Logistic reaction-diffusion-advection river network model: phase plane approach

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# Outline

• Logistic RDA model for a single river (V., Lutscher 2010)

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• Logistic RDA model for a river network (V. 2019)



+ upstream and downstream b.c.

u(x, t)=population density at point  $0 \le x \le L$  at time tq = advection speed



# RDA model for single river segment

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} - q \frac{\partial u}{\partial x} + ru(1-u)$$

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• 
$$D\left(\frac{\partial u}{\partial x}\right)|_{x=0} = qu(0,t)$$
 and  $u(L,t) = 0$  (hostile)

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• 
$$D\left(\frac{\partial u}{\partial x}\right)|_{x=0} = qu(0,t)$$
 and  $\left(\frac{\partial u}{\partial x}\right)|_{x=L} = 0$  (outflow)

# Critical domain size: hostile and outflow downstream b.c.

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For 
$$0 \le q < q_{cr} = 2\sqrt{Dr}$$
:

$$L_c^{host}(q) = rac{\pi - \arctan\left(rac{\sqrt{4rD - q^2}}{q}
ight)}{rac{\sqrt{4rD - q^2}}{2D}}$$

$$L_c^{out}(q) = \begin{cases} \frac{2D}{\sqrt{4rD - q^2}} \arctan\left(\frac{q\sqrt{4rD - q^2}}{2rD - q^2}\right), 0 < q \le \sqrt{2rD} \\ \frac{2D}{\sqrt{4rD - q^2}} \left(\pi + \arctan\left(\frac{q\sqrt{4rD - q^2}}{2rD - q^2}\right)\right), \sqrt{2rD} < q < 2\sqrt{rD} \end{cases}$$

 $L_c^{out}(q) < L_c^{host}(q).$ 

#### Steady state solutions of a BVP

Steady state solution of 
$$\begin{cases} \frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} - q \frac{\partial u}{\partial x} + f(u) \\ b.c. \end{cases}$$

is found by setting  $\frac{\partial u}{\partial t} = 0$ .

Look for a solution u = u(x) of

$$\begin{cases} Du'' - qu' + f(u) = 0\\ b.c. \end{cases} \text{ or } \begin{cases} u' = v\\ v' = \frac{q}{D}v - \frac{1}{D}f(u)\\ b.c. \end{cases}$$

#### Flow of the *uv*-system

The vector field of a system  $\begin{cases} u' = f(u, v) \\ v' = g(u, v) \end{cases}$  gives rise to the flow operator  $\Phi(x, -, -) : \mathbb{R}^2 \to \mathbb{R}^2$  describing the "movement along the trajectories" over the interval [0, x]:



# Phase plane method: outflow b.c.

$$\begin{cases} u' = v \\ v' = \frac{q}{D}v - \frac{r}{D}u(1-u) \\ v(0) = \frac{q}{D}u(0) \\ v(L) = 0 \end{cases}$$

# Phase plane method: outflow b.c.

• 
$$q \ge q_{cr} = 2\sqrt{Dr}$$



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# Phase plane method: outflow b.c.

• 
$$0 < q < q_{cr} = 2\sqrt{Dr}$$



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# Domain size L as the function of downstream density $\mu$



There is no explicit formula for  $L = L(\mu)$  (unlike the case of Fisher equation, see Ludwig et al. 1979), but we can show:

- $L(\mu)$  is an increasing continuous function of  $\mu$ .
- $L(\mu) \rightarrow L_c^{out}$  as  $\mu \rightarrow 0$ ;
- $L(\mu) \to \infty$  as  $\mu \to 1$ ;

It follows that for each  $L > L_c^{out}$  there exists a unique  $\mu \in (0, 1)$  such that  $L(\mu) = L$ . So, there is a unique orbit of "parametric length" L.

