Integrodifference Models with Temporally Varying Environments

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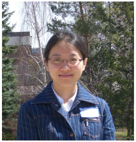

Yu Jin

Mark Lewis

Introduction

Motivation: Stream population

- local density dependent growth
- nonlocal dispersal in presence of unidirectional flow
- bounded habitat
- flow and growth regimes could depend on time

Background

Consider $n_t(x)$ modeled by

$$n_{t+1}(x) = \int_{\Omega} K(x,y) f(n_t(y))\, dy \tag{1}$$

- $\Omega = (0, L)$
- density dependent growth $f(n)$
- dispersal kernel $K(x,y)$

Advective Kernel (Lutscher et al., Siam Review, 2005)

Let $z(x,t)$ be density of moving individuals

$$z_t + vz_x = Dz_{xx} - \alpha z, \qquad z(x,0) = \delta_0(x-y) \tag{2}$$

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Density of settlers at x at time T is then

$$k_T(x) = \alpha \int_0^T z(x,s)\, ds$$

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For $T >> 1/\alpha$

$$K(x;y) = \alpha \int_0^\infty z(x,s)\,ds$$

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$$K(x;y) = \alpha \int_0^\infty z(x,s)\,ds$$

Integrate (2) from 0 to ∞

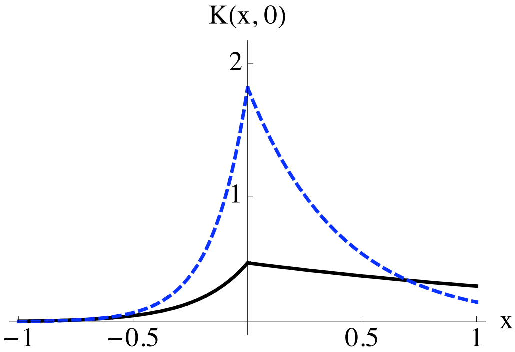
$$\frac{D}{\alpha} K_{xx} - \frac{v}{\alpha} K_x - K = -\delta_0(x-y) \tag{3}$$

with soln

Asymmetric Laplace Kernel (advective velocity v)

$$K(x,y) = \begin{cases} A\, e^{a_1(x-y)} & x < y \\ A\, e^{a_2(x-y)} & x \geq y \end{cases}$$

where $a_{1,2} = \frac{v}{2D} \pm \sqrt{\frac{v^2}{4D^2} + \frac{\alpha}{D}}$ and $A = \frac{a_1 a_2}{a_2 - a_1} = \frac{\alpha}{\sqrt{v^2 + 4\alpha D}}$



advective flow v; local diffusion D; setting rate α

Linear Stability

Assuming $f(0) = 0$, $f'(0) = R > 0$ one can consider the linear stability of (1) for small solutions via

$$n_{t+1}(x) = \mathscr{L}[n_t] = R \int_\Omega K(x, y)\, n_t(y)\, dy$$

Let $\lambda_1(K) = \rho(\mathscr{L})$. For well-behaved K, f (e.g., Hardin et al. '88)

- $\lambda_1(K) > 1$: trivial soln unstable, (1) admits stable $n_*(x)$
- $\lambda_1(K) < 1$: trivial soln $n_*(x) = 0$ stable

This allows study of relation between the organism's ability to persist and the biological parameters via the spectral radius of $\mathscr{L}$

Principal Eigenvalue λ_1

Consider

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

Differentiate

$$\lambda\phi''(x) = R\int_\Omega K_{xx}(x,y)\,\phi(y)\,dy$$

One can use K's DE to derive SLP for ϕ of the form

$$\phi'' + c(v)\phi' + d(\lambda)\phi = 0 \tag{4}$$

w/ associated Robin type BCs (n.b. $c(0) = 0$)

- facilitates study of dependence of $\lambda_1(K)$ on parameters (e.g., critical domain size)

Dispersal Success Function

We can also approximate λ_1.

