Integrodifference equations in spatial ecology

Lecture 18: Spatial Heterogeneity II

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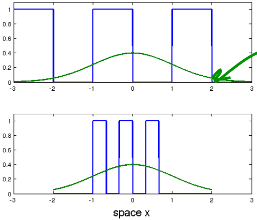
Small-scale Heterogeneity

$N_{t+1}(x) = \int K(x-y) F(N_t(y), y)\, dy$

What if landscape heterogeneity is much smaller than dispersal distance?



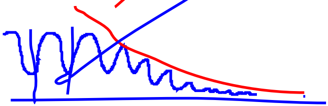
Heterogeneous linear IDE model

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

- Special case: Laplace kernel, piecewise constant growth function

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

- $q_i = \sqrt{1 - e^{sc} R_i}$
- Exact but implicit and specific to Laplace
- Goal today: approximate but explicit and general



The set-up

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

$a = a(y)$

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

- K depends on distance, but parameter(s) may depend on initial location
- R, K are L-periodic (in second argument)
- Ansatz $N_t(x) = \exp(-s(x-ct))\phi(x)$, where ϕ is L-periodic
- Goal: make parameter L appear in the equation, then let $L \to 0$.

$e^{-s(x-c(t+1))}\phi(x) = \int_{-\infty}^{\infty} K(x-y;y)R(y)e^{-s(y-ct)}\phi(y)\,dy$

x is L-periodic

$e^{x}\phi(x) = \int_{-\infty}^{\infty} K(x-y;y)e^{s(x-y)}R(y)\phi(y)\,dy$ $\quad x = L\omega$

The scaling

Apply $x = Lw$, $y = Lz$ to

$$e^{sc}\phi(x) = \int_{-\infty}^{\infty} K(x-y;y)e^{s(x-y)}R(y)\phi(y)dy$$

$$e^{sc}\phi(Lw) = \int_{-\infty}^{\infty} LK(L(w-z);Lz)\,e^{sL(w-z)}R(Lz)\phi(Lz)dz$$

$$e^{sc}\hat{\phi}(w) = \int_{-\infty}^{\infty} L\hat{K}(L(w-z);z)\,e^{sL(w-z)}\hat{R}(z)\hat{\phi}(z)dz$$

$\hat{\phi}$, $\hat{R}$, $\hat{K}(\cdot,z)$ are 1-periodic

$$e^{sc}\hat{\phi}(w) = \int_0^1 \underbrace{\sum_{n\in\mathbb{Z}} L\hat{K}(L(w-z-n);z)\,e^{sL(w-z-n)}}_{=M(s;z)}\hat{R}(z)\hat{\phi}(z)dz$$

The sum

$$\sum_{n=-\infty}^{\infty} L\hat{K}(L(w-z-n); z)e^{sL(w-z-n)}$$

as $L \to 0$

x_n

$$\int f(x)\,dx \approx \sum_n f(x_n)\cdot \Delta x \qquad \Delta x = L$$

as $L \to 0$ we get

$$\int_{-\infty}^{\infty} \hat{K}(w-z; z)e^{s(w-z)}\,dw = M(s, z)$$

The final step

$$e^{sc}\hat{\phi}(w) \approx \int_0^1 \hat{R}(z) M(s;z) \hat{\phi}(z)\, dz$$

$= \hat{\phi}$ indep. of w — indep of w

$$e^{sc} = \int_0^1 \hat{R}(z) M(s;z)\, dz = R \cdot M(s)$$

if $\hat{R}$, M are indep of z

$$\Rightarrow \quad c = \frac{1}{s} \ln \left(\int_0^1 \hat{R}(z) M(s;z)\, dz \right)$$

$$= \frac{1}{s} \ln \left(\int_0^1 \hat{R}(z)\, dz \cdot M(s) \right) \quad \text{if } M(s), \quad \int_0^1 \hat{R}(z)\, dz = \bar{R}$$

Illustrations

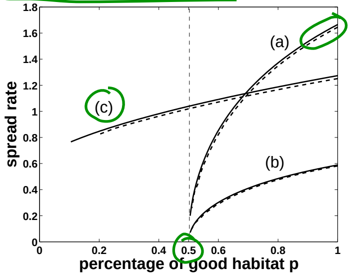
$N_{t+1}(x) = \int_{-\infty}^{\infty} K(x-y; y) R(y) N_t(y)\, dy$

Scaled $L = 1$ choose variance

large variance $\Leftrightarrow$ small L

$R = \begin{cases} R_1 > 1 \\ R_2 = 0 \end{cases}$ $\quad \frac{L_1}{L} = p$

Gaussian kernel



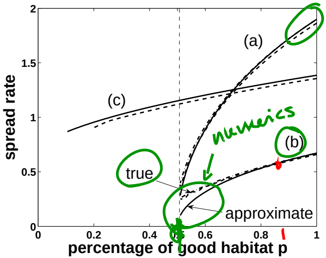
$L \to 0$

- (a) $R_2 = 0$, small period, large variance
- (b) $R_2 = 0$, large period, small variance — large L
- (c) $R_1 = R_2$, mixed variance

Dewhirst & L 2009

Illustrations

Laplace kernel



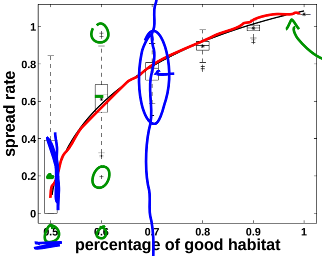
(a) $R_2 = 0$, small period, large variance