### Existence and Uniqueness <sup>1</sup>

Thus, if  $q < q_{cr}$  and  $L > L_c^{out}$ , one gets existence and uniqueness of the non-trivial solution of  $\begin{cases} u' = v \\ v' = \frac{q}{D}v - \frac{r}{D}u(1-u) \\ v(0) = \frac{q}{D}u(0) \\ v(L) = 0 \end{cases}$ 

or the non-trivial steady state solution of

$$\begin{cases} \frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} - q \frac{\partial u}{\partial x} + ru(1-u) \\ \frac{\partial u}{\partial x} = qu, \ x = 0 \\ \frac{\partial u}{\partial x} = 0, \ x = L \end{cases}$$

<sup>1</sup>O.V., F. Lutscher, Population Dynamics in Rivers: Analysis of Steady States, Can. Appl. Math. Quart., Vol. 18 (4) (2010), 439-469. ( = ) ( = ) ( = ) ( ⊂

# RDA models for river networks



#### RDA models for river networks

- Linear RDA model: J.M. Ramirez (2011)<sup>2</sup> and J. Sarhad, R. Carlson, K.E. Anderson (2014)<sup>3</sup>
- PDE-based approach to nonlinear RDA models: Y. Jin, R. Peng and J. Shi (2019)<sup>4</sup>
- Phase-plane-based approach to logistic RDA model: O.V. (2019) <sup>5</sup>

<sup>3</sup>J. Sarhad, R. Carlson, K.E. Anderson, *Population persistence in river networks*, J. Math. Biology 69(2), 401-448 (2014).

<sup>4</sup>Y. Jin, R. Peng and J. Shi, *Population Dynamics in River Networks*, J. Nonlin. Science 29, 2501-2545 (2019).

<sup>5</sup>O.V., Population Dynamics in River Networks: Analysis of Steady States, J. Math. Biology 79 (1) 63-100 (2019).

<sup>&</sup>lt;sup>2</sup>J.M. Ramirez, *Population persistence under advection-diffusion in river networks*, J. Math. Biology 65 (5), 919-942 (2011).

#### River network: metric graph + cross-section areas



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# General river network as a metric graph

- *D*, *q*, *r* and carrying capacity are assumed to be the same for all segments
- cross-section area A<sub>i</sub> is constant throughout the *i*th segment
- whole cross-section is habitable
- population is well mixed in the cross-section
- cross-section areas are additive in each junction (conservation of hydrological discharge)

# Basic case: Y-shaped network



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Population density functions on a metric graph

Identify segments with the intervals  $[-L_0, 0], [-L_1 - L_0, -L_0], [-L_2 - L_0, -L_0].$ 

Let  $u_i(x, t)$  represent the population density on the *i*th segment.



#### RDA model on a metric graph

On each segment, the density is subject to the same RDA equation:

$$\frac{\partial u_i}{\partial t} = D \frac{\partial^2 u_i}{\partial x^2} - q \frac{\partial u_i}{\partial x} + r u_i (1 - u_i).$$

No-flux boundary condition at each upstream vertex:

• 
$$D\frac{\partial u_1}{\partial x}(-L_1-L_0,t) = qu_1(-L_1-L_0,t)$$

• 
$$D\frac{\partial u_2}{\partial x}(-L_2-L_0,t)=qu_2(-L_2-L_0,t)$$

Outflow condition at the "root" vertex:

• 
$$\frac{\partial u_0}{\partial x}(0,t)=0.$$

# RDA model on a metric graph: junction conditions

At the junction, we have:

- the continuity conditions:  $u_0(-L_0, t) = u_1(-L_0, t) = u_2(-L_0, t).$
- the flux balancing condition: outgoing flux = sum of incoming fluxes (assuming that habitat cross-section areas satisfy A<sub>0</sub> = A<sub>1</sub> + A<sub>2</sub>)



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$$\frac{\partial u_0}{\partial x}(-L_0,t) = \frac{A_1}{A_0}\frac{\partial u_1}{\partial x}(-L_0,t) + \frac{A_2}{A_0}\frac{\partial u_2}{\partial x}(-L_0,t)$$

#### Translating to the phase plane setting

To find steady state solution, we set  $\frac{\partial u_i}{\partial t} = 0$ . We have  $u_i = u_i(x)$ ,  $v_i = v_i(x) = \frac{\partial u_i}{\partial x}$  satisfying:  $\begin{cases} u'_i = v_i & i = 0, 1, 2 \\ v'_i = \frac{q}{D}v_i - \frac{r}{D}u_i(1 - u_i) & i = 0, 1, 2 \end{cases}$ •  $v_1(-L_1 - L_0) = \frac{q}{D}u_1(-L_1 - L_0)$  (upstream condition) •  $v_2(-L_2 - L_0) = \frac{q}{D}u_2(-L_2 - L_0)$  (upstream condition) •  $v_0(0) = 0$  (downstream condition) •  $u_0(-L_0) = u_1(-L_0) = u_2(-L_0)$  (continuity conditions) •  $v_0(-L_0) = \frac{A_1}{A_0}v_1(-L_0) + \frac{A_2}{A_0}v_2(-L_0)$  (flux balancing condition)

What does a steady state look like in a phase plane?

