Metrics for Population Persistence in Rivers

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(Presentation at Everything Disperses to Miami, December 14, 2012)

Outline

Overview

Streams and rivers are important habitats for certain aquatic species.

The *drift paradox*: how stream-dwelling organisms can persist, without being washed out, when they are continuously subject to the unidirectional stream flow.

Instream flow needs (IFNs): the flows needed to maintain ecosystem integrity at a particular level.

Question: How does the water flow influence population growth and persistence?

Overview

Models

- Reaction-diffusion-advection models
  (Bencala and Walters (1983), DeAngelis et al. (1995), Speirs and Gurney (2001), Pachepsky et al. (2005), Lutscher et al (2006), etc.)
- Integro-differential/difference models
  (Lutscher et al (2005), Lutscher et al. (2010), etc.)
- Numerical flow models coupled to population dynamical equations
  (uses River2D, Steffler, Blackburn, Jin and Lewis (in prep)).
- etc.

Overview

Population spread and persistence in streams or rivers.

- Spreading speeds (asymptotic speeds of spread)
- Critical domain size
- **River metrics to provide useful ways to understand persistence in spatially variable rivers**

The model

$$
\begin{cases}
n_t = g(x,n)n - \frac{Q}{A(x)} n_x + \frac{1}{A(x)} \left(D(x)A(x)n_x \right)_x, & x \in (0,L),\ t > 0, \\
\alpha_1 n(0,t) - \beta_1 n_x(0,t) = 0, & t > 0, \\
\alpha_2 n(L,t) + \beta_2 n_x(L,t) = 0, & t > 0, \\
n(x,0) = n_0(x), & x \in (0,L),
\end{cases}
\tag{1}
$$

n: the population density
g: the per capita growth rate function
A: the cross-sectional area of the stream
D: the spatially variable diffusion coefficient
$Q > 0$: the constant stream discharge
α_i, β_i: nonnegative constants ($i = 1, 2$)
n_0: the initial distribution of the population
$g(x,0) = f(x) - v(x)$
$f(x) > 0$: spatially varying intrinsic birth rate
$v(x) > 0$: mortality rate

Two typical boundary conditions

Hostile conditions (zero-flux at the stream source and zero-density at the stream outflow:

$$Qn(0,t) - D(0)A(0)n_x(0,t) = 0 \text{ and } n(L,t) = 0. \tag{2}$$

Danckwerts conditions (zero-flux at the stream source and free-flow or insulated condition at the stream outflow:

$$Qn(0,t) - D(0)A(0)n_x(0,t) = 0 \text{ and } n_x(L,t) = 0. \tag{3}$$

Linearization

The strongly elliptic linear operator

$$\mathcal{L} := -\frac{Q}{A(x)}\frac{\partial}{\partial x} + \frac{1}{A(x)}\frac{\partial}{\partial x}\left(D(x)A(x)\frac{\partial}{\partial x}\right) \tag{4}$$

The linearized system of (1) at $n^* = 0$ is

$$\begin{cases} n_t = g(x,0)n + \mathcal{L}n, & x \in (0,L),\ t > 0, \\ \alpha_1 n(0,t) - \beta_1 n_x(0,t) = 0, & t > 0, \\ \alpha_2 n(L,t) + \beta_2 n_x(L,t) = 0, & t > 0, \\ n(x,0) = n_0(x), & x \in (0,L). \end{cases} \tag{5}$$

The next generation operator

The next generation operator $\Gamma : X = C[0, L] \to X$

$$\Gamma\psi_0(x) = \int_0^\infty f(x)\psi(x,t)\,dt = f(x)\int_0^\infty \psi(x,t)\,dt, \tag{6}$$

where $\psi(x, t)$, the distribution of initial individuals at t, is the solution of

$$\begin{cases} \psi_t = -v(x)\psi + \mathcal{L}\psi, & x \in (0, L),\ t > 0, \\ \psi(x, 0) = \psi_0(x), & x \in (0, L). \end{cases} \tag{7}$$

The next generation operator

Alternatively,

$$\Gamma\psi_0(x) = f(x)\int_0^L k(x,y)\psi_0(y)\,dy.$$

$k(x, y)$ is the solution of the ordinary boundary value problem

$$\begin{cases} \mathcal{L}k(x,y) - v(x)k(x,y) = -\delta(x-y), & x \in (0,L) \\ \alpha_1 k(0,y) - \beta_1 k'(0,y) = 0 \\ \alpha_2 k(L,y) + \beta_2 k'(L,y) = 0. \end{cases} \tag{8}$$

The function $k(x, y)$ can be considered the lifetime density of space use of an individual originally introduced at y.

