Integrodifference equations in spatial ecology

Lecture 17: Spatial Heterogeneity I

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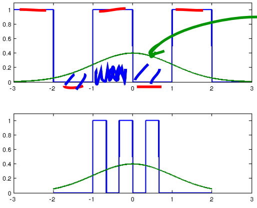
Spatial Heterogeneity

- landscapes vary in quality
- models so far: single patch and homogeneous
- idea 1: continuous variation (homework)
- idea 2: multiple patches
- analytically easier: infinitely many patches, periodic



$H(x)$

$K(x)$

Persistence in a patchy landscape.

Heterogeneous IDE model

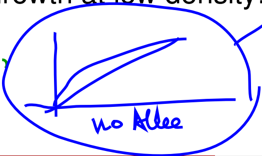
$K(x-y)$

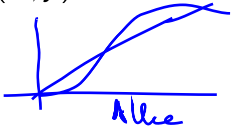
spatial variation in growth function

$$N_{t+1}(x) = Q[N_t](x) = \int_{-\infty}^{\infty} K(x,y) F(N_t(y), y)\, dy$$

?

- Case: dispersal is not affected by heterogeneity (seeds)
- $K(x,y) = \hat{K}(x-y)$ is a difference kernel (drop $\hat{}$)
- $F(N,y) < N$: bad place
- $F(N,y) > N$ for some N : good place
- Growth at low density: $F(N,y) > N$ for $N \in (0, N^*)$





Persistence question (grow from low density)

what if $F(0) \neq 0$

Linearize at $N = 0$:

Laplace

$$N_{t+1}(x) = Q'[N_t](x) = \int_{-\infty}^{\infty} K(x-y)R(y)N_t(y)dy$$

$N_t(x) = \lambda^t \phi(x)$

Set-up:

- $R(y) = \partial F / \partial N(0, y)$
- Good places: $R(y) > 1$. Bad places: $0 < R(y) < 1$.
- Scenario: source-sink landscape

Question: What fraction of good patches allows for persistence?

- simplification: periodicity

length L_1 bad L_2

Laplace kernel

$L_1 + L_2 = L$

assume periodicity; e.g.
ϕ is L-periodic

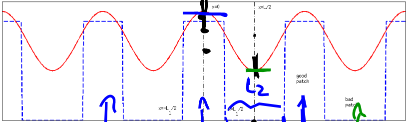
The eigenvalue equation

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

in the periodic case reduces to a Hill's equation

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

now:
$R(x) = R_1 > 1$ on good
$R(x) = R_2 < 1$ on bad.



L_2

0 $\frac{L_1}{2}$ good L bad

$L/2$

$\left[-\frac{L_1}{2}, \frac{L_1}{2}\right]$

$\left[\frac{L_1}{2}, \frac{L_1}{2} + L_2\right] = \left[\frac{L_1}{2}, L - \frac{L_1}{2}\right]$

Calculations

$$\phi'' = a^2\left(1 - \frac{R_1}{\lambda}\right)\phi \qquad \left[-\frac{L_1}{2}, \frac{L_1}{2}\right] \qquad \boxed{\phi\left(\frac{L_1}{2}\right) = \phi\left(\frac{L_1}{2}\right)}$$

$$\phi'' = a^2\left(1 - \frac{R_2}{\lambda}\right)\phi \qquad \left[\frac{L_1}{2}, L - \frac{L_1}{2}\right] \qquad \phi\left(-\frac{L_1}{2}\right) = \phi\left(L - \frac{L_1}{2}\right)$$

Connected by: continuity / periodicity: + for derivatives.

$\Rightarrow$ 4 coeff. and 4 matching conditions ✓

More clever: use symmetry: and half-intervals: $\phi'(0) = 0$

$$\phi'' = a^2\left(1 - \frac{R_1}{\lambda}\right)\phi \qquad \left[0, \frac{L_1}{2}\right]$$

$$\phi'' = a^2\left(1 - \frac{R_2}{\lambda}\right)\phi \qquad \left[\frac{L_1}{2}, \frac{L_2}{2}\right] \qquad \phi'\left(\frac{L_2}{2}\right) = 0$$

Observe: dominant λ:

$$R_2 < \lambda < R_1$$

$$1 - \frac{R_1}{\lambda} < 0 \qquad 1 - \frac{R_2}{\lambda} > 0$$

More calculations

$$\Rightarrow \boxed{\nu_1 \tan\left(\frac{\nu_1 L_1}{2}\right) = \nu_2 \tanh\left(\frac{\nu_2 L_2}{2}\right)}$$

Solvability condition

$$\phi'' = \underbrace{a^2\left(1-\frac{R_1}{\lambda}\right)}_{<0}\phi \quad : \quad \boxed{\phi(x) = A_1\cos(\nu_1 x)} + B_1\sin(\nu_1 x) \qquad \nu_1^2 = -a^2\left(1-\frac{R_1}{\lambda}\right)$$