# Steady state solution as an "orbit graph" in the uv-plane



Geometric interpretation of junction conditions:

- $u_0(-L_0) = u_1(-L_0) = u_2(-L_0) \iff$  vertical alignment
- $v_0(-L_0) = \frac{A_1}{A_0}v_1(-L_0) + \frac{A_2}{A_0}v_2(-L_0) \iff$  vertical coordinates satisfy the linear combination



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# "Local" preservation of concavity under flow



Given  $(\alpha_i, \beta_i)$ , i = 1, 2, 3, on a straight line with  $\alpha_1 < \alpha_2 < \alpha_3$  let  $m_{ij}(x)$  =slope of the line through  $\Phi(x, \alpha_i, \beta_i)$  and  $\Phi(x, \alpha_j, \beta_j)$ . Then for sufficiently small h > 0 we have:  $m_{12}(h) < m_{23}(h)$  and  $m_{12}(-h) > m_{23}(-h)$ .



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### Looking for intersection point: possible scenarios





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#### Looking for intersection point: possible scenarios





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#### Looking for intersection point: possible scenarios





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#### Existence and uniqueness of a positive steady state solution (for a Y-shaped network)

### Whenever a positive steady state exists, it is unique (by concavity).

Sufficient and necessary conditions for existence:

#### Looking for an intersection point

"Interesting case" (when river segments are relatively short) comes down to distinguishing between the following two situations:



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#### Looking for an intersection point



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#### Using Hartman-Grobman Theorem

Recall: 
$$\Phi(x, -, -)$$
 is the flow of the system  

$$\begin{cases}
u' = v \\
v' = \frac{q}{D}v - \frac{r}{D}u(1 - u)
\end{cases}$$
Let  $\Psi(x, -, -)$  be the flow of the linearized system  

$$\begin{cases}
u' = v \\
v' = \frac{q}{D}v - \frac{r}{D}u
\end{cases}$$

Note that 
$$\Psi(x, \alpha, \beta)$$
 is given by  $e^{Ax}(\alpha, \beta)^T$  where  $A = \begin{bmatrix} 0 & 1 \\ -\frac{r}{D} & \frac{q}{D} \end{bmatrix}$ 

By Hartman-Grobman Theorem, there exist open neighborhoods  $\Omega, \Omega'$  of (0,0) in  $\mathbb{R}^2$  and a homeomorphism  $\mathbf{h} : \Omega \to \Omega'$  given by  $\mathbf{h}(u,v) = (h_1(u,v), h_2(u,v))$  such that for any  $(\alpha, \beta) \in \Omega$ ,

$$\Phi(x,\alpha,\beta) = \mathbf{h}^{-1}\Psi(x,h_1(\alpha,\beta),h_2(\alpha,\beta)),$$

for all  $x \in \mathbb{R}$  such that  $\Phi(x, \alpha, \beta) \in \Omega$ .

By a result of Guysinsky et al.  $(2003)^6$  since  $f(u, v) = (v, \frac{q}{D}v - \frac{r}{D}u(1-u))$  is a  $C^{\infty}$  function, **h** can be chosen so that

- **h** is differentiable at (0,0)
- $D\mathbf{h}(0,0) = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$

<sup>&</sup>lt;sup>6</sup>M. Guysinski, B. Hasselblatt, V. Rayskin, *Differentiability of the Hartman-Grobman Linearization*, Discrete and Continuous Dynamical Systems, 9(4), 2003, 979-984





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#### Slopes at (0,0) under the action of the linear flow



Let S(m, L) = the slope of the image of the line v = mu under  $\Psi(L, -, -)$ .

Let  $\theta = \sqrt{\frac{r}{D} - \frac{q^2}{4D^2}}$ .

