Population persistence under advection-diffusion in river networks

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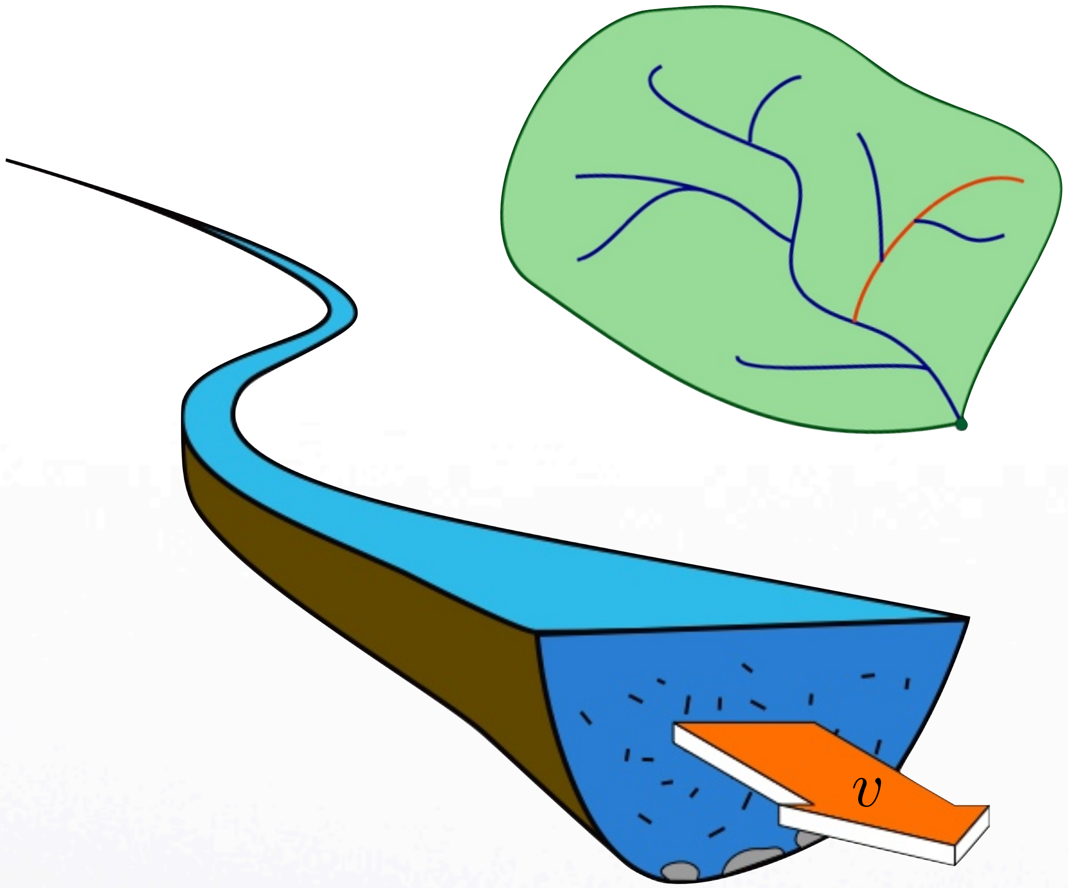
Motivation: the Drift Paradox



- During the larval stage, benthic organisms dwell on the bottom of streams.
- Organisms get eventually detached from the stream bottom and are dispersed (mostly) downstream.
- Dispersal distance depends on the physical properties of the river network.

Reproductive rate

Rate of detachment from bottom

VS

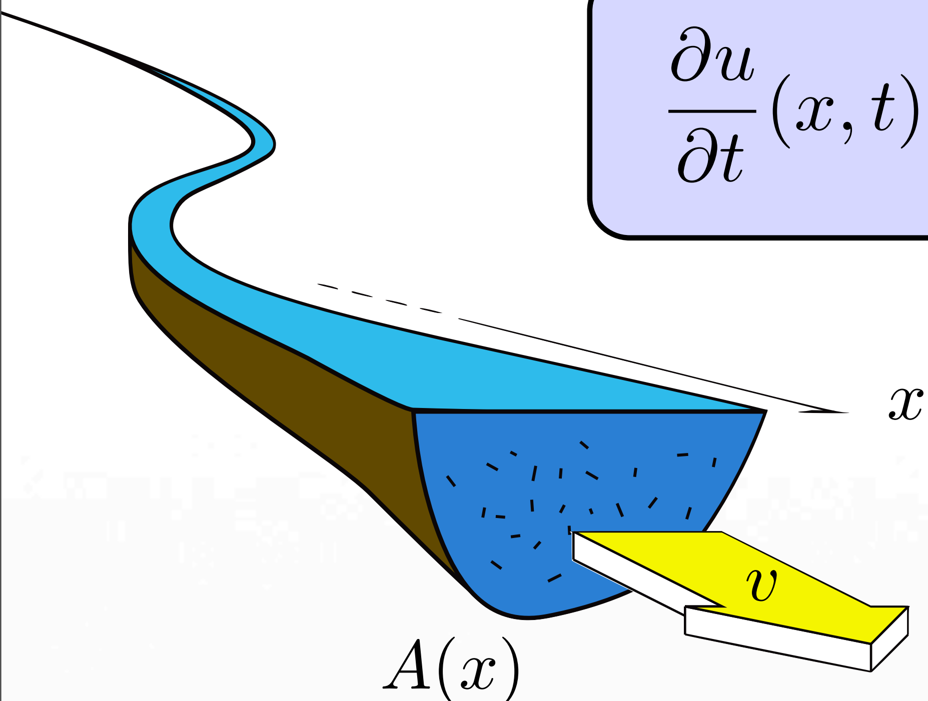
Direction and magnitude of dispersal

Problem:

Find conditions, in terms of physical and biological variables, that guarantee population persistence.

Mathematical model: jump process.

$$\frac{\partial u}{\partial t}(x,t) = ru(x,t) - \mu u(x,t) + \mu \int_\Gamma \mathcal{K}(y,x)u(y,t)\,\mathrm{d}y$$