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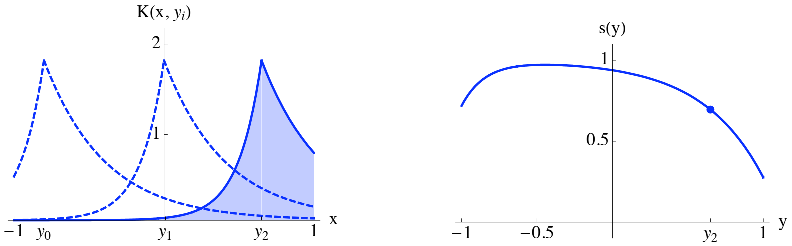
$$s(y) = \int_\Omega K(x, y)\, dx \qquad (5)$$



$s(y)$ indicates the probability an individual starting at y successfully settles in the habitat Ω after the dispersal event;

Dispersal Success Approximation

For principal eigenfunction ϕ we have

$$\lambda_1(K)\,\phi(x) = R\int_\Omega K(x,y)\phi(y)\,dy$$

Assume $\|\phi\|_1 = 1$ and integrate

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Assume $\|\phi\|_1 = 1$ and integrate

$$\begin{aligned}\lambda_1(K) &= R\int_\Omega\int_\Omega K(x,y)\phi(y)\,dy\,dx\\ &= R\int_\Omega s(y)\phi(y)\,dy\end{aligned}$$

Dispersal Success Approximation

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$$\begin{aligned}
\lambda_1(K) &= R\int_\Omega\int_\Omega K(x,y)\phi(y)\,dy\,dx \\
&= R\int_\Omega s(y)\phi(y)\,dy \\
&\approx \frac{R}{L}\int_\Omega s(y)\,dy
\end{aligned}$$

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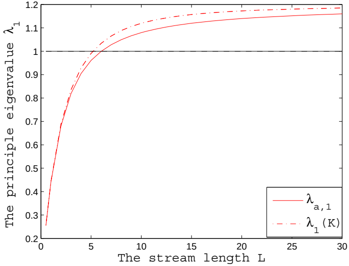

DSA tends to underestimate λ_1.

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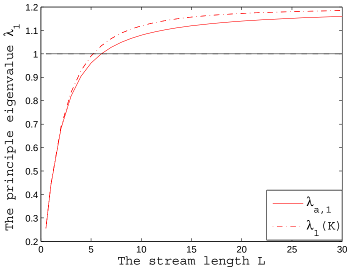


DSA tends to underestimate λ_1. We also have

$$\lambda_1(K) \le R\|s\|_\infty \|\phi\|_1 < R$$

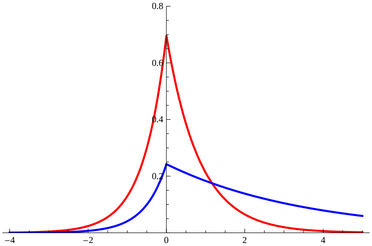
(dispersal loss will reduce growth rate from nonspatial model)

Temporal Variations

Consider variations in growth and dispersal

$$n_{t+1}(x) = \int_{\Omega} K_t(x,y) f_t(n_t(y))\, dy \tag{6}$$

- $K_t(x,y)$ kernel for dispersal event at step t
- $f_t(n)$ growth dynamics at step t



Example: Two kernel model

Consider linearized two kernel model K_1, R_1 and K_2, R_2 in succession:

$$n_{t+2}(x) = R_2 \int_\Omega K_2(x,y)\, n_{t+1}(y)\, dy$$

Example: Two kernel model

Consider linearized two kernel model K_1, R_1 and K_2, R_2 in succession:

$$
\begin{aligned}
n_{t+2}(x) &= R_2 \int_\Omega K_2(x,y)\, n_{t+1}(y)\, dy \\
&= R_2 \int_\Omega K_2(x,y) \left[R_1 \int_\Omega K_1(y,z)\, n_t(z)\, dz \right] dy \\
&= R_1 R_2 \int_\Omega \int_\Omega K_2(x,y) K_1(y,z)\, n_t(z)\, dz\, dy \\
&= R_1 R_2 \int_\Omega K(x,z)\, n_t(z) dz
\end{aligned}
$$