Because $\phi'(0)=0 \Rightarrow B_1 = 0$

$$\phi'' = \underbrace{a^2\left(1-\frac{R_2}{\lambda}\right)}_{>0}\phi \quad : \quad \boxed{\phi(x) = A_2\cosh\left(\nu_2\left(\tfrac{L}{2}-x\right)\right)} \qquad \nu_2^2 = a^2\left(1-\frac{R_2}{\lambda}\right)$$

$$+ B_2\sinh\left(\nu_2\left(\tfrac{L}{2}-x\right)\right)$$

Because $\phi'\left(\frac{L}{2}\right)=0 \Rightarrow B_2 = 0$

Now: find conditions on A_1, A_2 from matching conditions at $\frac{L_1}{2}$

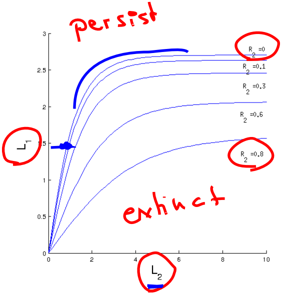
$$\phi\left(\tfrac{L_1}{2}\right) = \phi\left(\tfrac{L_1}{2}\right) \Rightarrow A_1\cos\left(\frac{\nu_1 L_1}{2}\right) = A_2\cosh\left(\frac{\nu_2 L_2}{2}\right)$$

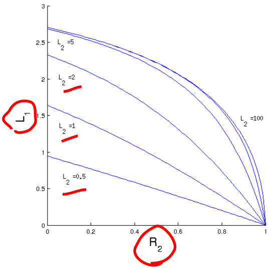
$$\frac{L}{2} - \frac{L_1}{2} = \frac{L_2}{2}$$

$$\phi'\left(\tfrac{L_1}{2}\right) = \phi'\left(\tfrac{L_1}{2}\right) \Rightarrow -\nu_1 A_1\sin\left(\frac{\nu_1 L_1}{2}\right) = -\nu_2 A_2\sinh\left(\frac{\nu_2 L_2}{2}\right)$$

Result

$$L_1 = \frac{2}{a\sqrt{R_1 - 1}} \arctan\left[\sqrt{\frac{1-R_2}{R_1-1}} \tanh\left(\frac{aL_2\sqrt{1-R_2}}{2}\right)\right].$$





$L_2 \to \infty$ tanh $\to 1$

$$L_1 = \frac{2}{a\sqrt{R_1-1}} \arctan\left(\frac{\sqrt{1-R_2}}{\sqrt{R_1-1}}\right)$$

now $R_2 \to 0$

$$L_1 = \frac{2}{a\sqrt{R_1-1}} \arctan\left(\frac{1}{\sqrt{R_1-1}}\right)$$

A lower bound

Know: $R_2 < \lambda < R_1$

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

Hill's equation solved for $R(x)$ is

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

Average over one period

$$\bar{R} = \frac{1}{L}\int_0^L R(x)\,dx = \lambda\left(1 - \frac{1}{a^2}\frac{1}{L}\int_0^L \frac{\phi''}{\phi}\,dx\right) \Rightarrow \bar{R} = \lambda\left(\overbrace{1 - \frac{1}{a^2 L}\,\circ}^{<1}\right)$$

$$\int_0^L \frac{\phi''}{\phi}\,dx = \frac{\phi'}{\phi}\Big|_0^L - \int_0^L \phi'\left(-\frac{1}{\phi^2}\right)\cdot\phi'\,dx = + \int_0^L \frac{\phi'^2}{\phi^2}\,dx > 0$$

$\phi'' \cdot \frac{1}{\phi}$

$f' \quad g$

periodic

$\Rightarrow \lambda > \bar{R}$

$\Rightarrow$ growth rate > average growth rate.

More theory

Start with:

$$\underline{N_{t+1}(x)} = Q[N_t](x) = \int_{-\infty}^{\infty} K(x,y)F(\underline{N_t(y)}, y)dy \Bigg]$$

where $\underbrace{F(\cdot, x+L) = F(\cdot, x)}$, and $\underbrace{K(x+L, y+L) = K(x,y)}_{K(x-y)}$

1) Lemma:
Then Q leaves the subspace of L-periodic functions on $\mathbb{R}$ invariant.

$\Rightarrow$ can restrict Q to periodic functions.

More theory

2 Lemma:

If N is an L-periodic fixed point of Q, then N is precisely the L-periodic extension of a fixed point of operator Q_L, defined by

$$Q_L[N](x) = \int_0^L \widehat{K}(x,y)F(N(y),y)dy, \qquad \subset [0,L]$$

where

$$\widehat{K}(x,y) = \sum_{m\in\mathbb{Z}} K(x,y+mL), \qquad x,y \in [0,L],$$

on the space of bounded functions on $[0,L]$. Vice versa, if N is a fixed point of Q_L, then its L-periodic extension to $\mathbb{R}$ is a fixed point of Q.