Volumetric density of individuals = $A(x)u(x,t)$

$r =$ net growth rate at low population values

$\mu =$ rate of detachment

$\Gamma =$ river network

$\mathcal{K}(y,x) =$ probability of dispersal to x starting at y

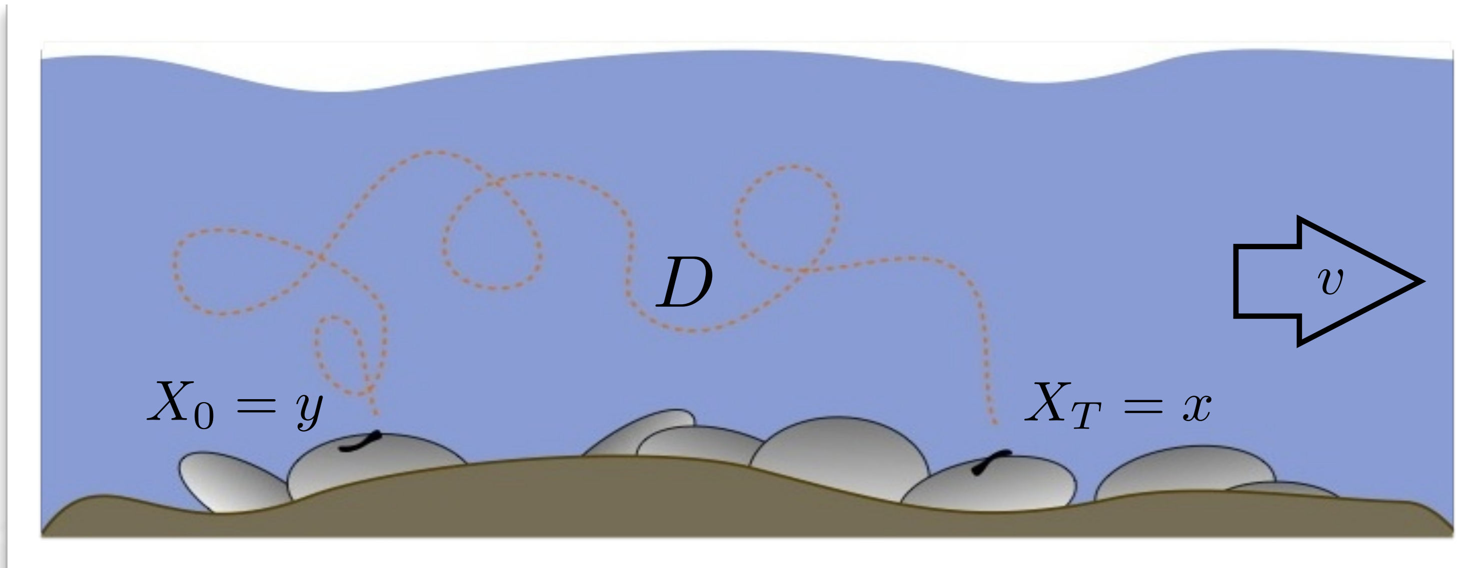
Persistence $\not\equiv$ **Imminent extinction** $\Longleftrightarrow$ **$u \equiv 0$ is asymptotically stable**

$\Uparrow$

$$\boldsymbol{r - \mu + \mu\omega_{\mathcal{K}} < 0}$$

$\omega_{\mathcal{K}} :=$ max eigenvalue of $\mathcal{K}f := \int_\Gamma \mathcal{K}(y,x)f(y)\,\mathrm{d}y$

Microscopic model: the dispersion kernel $\mathcal{K}$



Individual trajectories:
advection-diffusion in Γ

$$X := \{X_t : t \geqslant 0\}$$

$v =$ water velocity
$D =$ diffusion coefficient.

Transition probabilities:

$$P(y,x,t)\,\mathrm{d}x := \mathbb{P}(X_t \in \mathrm{d}x | X_0 = y)$$

Backwards operator:

$$\frac{\partial P}{\partial t} = \mathcal{A}P(\cdot,x,t) = D\frac{\partial^2 P}{\partial y^2} - v\frac{\partial P}{\partial y}$$

+ boundary conditions

Individuals remain mobile for a random exponential time: $T \sim \exp(\sigma)$

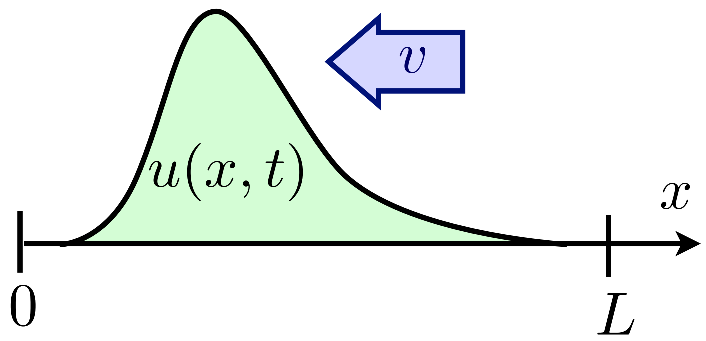
$$\mathcal{K}(y,x) = \mathbb{P}(X_T \in \mathrm{d}x | X_0 = y) = \int_0^\infty \sigma e^{-\sigma t} P(y,x,t)\,\mathrm{d}t$$

Review of the 1D case.

Habitat = river stretch of length L.

Lutscher, Pachepsky, Lewis (2005)

The mathematical model in 1D



$\mu =$ detachment rate

$$\frac{\partial u}{\partial t}(x,t) = ru(x,t) - \mu u(x,t) + \mu \int_0^L \mathcal{K}(y,x)u(y,t)\,\mathrm{d}y$$

$r =$ net population growth

$\mathcal{K}(y,x) =$ probability of dispersal from y to x

Change of time units to μt :

$$\frac{\partial u}{\partial t}(x,t) = (r/\mu - 1)u(x,t) + \int_0^L \mathcal{K}(y,x)u(y,t)\,\mathrm{d}y$$

Theorem (critical reproductive rate)

Let $\omega_{\mathcal{K}}$ be the largest eigenvalue of $\mathcal{K}$

$$r < r_{\text{crit}} := \mu(1 - \omega_{\mathcal{K}})$$

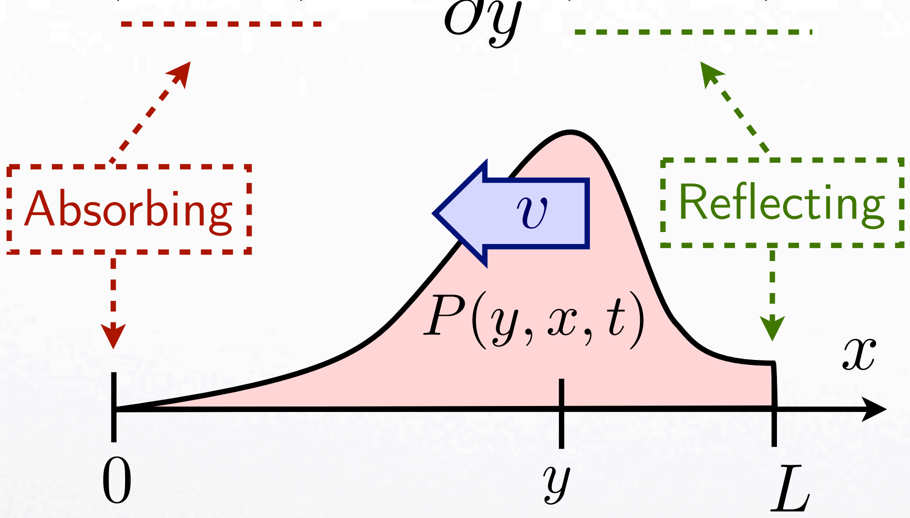
implies $u \equiv 0$ is stable **(imminent extinction)**.