Effective two-stage kernel

Single kernel for two-stage succession

$$n_{t+1}(x) = R \int_\Omega K(x,y)\, n_t(y)\, dy$$

where $R = R_1 R_2$ and

$$K(x,y) = \int_\Omega K_2(x,z) K_1(z,y)\, dz$$

Similar calculation for eigenfunction as before shows

$$\lambda_1(K) < R_1 R_2$$

- $\sqrt{\lambda_1(K)}$ would be effective single rate for two stage process

BVP for advective kernels

Consider eigenfunction

$$\lambda\phi(x) = R_1 R_2 \int_\Omega K(x,y)\,\phi(y)\,dy \tag{7}$$

Let

$$\psi(x) = R_1 \int_\Omega K_1(x,y)\,\phi(y)\,dy$$

Then by (7),

$$\phi(x) = \frac{R_2}{\lambda} \int_\Omega K_2(x,y)\psi(y)\,dy$$

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Thus

$$\psi''(x) = \frac{v_1}{D_1}\psi'(x) + \frac{\alpha_1}{D_1}\psi(x) - \frac{\alpha_1}{D_1}R_1\,\phi(x)$$

$$\phi''(x) = \frac{v_2}{D_2}\phi'(x) + \frac{\alpha_2}{D_2}\phi(x) - \frac{\alpha_2}{D_2}\frac{R_2}{\lambda}\,\psi(x)$$

Sturm-Liouville Problem for two stage process

Differentiating ϕ'' two more times and using ψ's equations yields:

$$\phi^{(4)} - B\phi^{(3)} - \left(\frac{\alpha_1}{D_1} + \frac{\alpha_2}{D_2} - \frac{v_1 v_2}{D_1 D_2}\right)\phi^{(2)} + C\phi' + \frac{\alpha_1\alpha_2}{D_1 D_2}\left(1 - \frac{R_1 R_2}{\lambda}\right)\phi = 0$$

where $B = \left[\frac{v_1}{D_1} + \frac{v_2}{D_2}\right]$ and $C = \left[\frac{v_1\alpha_2 + \alpha_1 v_2}{D_1 D_2}\right]$

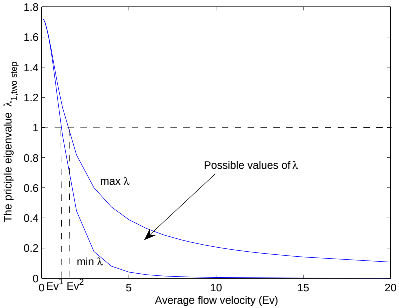
and associated boundary conditions:

$$\begin{aligned}
\phi'(0) &= a_{1,2}\,\phi(0) \\
\phi'(L) &= a_{2,2}\,\phi(L) \\
\phi'''(0) &= \left(a_{1,1} + \frac{v_2}{D_2}\right)\phi''(0) - a_{1,1}\frac{v_2}{D_2}\phi'(0) + \frac{\alpha_2}{D_2}(a_{1,2} - a_{1,1})\,\phi(0) \\
\phi'''(L) &= \left(a_{2,1} + \frac{v_2}{D_2}\right)\phi''(L) - a_{2,1}\frac{v_2}{D_2}\phi'(L) + \frac{\alpha_2}{D_2}(a_{2,2} - a_{2,1})\,\phi(L)
\end{aligned}$$

where $a_{i,j}$ are the exponential coefficients for K_i

Example: λ vs. flow rate

Consider two flow rates v_1 and v_2, keeping fixed average Ev

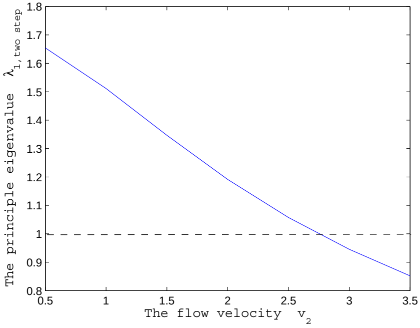


For fixed Ev, as v_1 and v_2 vary, the principal eigenvalue λ_1 varies between two values

- $Ev < Ev^1$ implies $\lambda_1 > 1$
- $Ev > Ev^2$ implies $\lambda_1 < 1$
- Interesting regime for modest averages $Ev^1 < Ev < Ev^2$

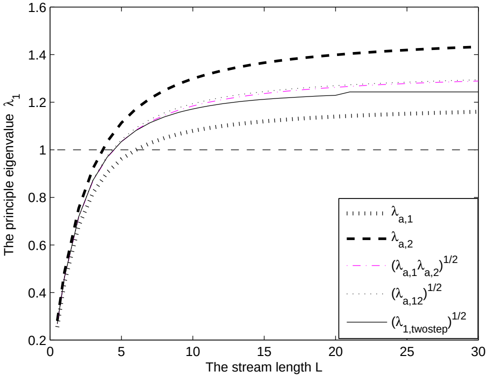
Example: λ_1 vs. variation in flow rate

Fix $v_1 = 0.1$, let v_2 vary



- λ_1 is a decreasing function of v_2 (the larger the second flow velocity, the harder it is for the population to persist)