Still more theory

Under the usual conditions, operator Q_L is a completely continuous operator on $\mathcal{L}^2(0, L)$. It is Fréchet differentiable at 0, and the derivative is the completely continuous operator

$$Q_L'[N](x) = \int_0^L \widehat{K}(x, y)R(y)N(y)dy,$$

where $R(x) = \partial F/\partial N(0, x)$.

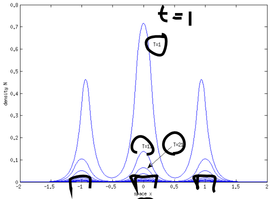
The final piece of the puzzle

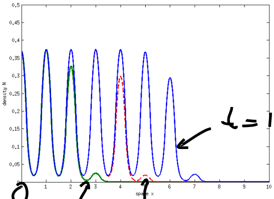
Theorem: (Musgrave 2014)
The trivial solution for Q is stable (locally asymptotically stable) if and only if it is stable (locally asymptotically stable) for Q_L.

Spreading in heterogeneous landscapes

If persistence is given, how would a local introduction propagate?

$$N_{t+1}(x) = Q[N_t](x) = \int_{-\infty}^{\infty} K(x-y)F(N_t(y),y)dy$$





Travelling Periodic Wave (TPW)

Numerical observation: periodic travelling waves

no persistence

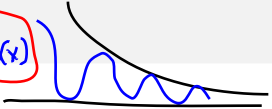
persistence ✓

c?

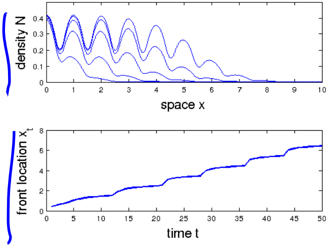
for TW: $N \sim e^{-s(x-ct)}$

More simulations

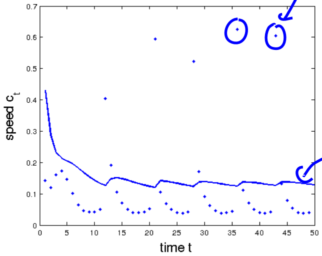
$$\boxed{N_t(x) \sim e^{-s(x-ct)}\phi(x)}$$



ϕ is L-periodic



instantaneous



average up to $\to c^*$ here.

$$c_t = \frac{x_t}{t}$$

Heuristic calculations

Start with the linear equation

$$N_{t+1}(x) = Q[N_t](x) = \int_{-\infty}^{\infty} \frac{a}{2} e^{-a|x-y|} R(y) N_t(y) dy$$

Substitute the ansatz $N_t = \exp(-s(x-ct))\phi(x)$ to get

$$e^{sc} N_t(x) = \int_{-\infty}^{\infty} \frac{1}{2} e^{-|x-y|} R(y) N_t(y) dy$$

and differentiate to get

$$N_t''(x) = (1 - e^{-sc} R(x)) N_t(x)$$

$N_t' = -s e^{-s(x-ct)} \phi + e^{-s(x-ct)} \phi'$. $N_t'' = (s^2\phi - 2s\phi' + \phi'') e^{-s(x-ct)}$

Heuristic calculations II

no symmetry $x \to -x$

Substitute the definition of ϕ and find

$$\boxed{\phi'' - 2s\phi' + (s^2 - 1 + e^{-sc}R(x))\phi = 0}$$

- Linear second-order ✓
- periodic ✓
- piecewise constant R ✓ $R(x) = \begin{cases} R_1 \\ R_2 \end{cases}$
- periodic matching conditions ✓
- 4×4 matrix

$\phi(x) = A_1 \ldots A_2$ in $[-\frac{L_1}{2}, \frac{L_1}{2}]$

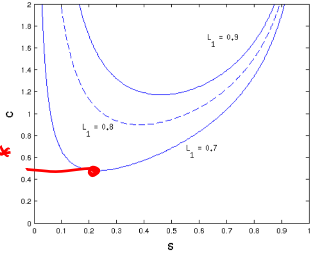
$\phi(x) = B_1 \ldots B_2$ in $[\frac{L_1}{2}, L - \frac{L_1}{2}]$

Dispersion relation

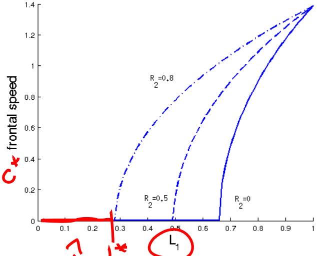
q_i contain s, c

$$\boxed{\cosh(sL) = \cosh(q_1 L_1)\cosh(q_2 L_2) + \frac{q_1^2 + q_2^2}{2q_1 q_2}\sinh(q_1 L_1)\sinh(q_2 L_2),}$$

c^*



c^*



$C = c(s)$

L_1^*

no persistence

param.