Finding eigenvalues: a related Sturm Liouville problem

Backwards operator:

$$\frac{\partial P}{\partial t} = \mathcal{A}P = D\frac{\partial^2 P}{\partial y^2} - v\frac{\partial P}{\partial y}$$

$$P(0,x,t) = \frac{\partial P}{\partial y}(L,x,t) = 0$$



Infinitesimal Generator:

$\mathcal{A}f = Df'' - vf'$

$\mathrm{Dom}(\mathcal{A}) = \{f \in \mathcal{C}^2_{[0,L]} : f(0) = f'(L) = 0\}$

$$\mathcal{K}(y,x) = \int_0^\infty \sigma e^{-\sigma t} P(y,x,t)\,\mathrm{d}t$$

Resolvent of $\mathcal{A}$: $(\sigma I - \mathcal{A})u = \frac{D}{p}\mathcal{L}u$

$$\mathcal{L}u = -(pu')' + qu$$

$$p(x) := e^{-\frac{v}{D}x} \quad q(x) := \frac{\sigma}{D}p(x)$$

Sturm-Liouville operator:

$$\mathcal{L}f = -(pf')' + qf$$

$$f(0) = f'(L) = 0$$

$$\mathrm{Dom}(\mathcal{L}) = \mathcal{C}^2_{[0,L]}$$

Finding eigenvalues: $\mathcal{K}$ and $\mathcal{L}$

$$\mathcal{L}u = -(pu')' + qu$$
$$u(0) = u'(L) = 0$$

$$\mathcal{L}\left(\int_\Gamma \mathcal{K}(y,x) f(x)\,\mathrm{d}x\right) = \frac{f(y)}{q(y)}$$

$G(y,x) =$ Green's function for $\mathcal{L}$

$\mathcal{L}u = f \Longleftrightarrow u(y) = \int_0^L G(y,x) f(x)\,\mathrm{d}x$

$$\mathcal{K}(y,x) = q(x)G(y,x)$$

Eigenvalue equivalence: $\mathcal{K}u = \omega u \Leftrightarrow \mathcal{L}v = \frac{1}{\omega} qv$

Theorem

The largest eigenvalue of $\mathcal{K}$ is $\omega_{\mathcal{K}} = 1/\nu_1$, where ν_1 is the smallest q-eigenvalue of $\mathcal{L}$.

$$1 + \frac{1}{4}\mathsf{QP} + \frac{\pi^2}{4}\frac{\mathsf{Q}}{\mathsf{P}} < \nu_1 < 1 + \frac{1}{4}\mathsf{QP} + \pi^2\frac{\mathsf{Q}}{\mathsf{P}}.$$

Non-dimensional numbers: $\mathsf{P} := \frac{vl}{D}$, $\mathsf{Q} := \frac{v}{\sigma l}$

Proof:

Eigenfunctions:

$$u(x;\nu) = Ae^{\left(\frac{v}{2D}+b(\nu)i\right)x} + Be^{\left(\frac{v}{2D}-b(\nu)i\right)x}$$
$$b(\nu) := \tfrac{1}{2D}\sqrt{v^2 - 4D\sigma(\nu-1)}$$

Eigenvalues:

$$\tan(lb(\nu)) = -\frac{2lb(\nu)}{\mathsf{P}}$$

$$\nu = \frac{(lb(\nu))^2 + \mathsf{P}^2/4}{\mathsf{P}/\mathsf{Q}} + 1$$

Critical reproductive rate (1D case)

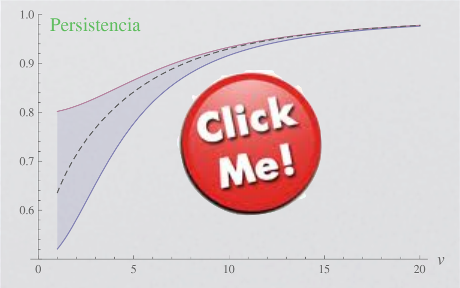
$$r_{\text{crit}} := \mu\left(1-\frac{1}{\nu_1}\right) \qquad \mathsf{P} := \frac{vl}{D},\ \mathsf{Q} := \frac{v}{\sigma l}$$

Small values of r_{crit} are good!

Theorem (Lutscher et.al. 05, JMR'11)

- $r > \mu \Rightarrow$ population peristence
- $r < r_{\text{crit}} \Rightarrow$ imminent extinction
- $r_{\text{crit}}(\sigma)\downarrow, \quad r_{\text{crit}}(l)\downarrow, \quad r_{\text{crit}}(v)\uparrow.$
- $r_{\text{crit}}(D)\downarrow$ for $\mathsf{P} > 2\pi$.
- $\displaystyle\lim_{l\to\infty}\frac{r_{\text{crit}}}{\mu} = \frac{v^2}{v^2+4D\sigma}$ It's not enough to have a large habitat!!!

Useful bounds: $$\frac{4\mathsf{P}}{4\mathsf{P}+\mathsf{Q}(\mathsf{P}^2+4\pi^2)} < \frac{r_{\text{crit}}}{\mu} - 1 < \frac{4\mathsf{P}}{4\mathsf{P}+\mathsf{Q}(\mathsf{P}^2+\pi^2)}$$