The next generation operator

$$\Gamma : C([0,L]) \to C([0,L]),$$

$$\underbrace{\Gamma\psi_0(x)}_{\text{density of new individuals produced by } \psi_0(x)} = \underbrace{f(x)}_{\text{birth}} \int_0^\infty \underbrace{\psi(x,t)}_{\text{density of initially introduced individuals still present at time t}} \, dt$$

$$\psi_t = -v\psi + \mathcal{L}\psi, \quad x \in (0,L), t > 0$$
$$\psi(x,0) = \psi_0(x), \quad x \in (0,L)$$
+ BC

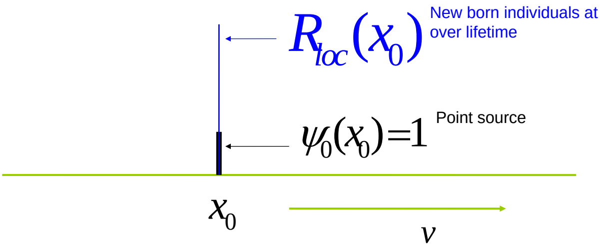
$$= f(x) \int_0^L \underbrace{k(x,y)}_{\text{lifetime spatial density of an individual introduced at y}} \psi_0(y) \, dy$$

$$-vk(x,y) + \mathcal{L}k(x,y) = -\delta(x-y)$$
+ BC

Three metrics for population persistence

1. $R_{loc}(x_0)$: number of offspring produced by an individual introduced at x (dispersal excluded), distribution of a species' fundamental niche. (see Krkosek and Lewis (2010))

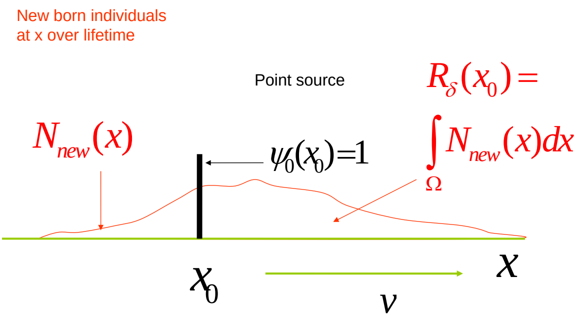
$$R_{\mathrm{loc}}(x_0) = \Gamma(\psi_0)(x_0) = f(x_0) \int_0^{\infty} e^{-v(x_0)t}\, dt = \frac{f(x_0)}{v(x_0)}. \qquad (9)$$



Three metrics for population persistence

2. R_δ: number of offspring produced by an individual introduced at dispersal included), realized niche. Source-sink regions? (see Krkosek and Lewis (2010))

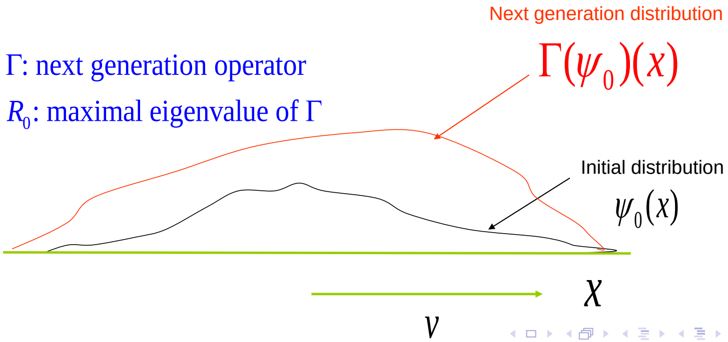
$$R_\delta(x_0) = \int_0^L \Gamma\psi_0(z)\,dz = \int_0^L f(z)k(z,x_0)\,dz, \tag{10}$$



3. R_0: net reproductive rate - number of offspring produced over an individuals lifetime, given that the individual is distributed spatially in a manner appropriate for maximizing long-term growth. Globally persist?

$$R_0 := r(\Gamma). \tag{11}$$

$r(\Gamma)$ is the spectral radius of the linear operator Γ.



Spectral properties of the next generation operator

1. Γ is a well-defined, bounded, compact, linear operator.
2. Krein-Rutman Theorem: $R_0 = r(\Gamma)$ is a simple eigenvalue and is the dominant eigenvalue of Γ. Furthermore, R_0 is the only eigenvalue with an eigenvector that is positive on $(0, L)$.
3. Based on Thieme (2009), R_0 determines the stability of the trivial solution.
4. Chatelin(1981): It is possible to approximate R_0 numerically.

Remark:
The *spectrum* of Γ: $\sigma(\Gamma) = \{\lambda \in \mathbb{C} \mid \lambda I - \Gamma$ is not invertible$\}$.
The *spectral radius* of Γ: $r(\Gamma) = \sup\{ |\lambda| : \lambda \in \sigma(\Gamma)\}$.

Preliminary theory

Theorem [Thieme (2009), Thm 3.5]. Let B be a resolvent-positive operator in the ordered Banach space S with $s(B) < 0$. If C is a positive linear operator such that $A = B + C$ is also resolvent-positive, then $s(A)$ has the same sign as $r(-CB^{-1})$.

Remark:
The *spectral bound* of T: $s(T) = \sup\{\mathrm{Re}(\lambda) : \lambda \in \sigma(T)\}$.
The *resolvent set* of T: $\rho(T) = \mathbb{C} \setminus \sigma(T)$, i.e., the complement of $\sigma(T)$.
The operator T is *resolvent-positive* if the resolvent set $\rho(T)$ contains a ray (ω, ∞) and $(\lambda I - T)^{-1}$ is a positive operator for all $\lambda > \omega$ [Thieme 2009].