Comparison of Eigenvalue Approximations



- $(\lambda_{a,1}\lambda_{a,2})^{1/2} \approx (\lambda_{1,\text{twostep}})^{1/2}$ for small L
- $(\lambda_{a,1}\lambda_{a,2})^{1/2} > (\lambda_{1,\text{twostep}})^{1/2}$ for larger L
- DSA $\lambda_{a,12}$ underestimates $\lambda_{1,\text{twostep}}$ for larger L

Random Kernels

We now consider

$$n_t(x) = \int_\Omega K_{\alpha_t}(x-y) f_{\alpha_t}(n_{t-1}(y))dy \tag{8}$$

where kernel parameters come from some distribution

K_{α_t} and f_{α_t} denote "random" growth and dispersal kernels at step t

Linearized operator time dependent so no eigenvalue analysis, but one expects, at least with certain assumptions on the parameters, some asymptotic analogue of λ_1.

Abstract Result

Hardin et al. '88 consider

$$X_{t+1} = \int_{\Omega} K(x,y) r(\alpha_t, y) f(X_t(y)) = H_{\alpha_t}(X_t), \tag{9}$$

Given various conditions of H_α, such as,

Abstract Result

Hardin et al. '88 consider

$$X_{t+1} = \int_\Omega K(x,y) r(\alpha_t, y) f(X_t(y)) = H_{\alpha_t}(X_t), \tag{9}$$

Given various conditions of H_α, such as,

(H1) $H_\alpha : C_+(\Omega) \to C_+(\Omega)$ continuous

(H2) If $x, y \in C_+(\Omega)$ and $x \geq y$ then $H_\alpha(x) \geq H_\alpha(y)$

(H4) There exists a compact set $D \subset C_+(\Omega)$ such that $H_\alpha(B_b) \subset D$ for all $\alpha \in \mathcal{A}$.

(H8) $A_\alpha = H'_\alpha(0)$ exists.

(H10)
- (a) If $x, y \in C(\Omega)$ and $x \leq y$ then $A_\alpha x \leq A_\alpha y$ for all $\alpha \in \mathcal{A}$.
- (b) $||A_\alpha|| \leq h$ for all $\alpha \in \mathcal{A}$.

Theorem (Hardin et al '88)

The limit $r = \lim_{t\to\infty} ||A_{\alpha_t} \circ \cdots \circ A_{\alpha_1}||^{1/t}$ *exists with probability one.*

(a) *If* $r < 1$, *the population becomes extinct;*

(b) *If* $r > 1$, *then population persists*

Random Kernels

The limit

$$r = \lim_{t\to\infty} ||A_{\alpha_t} \circ \cdots \circ A_{\alpha_1}||^{1/t}$$

is an analogue of the Gelfand formula for a bounded linear operator

$$\rho(A) = \lim_{n\to\infty} \|A^n\|^{1/n}$$

The abstract result in Hardin et al. can be adapted to

$$n_t(x) = \int_\Omega K_{\alpha_t}(x-y) f_{\alpha_t}(n_{t-1}(y))dy$$

w/ $\{\alpha_t\}_{t\geq 0}$ independent identically distributed from $\mathcal{A} = [\underline{\alpha}, \bar{\alpha}]$ with the following assumptions of f and K:

Assumptions

(C1) (a) $K_\alpha(x-y)$ is strictly positive and continuous for $x, y \in \Omega$;
(b) There exist $\underline{K}$, $\bar{K} > 0$ such that $\underline{K} \leq K_\alpha(x-y) \leq \bar{K}$ for all $\alpha \in \mathcal{A}$