Critical reproductive rate values

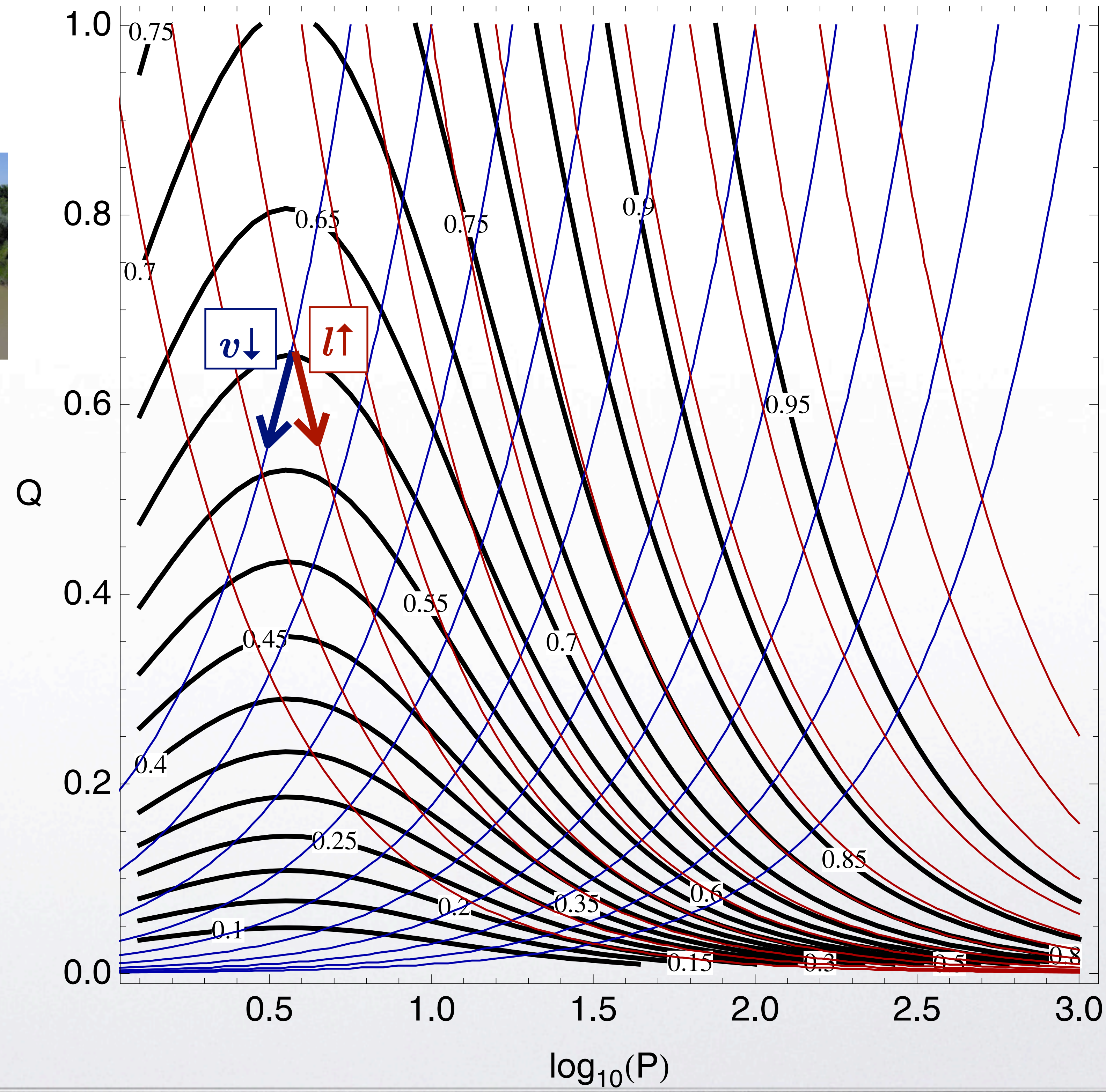
$$\mathsf{P} := \frac{vl}{D}, \qquad \mathsf{Q} := \frac{v}{\sigma l}$$

— constant r_{crit}

— constant $\dfrac{\mathsf{Q}}{\mathsf{P}} = \dfrac{D}{\sigma l^2}$

— constant $\mathsf{QP} = \dfrac{v^2}{\sigma D}$

Different strategies to reduce $\mathbf{r}_{\mathsf{crit}}$

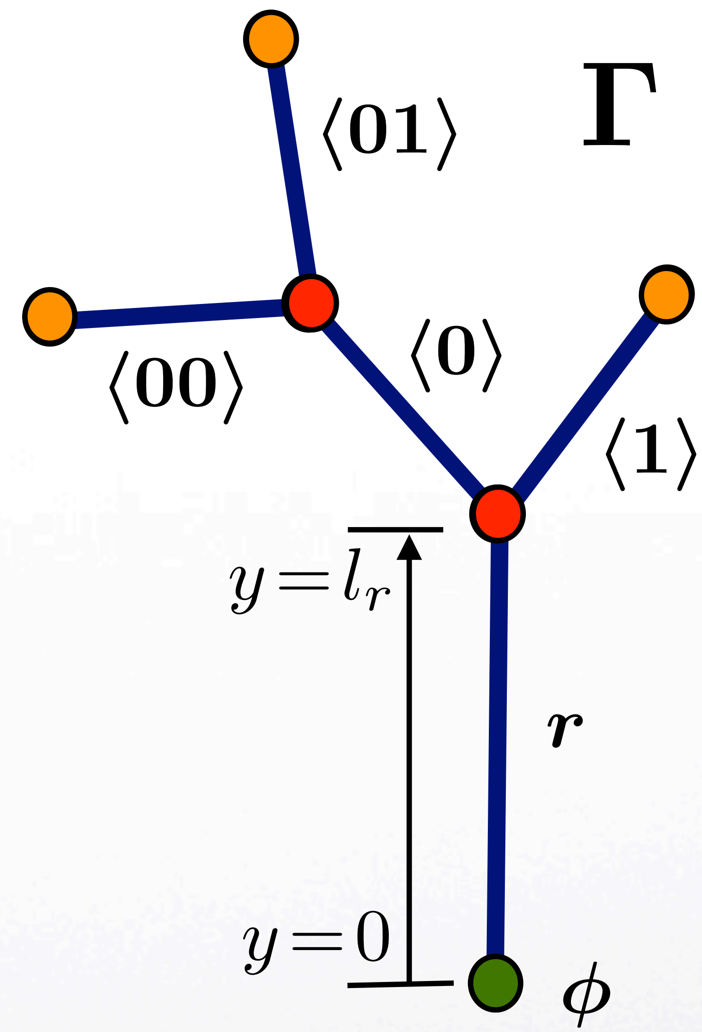


The binary tree case

Habitat = river network.

Binary graphs: a model for river networks

$$\frac{\partial u}{\partial t}(x,t) = (\bar{r}-1)u(x,t) + \int_\Gamma \mathcal{K}(y,x)u(y,t)\,\mathrm{d}y$$



Variables per edge	Area	Length	Drift	Diffusivity
	A_e	l_e	v_e	D_e

Transition kernel $\mathcal{K}$ … $\mathrm{d}t, \quad y, x \in \Gamma$

Conservation of water
$$A_{e0}v_{e0} + A_{e1}v_{e1} = A_e v_e$$

Dispersion operator $\quad \frac{\partial P}{\partial t} = \mathcal{A}P$

$$\mathcal{A}u|_e = D_e \frac{\partial^2 u_e}{\partial y^2} - v_e \frac{\partial u_e}{\partial y}$$

Dom$(\mathcal{A})$

Match fluxes $\quad A_e D_e\, u'_e(l_e) = \sum_{i=0,1} A_{ei} D_{ei}\, u'_{ei}(0)$