The sign of $R_0 - 1$

The next generation operator defined in (6) satisfies $\Gamma = -CB^{-1}$ where B and C are defined by

$$Bw(x) = \mathcal{L}w(x) - v(x)w(x) \tag{12}$$

$$Cw(x) = f(x)w(x). \tag{13}$$

Moreover, for

$$A = B + C, \tag{14}$$

the spectral bound $s(A)$ has the same sign as $R_0 - 1$, where $R_0 = r(-CB^{-1}) = r(\Gamma)$.

Stability of the trivial solution $n^* \equiv 0$

Proposition For (1), the following statements are valid.

1. If $s(A) < 0$, then the trivial steady state n^* for (1) is locally asymptotically stable.
2. If $s(A) > 0$, then n^* is unstable. Moreover, (1) admits a minimal positive equilibrium $\hat{n}(x)$ and all solutions to (1) which are initially positive on an open subset of $[0, L]$ are eventually bounded below by orbits which increase toward $\hat{n}$ as $t \to \infty$.

Uniform persistence when $s(A) > 0$

If $s(A) > 0$, then (1) is *uniform persistent* in the sense that there exists $\delta > 0$ such that for any solution $n(x,t)$ of (1) with $n(x,0) = n_0 \in X_+ \backslash \{0\}$ we have

$$\liminf_{t\to\infty} \min_{x\in[0,L]} n(x,t) \geq \delta \tag{15}$$

when the boundary conditions in (1) are Neumann or Robin conditions and

$$\liminf_{t\to\infty} \max_{x\in[0,L]} n(x,t) \geq \delta \tag{16}$$

when at least one of the boundary conditions in (1) are Dirichlet conditions.

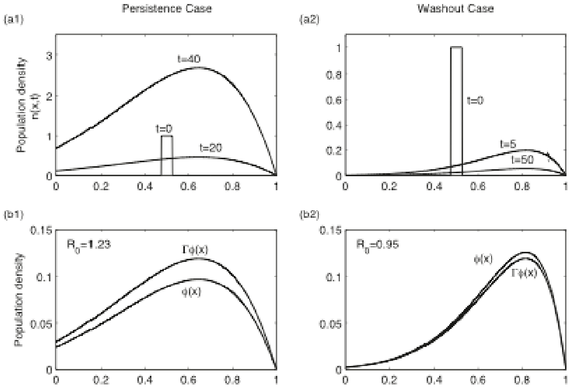
R_0 determines population persistence

Theorem

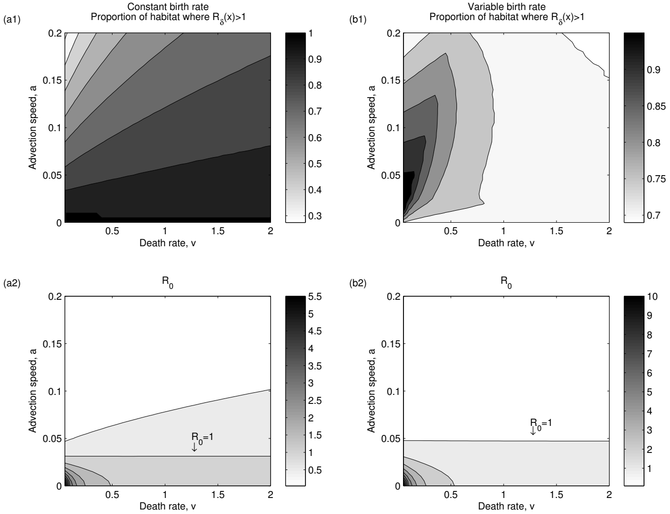
Let Γ be the next generation operator defined by (6) *and let $R_0 = r(\Gamma)$ be the spectral radius of Γ. For the population model* (1)*, the homogeneous trivial steady state solution $n^* \equiv 0$ is locally asymptotically stable when $R_0 < 1$ and unstable when $R_0 > 1$. Moreover, if $R_0 > 1$, then the population is uniformly persistent.*

A numerical example

Net Reproductive Rate



A numerical example



The extensions of the work

- Metrics of the two-dimensional version of the model
- Metrics of a benthic-drift model in a one-dimensional river
- Metrics of a benthic-drift model in a two-dimensional river

Acknowledgement

People

Mark A. Lewis, Peter Steffler, Julia Blackburn, Hannah Mckenzie, Jon Jacobsen, Frithof Lutscher, Qihua Huang
Lewis Research Group
Centre for Mathematical Biology at University of Alberta
Department of Mathematical and Statistical Sciences, University of Alberta
Department of Mathematics, University of Nebraska-Lincoln

Funding

MITACS Network for Biological Invasions and Dispersal
National Sciences and Engineering Research Council of Canada
Sustainable Resource Development Alberta
Alberta Water Research Institute

Thank you!