(C2) (a) $f_\alpha : \mathbb{R} \to \mathbb{R}_+$ continuous; $f_\alpha(u) = 0$ for all $u \leq 0$. Moreover, $f_\alpha(u)$ is continuous in $\alpha \in \mathcal{A}$ uniformly in $u \in \mathbb{R}$.
(b) For any $\alpha \in \mathcal{A}$,
  (i) $f_\alpha(u)$ is an increasing function in u;
  (ii) $\frac{f_\alpha(u)}{u} < \frac{f_\alpha(v)}{v}$ if $u > v > 0$.
(c) (i) f_α is right differentiable at 0
  (ii) $\frac{f_\alpha(u)}{u} \to f'_\alpha(0)$ as $u \to 0^+$ uniformly for $\alpha \in \mathcal{A}$,
  (iii) There exist $\underline{f}$, $\bar{f} > 0$ such that $\underline{f} = \inf_{\alpha \in \mathcal{A}} f'_\alpha(0) \leq f'_\alpha(0) \leq \bar{f}$
(d) (i) There exists $m > 0$ such that $0 \leq f_\alpha(u) \leq m$ for all $u \in C_+(\Omega)$
  (ii) For $b = m\bar{k} \int_\Omega dy$, there exists $\underline{f_1} = \inf_{\alpha \in \mathcal{A}} f_\alpha(b) > 0$.

Then

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(b) For any $\alpha \in \mathcal{A}$,
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(d) (i) There exists $m > 0$ such that $0 \le f_\alpha(u) \le m$ for all $u \in C_+(\Omega)$
  (ii) For $b = m\bar{k}\int_\Omega dy$, there exists $\underline{f_1} = \inf_{\alpha \in \mathcal{A}} f_\alpha(b) > 0$.

Then $r = \lim_{t \to \infty} ||A_{\alpha_t} \circ \cdots \circ A_{\alpha_1}||^{1/t}$ exists...

λ_1 analogue for random model

Instead of $r = \lim_{t\to\infty} ||A_{\alpha_t} \circ \cdots \circ A_{\alpha_1}||^{1/t}$, consider

$$\Lambda = \lim_{t\to\infty} \left[\int_\Omega \tilde{n}_t(x)\, dx \right]^{1/t} \tag{10}$$

where

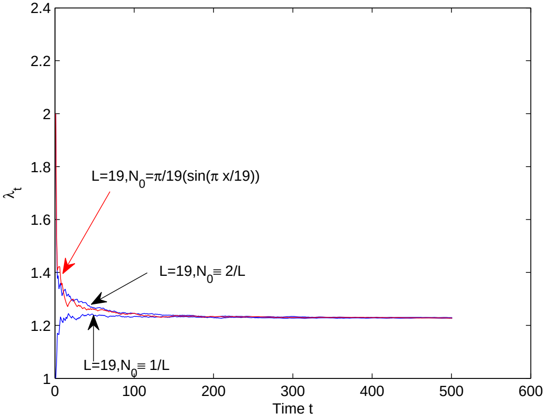
$$\tilde{n}_t(x) = \int_\Omega K_t(x-y) f'_{\alpha_t}(0) \tilde{n}_{t-1}(y)\, dy,$$

- $\Lambda \approx$ asymptotic growth rate of the population

Conjecture: Λ and r cross 1 at same time

Example: convergence of $\Lambda_t = \left(\int_\Omega n_t(x)\,dx\right)^{1/t}$

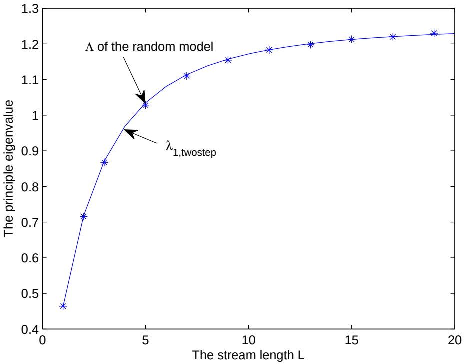
Suppose $K_t \in \{K_1, K_2\}$, chosen with 50/50 probability (CFK)



Regardless of IC or flip sequence, $\Lambda_t \to \Lambda \approx 1.22$

Two-step vs. Coin-Flip

For comparison, consider limit Λ for CFK model vs. exact $\lambda_1(K)$ for two-step model:

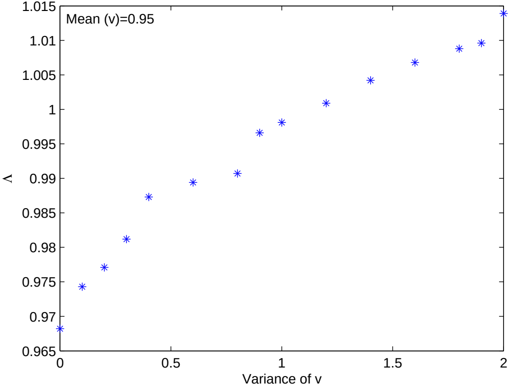


Note: For $L = 19$, $\Lambda \approx 1.22$ as in previous plot.