(b) $R_2 = 0$, large period, small variance

(c) $R_1 = R_2$, mixed variance

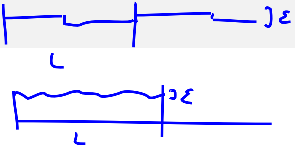
Illustrations

Random Landscape



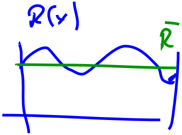
- Gaussian kernels
- 100 landscapes each
- mean, median, percentile, outliers

Small variation



Start again with

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



and assume

$$R(x) = \bar{R}(1 + \epsilon R_1 + O(\epsilon^2))$$

where

$$\bar{R} = \frac{1}{L}\int_0^L R(x)dx, \quad \int_0^L R_1(x)dx = 0.$$

$$N_{t+1}(x) = \underbrace{\int K(x-y)\bar{R}N_t(y)dy}_{K_0[N_t]} + \varepsilon \underbrace{\int K(x-y)\bar{R}R_1(y)N_t(y)dy}_{K_1[N_t]} + O(\varepsilon^2)$$

Expansion in ϵ

$$N_t(x) = e^{-s(x-ct)}\phi(x) \Longrightarrow e^{sc}\phi(x) = (\mathcal{K}_0 + \varepsilon \mathcal{K}_1)[\phi] + O(\varepsilon^2)$$

$$c(s,\varepsilon) = c_0(s) + \varepsilon c_1(s) + O(\varepsilon^2) \qquad \phi(x,\varepsilon) = \phi_0(x) + \varepsilon \phi_1(x) + O(\varepsilon^2)$$

$$\Rightarrow e^{sc} = e^{s(c_0 + \varepsilon c_1 + \dots)} = e^{sc_0} + \varepsilon c_1 e^{sc_0} + \varepsilon^2 \dots$$

$$\left(e^{sc_0} + \varepsilon c_1 e^{sc_0}\right)\left(\phi_0 + \varepsilon \phi_1\right) = \mathcal{K}_0\phi_0 + \varepsilon\left(\mathcal{K}_1\phi_0 + \mathcal{K}_0\phi_1\right) + \varepsilon^2 \dots$$

$$\mathcal{K}_0[\phi] = \int K(x-y) e^{s(x-y)} \bar{R} \phi \, dy$$

$$\mathcal{K}_1[\phi] = \int K(x-y) e^{s(x-y)} \bar{R} R_1(y) \phi \, dy$$

The lowest terms

$$(e^{sc_0} + \epsilon c_1 e^{sc_0})(\phi_0 + \epsilon\phi_1) = \mathcal{K}_0\phi_0 + \epsilon(\mathcal{K}_0\phi_1 + \mathcal{K}_1\phi_0)$$

ε^0: $e^{sc_0}\phi_0 = \mathcal{K}_0\phi_0 = \int k(x-y)\bar{R}\,\phi_0(y)\,dy$, $\phi_0(y) = \text{const}$

$k(x-y) \to e^{s(x-y)}$, $\to M(s)\cdot\bar{R}$

$\Rightarrow c_0 = \frac{1}{s}\ln\left(M(s)\bar{R}\right)$

ε^1: $e^{sc_0}c_1\phi_0 + e^{sc_0}\phi_1 = \mathcal{K}_0\phi_1 + \mathcal{K}_1\phi_0$

$e^{sc}c_1\phi_0 - \mathcal{K}_1\phi_0 = -e^{sc_0}\phi_1 + \mathcal{K}_0\phi_1$

Claim: $c_1 = 0$

L-periodic functions $\mathcal{L}^2[0,L]$ with $\langle \, , \, \rangle$

$e^{sc_0}\phi_0 - \mathcal{K}_0\phi_0 = 0$

$$\langle \phi_0^*, e^{sc_0}\phi_1 - \mathcal{K}_0\phi_1 \rangle$$

$$= \langle \underbrace{e^{sc_0}\phi_0^* - \mathcal{K}_0^*\phi_0^*}_{=0}, \phi_1 \rangle = 0$$

$$= \langle \phi_0^*, e^{sc_0}c_1\phi_0 - \mathcal{K}_1\phi_0 \rangle = 0$$

$$\Rightarrow \langle \phi_0^*, e^{sc_0}c_1\phi_0 \rangle - \langle \phi_0^*, \mathcal{K}_1\phi_1 \rangle = 0$$

$$\Leftrightarrow c_1 = \frac{\langle \phi_0^*, \mathcal{K}_1\phi_0 \rangle}{\langle \phi_0^*, e^{sc_0}\phi_0 \rangle} \stackrel{!}{=} 0$$

$$\int_0^L \phi_0^*(x) \int_0^L k(x-y)\bar{R}R_1(y)\phi_0(y)\,dy\,dx$$

$$= \phi_0^*\phi_0\bar{R}\int_0^L\int_0^L k(\underbrace{x-y}_{w})R_1(y)\,dy\,dx$$

$$= \phi_0^*\phi_0\bar{R}\int\int_0^L k(w)R_1(y)\,dy\,dw$$

$$= \phi_1^*\phi_0\bar{R}\int k(w)\underbrace{\left[\int_0^L R_1(y)\,dy\right]}_{=0}dw$$

Summary

- Averaging over fine-grained landscapes
- Averaging over small variation
- $c(s,\epsilon) = c_0(s) + O(\epsilon^2)$