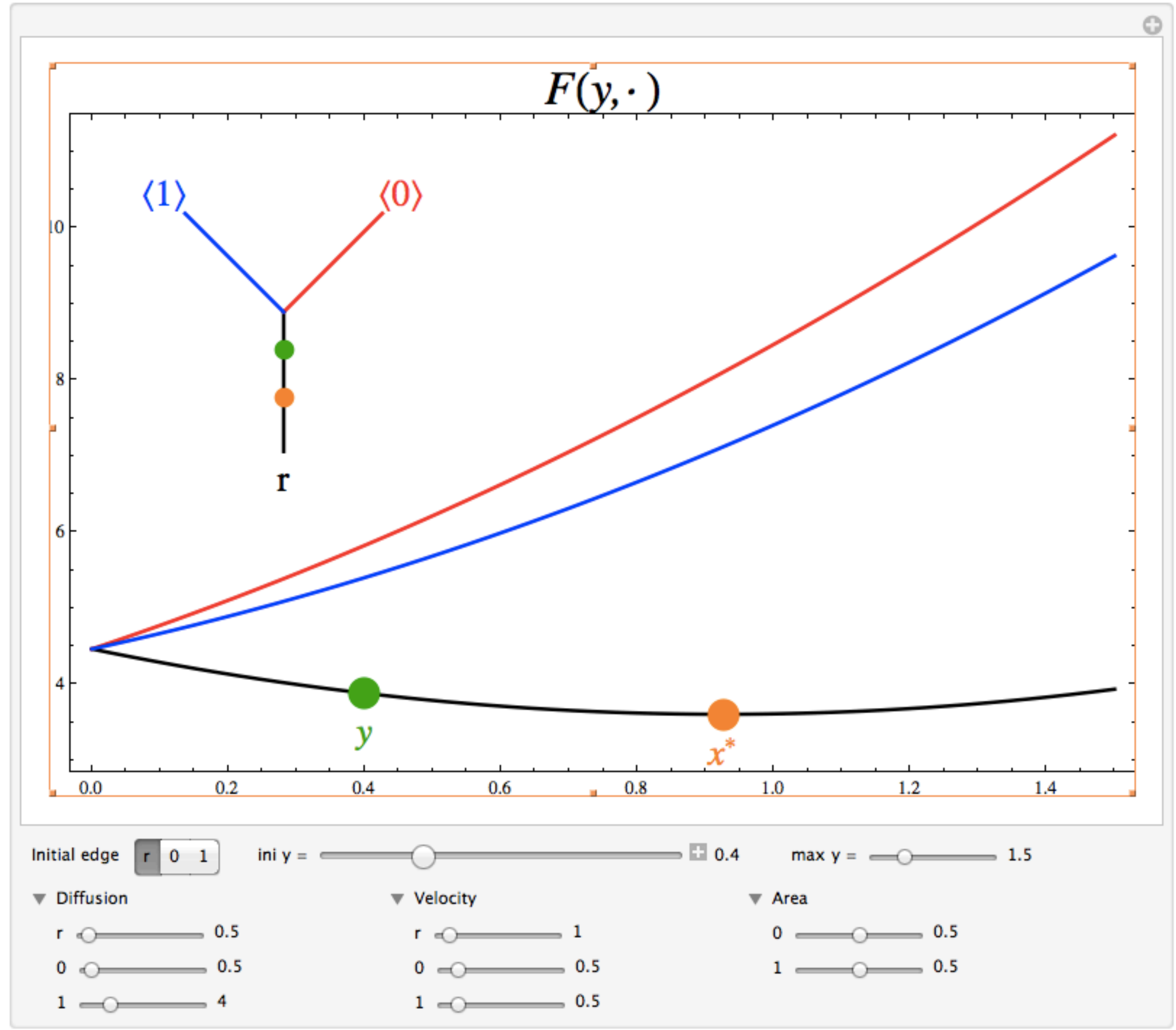
Continuity $\quad u_e(l_e) = u_{e0}(0) = u_{e1}(0)$

$u'_e(l_e) = 0$ **Reflecting Upstream**

$u_r(0) = 0$ **Absorbing Downstream**

The stochastic process in a graph

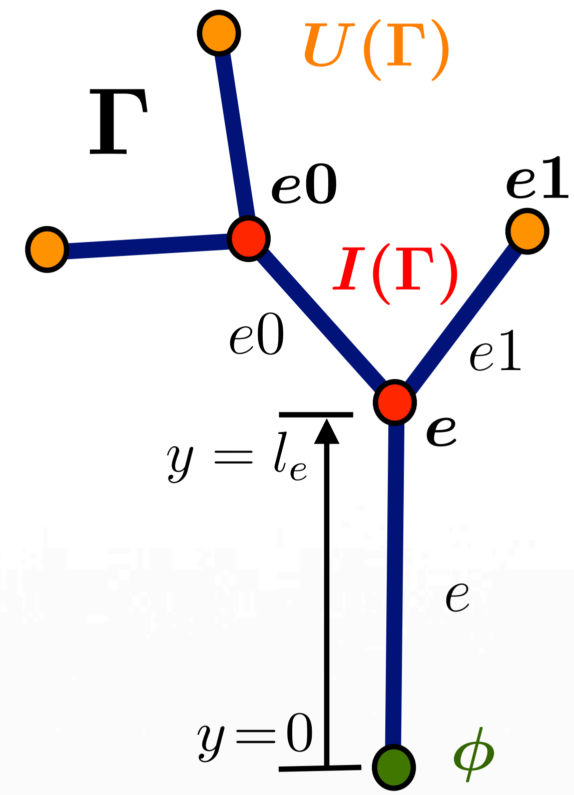
Existence: Freidlin, Wentzell '93. **No info on sample paths!!**



The Sturm-Liouville problem on a graph

$$p(x) := e^{-\int_{\phi}^{x} \frac{v(y)}{D(y)}\,\mathrm{d}y}$$
$$q(x) := \frac{\sigma}{D} p(x)$$

$$(\sigma I - \mathcal{A}) f = \frac{D}{p} \mathcal{L} f$$



Operator: $\mathcal{L} f|_e = -(p f_e')' + q f_e$

$$\mathrm{Dom}(\mathcal{L}) = \left\{ f \in \mathcal{C}(\bar{\Gamma}) \cap \mathcal{C}^2(\Gamma);\ \frac{\mathrm{d}f}{\mathrm{d}_{AD}}(\boldsymbol{e}) = 0,\ \boldsymbol{e} \in I(\Gamma) \right\}$$

"Hydrologic" boundary conditions:

$$B_H(\Gamma) = \{ f : \Gamma \to \mathbb{R};\ f(\boldsymbol{\phi}) = f'(\boldsymbol{e}) = 0,\ \boldsymbol{e} \in U(\Gamma) \}$$

Theorem (JMR'11).