$(v_1 = 0.1, v_2 = 1, R_1 = 1.2, R_2 = 1.5, D_1 = 1, D_2 = 1, \alpha_1 = 1, \alpha_2 = 1)$

Example: Random flow speed

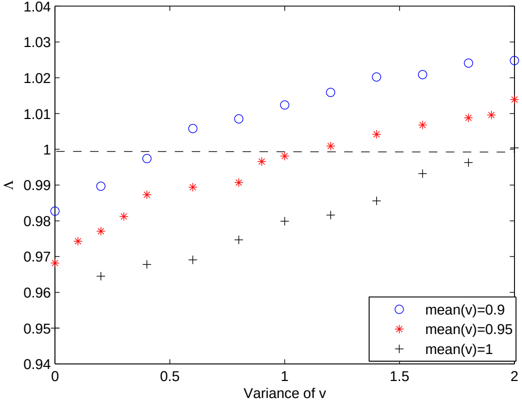
Consider Λ for random model with flow velocity chosen from log normal distribution with $\mu = 0.95$, as a function of the variance:



Other parameters fixed with $R = 1.2$, $D = 1$, $\alpha = 1$.

Example 2: Different means

Similar scenario, with three different means:



Explicit calculation for Λ

Let $n_0(x) = \frac{1}{L}$.

$$\Lambda_1 = \int_\Omega n_1(x)\,dx = \frac{R_1}{L}\int_\Omega\int_\Omega K_1(x,y)\,dx\,dy \quad = \quad \frac{R_1}{L}\int_\Omega s_1(y)\,dy$$

Continuing,

Explicit calculation for Λ

Let $n_0(x) = \frac{1}{L}$.

$$\Lambda_1 = \int_\Omega n_1(x)\,dx = \frac{R_1}{L}\int_\Omega\int_\Omega K_1(x,y)\,dx\,dy \quad = \quad \frac{R_1}{L}\int_\Omega s_1(y)\,dy$$

Continuing,

$$\Lambda_2 \quad = \quad \left(R_2\int_\Omega\int_\Omega K_2(x,y)\,n_1(y)\,dy\,dx\right)^{1/2} = \left(\frac{R_1R_2}{L}\int_\Omega s_2(y)\,r_1(y)\,dy\right)^{1/2}$$

$$\Lambda_3 \quad = \quad \left(\frac{R_1R_2R_3}{L}\int_\Omega\int_\Omega s_3(y)\,K_2(y,z)\,r_1(z)\,dy\,dz\right)^{1/3}$$

$$\Lambda_4 \quad = \quad \left(\frac{R_1R_2R_3R_4}{L}\int_\Omega\int_\Omega\int_\Omega s_4(z_3)\,K_3(z_3,z_2)\,K_2(z_2,z_1)\,r_1(z_1)\,dz_3\,dz_2\,dz_1\right)$$

$$\vdots$$

$$\Lambda_n \quad = \quad \left(\frac{\mathcal{R}}{L}\underbrace{\int_\Omega\cdots\int_\Omega}_{n-1 \text{ terms}} s_n(z_{n-1})\prod_{i=2}^{n-1}K_i(z_i,z_{i-1})\,r_1(z_1)\,dz_{n-1}\ldots dz_1\right)^{1/n}$$

Asymmetric Laplace Kernels

We can compute this exactly for random asymmetric Laplace kernels since, essentially,

$$n_t(x) = \frac{\mathcal{R}}{L}\left(\alpha_{1,t} + \sum_{j=2}^{2t+1} \alpha_{j,t}\, e^{\gamma_j x}\right) \tag{11}$$

where $\alpha_{j,t}$ are certain computable coefficients that depend on the kernels and the γ_j's are front/back kernel coefficients from the random kernels. Integrating (11) yields

$$\Lambda_t = [\mathcal{R}]^{1/t}\left[\alpha_{1,t} + \frac{2}{L}\sum_{j=2}^{2t+1} \frac{\alpha_{j,t}}{\gamma_j}\sinh\frac{\gamma_j L}{2}\right]^{1/t} \tag{12}$$

Nice closed form solution, but proving computationally unstable due to small divisors; further complicated by the fact that we need $t >> 1$

References

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- F.Lutscher, E. Pachepsky, M. Lewis, *The effect of dispersal patterns on stream populations*, Siam Review, 2005

Thanks for your attention!