 \boxed{\int K_2^{(1)} K_1^{(1)} R\, dz} \cdot K_1^{(1)}(\omega) + c_2 \boxed{\int K_2^{(1)} K_1^{(2)} R\, dz}\, K_1^{(1)}(\omega)$$

$K_1^{(1)}, K_1^{(2)}$ are lin. indep.

The cosine kernel III

$\int K_1^{(1)} \cdot K_1^{(1)} \cdot R \, dz$

$$\lambda \begin{bmatrix} c_1 \\ c_2 \end{bmatrix} = \frac{\pi}{2} \begin{bmatrix} \int \cos^2(\pi z) R(z) dz & \int \cos(\pi z) R(z) \sin(\pi z) dz \\ \underbrace{\int \cos(\pi z) R(z) \sin(\pi z) dz}_{=0} & \int \sin^2(\pi z) R(z) dz \end{bmatrix} \begin{bmatrix} c_1 \\ c_2 \end{bmatrix}$$

$= 0$

Evaluate for constant R:

$$\lambda \begin{bmatrix} c_1 \\ c_2 \end{bmatrix} = \frac{R}{4} \begin{bmatrix} 2\pi l + \sin(2\pi l) & 0 \\ 0 & \underbrace{2\pi l - \sin(2\pi l)}_{>0} \end{bmatrix} \begin{bmatrix} c_1 \\ c_2 \end{bmatrix}.$$

Use $l < 0.5$ to calculate R^*.

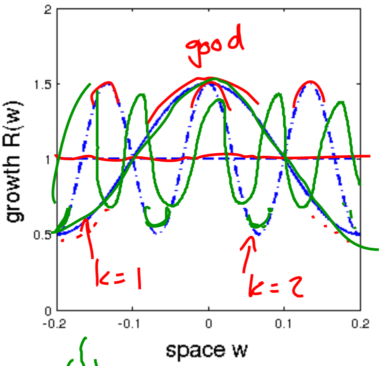
$$\lambda^+ = \frac{R}{4}\left(2\pi l + \sin(2\pi l)\right)$$

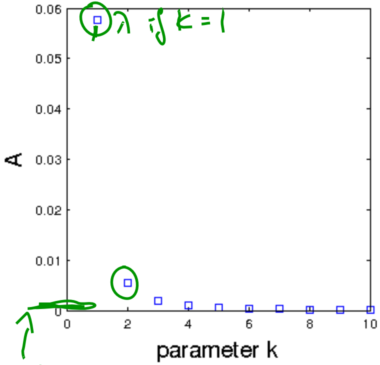
The cosine kernel IV

average – same for all k

Use carefully chosen $R(x) = \bar{R}[1 + \epsilon \cos((2k - 1)\pi z/l)]$.

variation





Why is better than

λ if R = const.

Approximation by separable kernels

Gauss
$$K(x,y) = \frac{1}{\sqrt{2\pi\sigma^2}} e^{-\frac{(x-y)^2}{2\sigma^2}} = \frac{1}{\sqrt{2\pi\sigma^2}} e^{-\frac{x^2}{2\sigma^2}} e^{-\frac{y^2}{2\sigma^2}} e^{\frac{xy}{\sigma^2}}.$$

$$e^{\frac{xy}{\sigma^2}} = \sum_k \frac{\left(\frac{xy}{\sigma^2}\right)^k}{k!} = \sum_k \frac{\left(\frac{x}{\sigma}\right)^k \left(\frac{y}{\sigma}\right)^k}{\sqrt{k!}\sqrt{k!}}$$

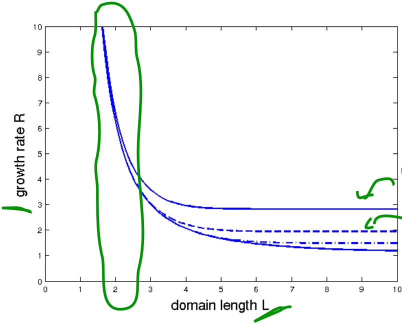
truncate

$$\underline{K(x,y)} = \cancel{\frac{1}{\sqrt{2\pi\sigma^2}}} \sum_k^{M} \underbrace{\frac{1}{\sqrt{\sqrt{2\pi\sigma^2}}} \frac{1}{\sqrt{k!}} \left(\frac{x}{\sigma}\right)^k e^{-\frac{x^2}{2\sigma^2}}}_{K_1^{(k)}(x)} \underbrace{\frac{1}{\sqrt{\sqrt{2\pi\sigma^2}}} \frac{1}{\sqrt{k!}} \left(\frac{y}{\sigma}\right)^k e^{-\frac{y^2}{2\sigma^2}}}_{K_2^{(k)}(y)}$$

Approximation by separable kernels

$$\lambda c_j = R \sum_{k=0}^{m} K_{jk} c_k,$$

$$K_{jk} = \int_{-L/2}^{L/2} K_1^{(j)}(y) K_2^{(k)}(y) dy = \frac{1}{\sqrt{2\pi\sigma^2 j! k!}} \int_{-L/2}^{L/2} \left(\frac{y}{\sigma}\right)^{(j+k)} \exp\left(-\frac{y^2}{\sigma^2}\right) dy.$$



m = 1

m = 2