- ✓ $\mathcal{L}$ is self-adjoint w.r.t. $\mathrm{d}AD$.
- ✓ Let $f \in \mathcal{C}(\bar{\Gamma})$. Then,
  $$\frac{1}{pA} \mathcal{K} f \in \mathrm{Dom}(\mathcal{L}) \cap B_H,\ \mathcal{L}\left(\frac{1}{pA} \mathcal{K} f \right) = \frac{1}{AD} f$$

1. Dispersion kernel:

$$\boldsymbol{\mathcal{K}(y, x) = q(x) G(y, x)}$$

2. Eigenvalue equivalence:

$$\boldsymbol{\mathcal{K} u = \omega u \Leftrightarrow \mathcal{L} v = \frac{1}{\omega} q v}$$

The Green's function G y el kernel $\mathcal{K}$

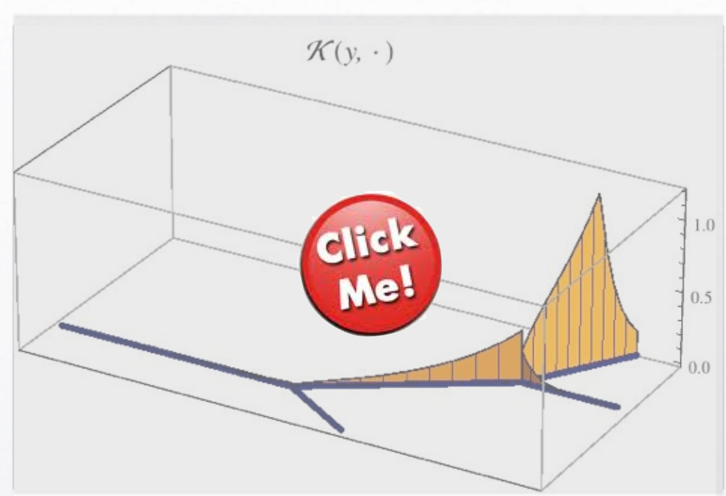
Computing G in a graph:

$$\mathcal{L}u = f \iff u(y) = \int_\Gamma G(y,x) f(x)\, \mathrm{d}x$$

$$\mathcal{K}(y,x) = q(x) G(y,x)$$

Lagrange's method for graphs:

(JMR '12) "Green's functions for Sturm-Liouville problems on directed tree graphs"



Bounds for the eigenvalues of $\mathcal{L}$ and criteria for persistence

$$\mathcal{K}u = \omega u \Leftrightarrow \mathcal{L}v = \frac{1}{\omega} q v$$

Variational formulation

Solve: $u \in \text{Dom}(\mathcal{L}) \cap B_H, \qquad -(pu_e')' + (1-\nu)qu_e = 0$

Extended operator:

$$\text{Dom}(\mathcal{L}) = \left\{ f \in \mathcal{C}(\bar{\Gamma}) \cap H^1(\Gamma);\ pu' \in H^1(\Gamma),\ \frac{\mathrm{d}f}{\mathrm{d}_{AD}}(\boldsymbol{e}) = 0,\ \boldsymbol{e} \in I(\Gamma) \right\}$$

$$B_H(\Gamma) = \{ f : \Gamma \to \mathbb{R};\ f(\boldsymbol{\phi}) = f'(\boldsymbol{e}) = 0,\ \boldsymbol{e} \in U(\Gamma) \}$$

Associated bilinear form:

$$\mathcal{F}(u,v) = \int_\Gamma pu'v' + quv \, \mathrm{d}AD, \qquad u, v \in \text{Dom}(\mathcal{F}).$$

$$\text{Dom}(\mathcal{F}) = \{ u \in H^1(\Gamma) \cap \mathcal{C}(\bar{\Gamma});\ u(\boldsymbol{\phi}) = 0 \}.$$

Theorem:

$$\nu_1(\Gamma) = \inf_{v \in \text{Dom}(\mathcal{F})} \frac{\mathcal{F}(v,v)}{(qv,v)_{AD}}$$

All sorts of upper bounds for the smallest eigenvalue!!!

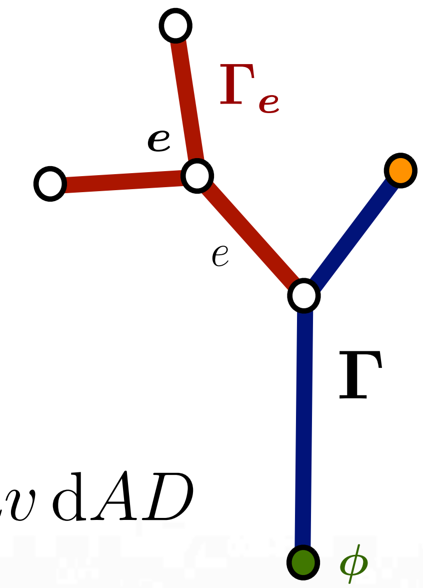
Consequences ...

Problem in sub-graph Γ_e:

$$\mathcal{L}^{(e)}u = (-p^{(e)}u')' + q^{(e)}u$$

$$u \in \mathrm{Dom}(\mathcal{L}^{(e)}) \cap B_H(\Gamma_e)$$

$$\mathcal{F}^{(e)}(u,v) = \int_{\Gamma_e} p^{(e)}u'v' + q^{(e)}uv\,\mathrm{d}AD$$



Theorem (JMR'11)

$\nu_1(\Gamma_e) =$ min eigenvalue of $\mathcal{L}^{(e)}$ in $\Gamma(e)$

$$\Longrightarrow \quad \nu_1(\Gamma) \leqslant \nu_1(\Gamma_e)$$

Proof:

$$\mathcal{F}^{(e)}(u^{(e)}, u^{(e)}) = \nu_1(\Gamma_e)(q^{(e)}u^{(e)}, u^{(e)})_{AD(\Gamma_e)}$$

$u := u^{(e)}\mathbb{1}_e \in \mathrm{Dom}(\mathcal{F})$

$\times p(e,0)$ both sides

$$\mathcal{F}(u,u) = \nu_1(\Gamma_e)(qu,u)_{AD}$$

Application:

$$r_{\text{crit}}(\Gamma) \leqslant r_{\text{crit}}(\Gamma_e)$$

Upstream subnetworks are very important for population persistence:

- If there is persistence in any upstream sub-network, there is persistence on the whole network.
- If we want a small r_{crit} on the whole network, it is enough to reduce it in some upstream sub-network.

Relationship with Dirichlet boundary conditions.