Then

$$S(m,L) = \frac{2Dm\theta\cos(\theta L) + (mq - 2r)\sin(\theta L)}{2D\theta\cos(\theta L) + (2mD - q)\sin(\theta L)}.$$

#### Slopes at (0,0) under the action of the linear flow



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Let 
$$\theta = \sqrt{\frac{r}{D} - \frac{q^2}{4D^2}}.$$

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# Slopes at (0,0) under the action of the linear flow



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Let 
$$\theta = \sqrt{\frac{r}{D} - \frac{q^2}{4D^2}}$$
.

Then

$$S(m,L) = \frac{2Dm\theta\cos(\theta L) + (mq - 2r)\sin(\theta L)}{2D\theta\cos(\theta L) + (2mD - q)\sin(\theta L)}.$$





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For intersection, we need  $S(0, -L_0) > \frac{A_1}{A_0} S\left(\frac{q}{D}, L_1\right) + \frac{A_2}{A_0} S\left(\frac{q}{D}, L_2\right)$ 

Sufficient and necessary condition for the existence of a positive steady state solution

There exists a (unique) positive steady state solution for a Y-shaped network if and only if one of the following holds:

- 1.  $L_0 > L_c^{out}$  (or just  $L_0 + L_1, L_0 + L_2 > L_c^{out}$ )
- 2.  $L_1 > L_c^{host}$  or  $L_2 > L_c^{host}$
- 3. neither (1) nor (2) hold, and

$$S(0,-L_0) > rac{A_1}{A_0}S\left(rac{q}{D},L_1
ight) + rac{A_2}{A_0}S\left(rac{q}{D},L_2
ight).$$

# Steady state solution as an "orbit graph" in the *uv*-plane: the general case



#### Existence and uniqueness in the general case

Given an arbitrary river network, we can look for the corresponding configuration of orbits by starting with the line  $v = \frac{q}{D}u$  and iterating the following steps, starting with the upstream segments and moving towards the root segment:

- for each segment of length L, apply the flow φ(L, −, −) to the curve obtained on a previous step;
- for each junction, produce the "vertical weighted average" of the curves obtained on the previous steps.

The curves produced at each iteration will stay concave up. The last step is the same as for the Y-shaped network.

#### Existence and uniqueness in the general case

Uniqueness is guaranteed. Existence conditions are similar. E.g. for a tree like this



we get the condition

$$S(0, -L_0) > \frac{A_{00}}{A_0} S\left(\frac{A_{000}}{A_{00}} S\left(\frac{q}{D}, L_{000}\right) + \frac{A_{001}}{A_{00}} S\left(\frac{q}{D}, L_{001}\right), L_{00}\right) + \frac{A_{01}}{A_0} S\left(\frac{q}{D}, L_{01}\right)$$

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### Effect of network geometry on persistence and steady state

- One-dimensional case (single river): the length *L* of the river is the only **geometric** parameter that affects persistence and steady state profile.
- River network: even in the simple Y-shaped network, there are multiple geometric parameters (lengths of segments, ratios of cross-section areas).
- Is there a single parameter that can be (up to some extent) used as an analogue of river length?
- Sarhad et al.<sup>7</sup> considered measures such as:
  - total water volume  $(\sum L_i A_i)$
  - radius of a circle centered at the root vertex that contains half of the total water volume

<sup>7</sup>J. Sarhad, S. Manifold, K.E. Anderson, Geometric indicators of population persistence in branching continuous-space networks, J. Math. Biol. (2017) 74: 981-1009.

#### Effect of network geometry on persistence and steady state

For a Y-shaped network:

- fix ratios of cross-section areas  $(\frac{A_1}{A_0} \text{ and } \frac{A_2}{A_0})$ , q, D, r
- $L = L_0 + L_1 + L_2$
- $\frac{L_0}{L} + \frac{L_1}{L} + \frac{L_2}{L} = 1$
- network geometry is determined by the ratios

$$\ell_1=rac{L_1}{L}$$
 and  $\ell_2=rac{L_2}{L}$  (where  $\ell_1+\ell_2\leq 1$ )



#### Effect of network geometry on persistence and steady state

- For each pair of ratios (l<sub>1</sub>, l<sub>2</sub>) in the triangle region we can determine the critical total length L<sub>c</sub>(l<sub>1</sub>, l<sub>2</sub>).
- Geometry of the network will affect the profile of the steady state, e.g. the location of the maximal density.
- Understanding density profile can help in analyzing competition in river networks: e.g. low density areas can be invaded by a competitor.



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## Effect of network geometry on critical total length: a first look



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