Hydrologic b.c. $B_H(\Gamma) = \{f : \Gamma \to \mathbb{R};\ f(\boldsymbol{\phi}) = f'(\boldsymbol{e}) = 0,\ \boldsymbol{e} \in U(\Gamma)\}$

Dirichlet b.c. $B_D(\Gamma) = \{f : \Gamma \to \mathbb{R};\ f(\boldsymbol{e}) = 0,\ \boldsymbol{e} \in \partial\Gamma\}$

$$\eta_1(\Gamma) = \text{Least evalue of} \begin{cases} u \in \mathrm{Dom}(\mathcal{L}) \cap B_D \\ \mathcal{L}u = \eta q u \end{cases}$$

Variational formulation:

$\Rightarrow\ \nu_1(\Gamma) < \eta_1(\Gamma)$

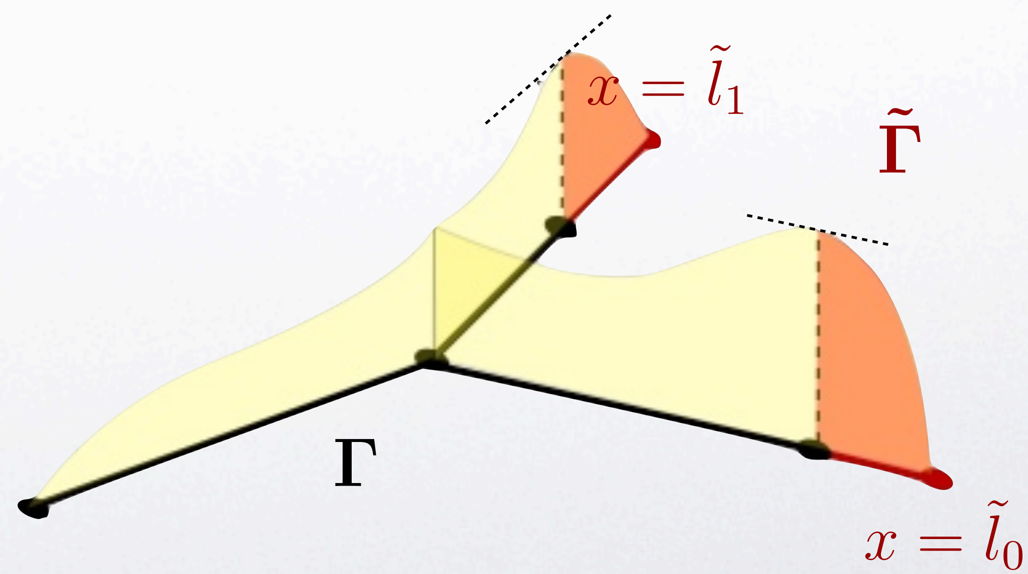
Lema

Every segmento e of $U(\Gamma)$ can be enlarged to a length $\tilde{l}_e$ such that

$$u_e(\tilde{l}_e, \nu_1(\Gamma)) = 0.$$

Let $\tilde{\Gamma}$ be the resulting network; $\tilde{p}$, $\tilde{q}$, and $\tilde{\mathcal{L}}$ the extensions to $\tilde{\Gamma}$, then

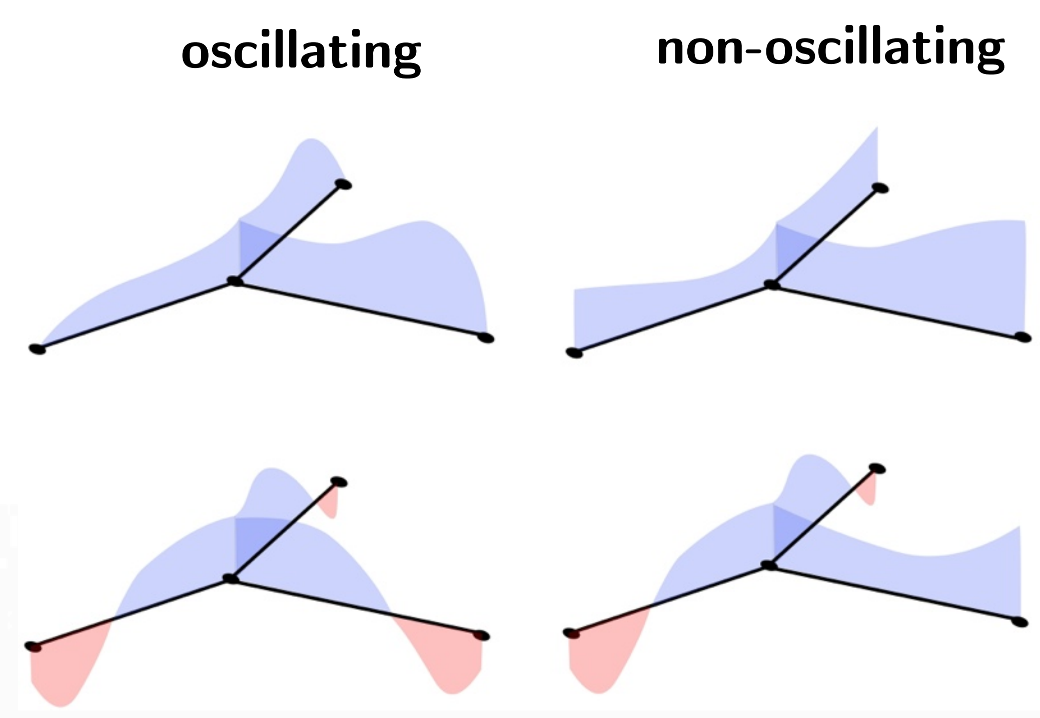
$$\eta_1(\tilde{\Gamma}) \leqslant \nu_1(\Gamma).$$



Oscillation theory on graphs

Definition

$(\mathcal{L}, \nu)$ **oscillates in** Γ if there exists a solution to $\mathcal{L}u = \nu q u$, $u \in \mathrm{Dom}(\mathcal{L})$, such that $|u| > 0$ in a sub-graph $S \subseteq \Gamma$, and $u = 0$ in ∂S.



Pokornyi, et.al. (2004)

$$\eta_1(\Gamma) = \sup_{\nu} \{(\mathcal{L}, \nu) \text{ in non-oscillating in } \Gamma\}$$

Lema Let $\nu^*(\Gamma) := \min_e \left\{1 + \frac{v_e}{4D_e\sigma}\right\}$.

$\nu < \nu^*(\Gamma) \Rightarrow (\tilde{\mathcal{L}}, \nu)$ is non-oscillating in $\tilde{\Gamma}$.

$$\boldsymbol{\nu^*(\Gamma) \leqslant \eta_1(\tilde{\Gamma}) \leqslant \nu_1(\Gamma)}$$

Proof:

Solution to $\tilde{\mathcal{L}}u = \nu \tilde{q} u$,

$$\tilde{u}(x;\nu) = \sum_{e \in \Gamma} (C_e^{\alpha} e^{\alpha_e x} + C_e^{\beta} e^{\beta_e x}) \mathbb{1}_e(x)$$

If $\nu < \nu^*(\Gamma)$, $\alpha_e, \beta_e \in \mathbb{R}$, there are $C_e^{\alpha}, C_e^{\beta}$ such that $\tilde{u}(\nu;x) > 0$ for all $x \in \tilde{\Gamma}$.

Summary: $\nu^*(\Gamma) \leqslant \nu_1(\Gamma) \leqslant \nu_1(\Gamma_e)$

Theorem:

The largest rvalue of $\mathcal{K}$ is $\omega_{\mathcal{K}} = 1/\nu_1(\Gamma)$.
The **critical reproductive rate** satisfy:

$$r_{\text{crit}}(\Gamma) = \mu(1 - \omega_{\mathcal{K}}),$$

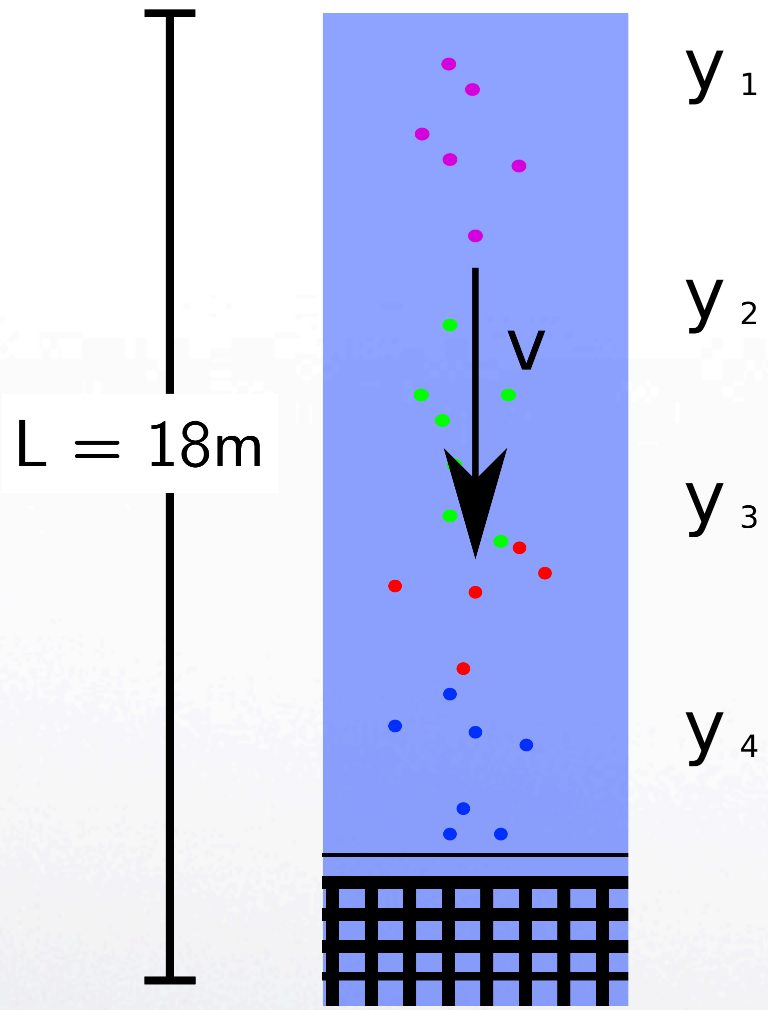
$$\min_{e \in \Gamma} \frac{\mathsf{P}_e \mathsf{Q}_e}{4 + \mathsf{P}_e \mathsf{Q}_e} < \frac{r_{\text{crit}}(\Gamma)}{\mu}$$

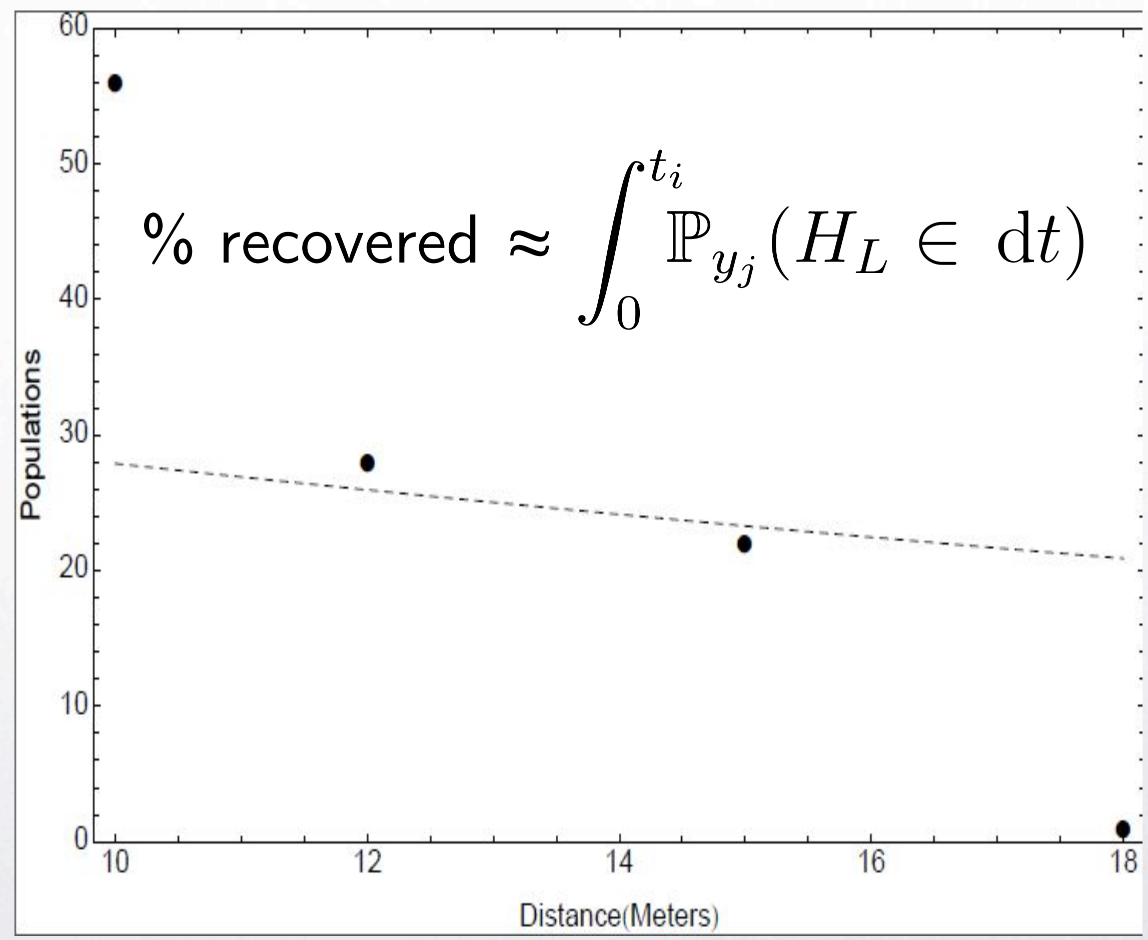
$$< \frac{r_{\text{crit}}(\Gamma_e)}{\mu} \leqslant \min_{e \in U(\Gamma)} 1 - \frac{4\mathsf{P}_e}{4\mathsf{P}_e + \mathsf{Q}_e(\mathsf{P}_e^2 + 4\pi^2)} \blacksquare$$

An example:

An experiment? Please?

At t = t_1, t_2, t_3, t_4





$$v = 0.35\, m/s, \;\; D = 5.6\, m^2/s$$

Thank you very much!