Persistence and Competition in River and River Networks

By

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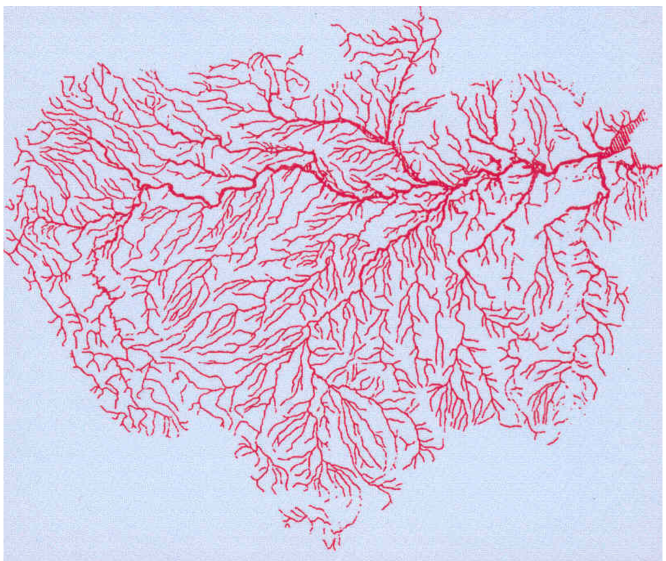
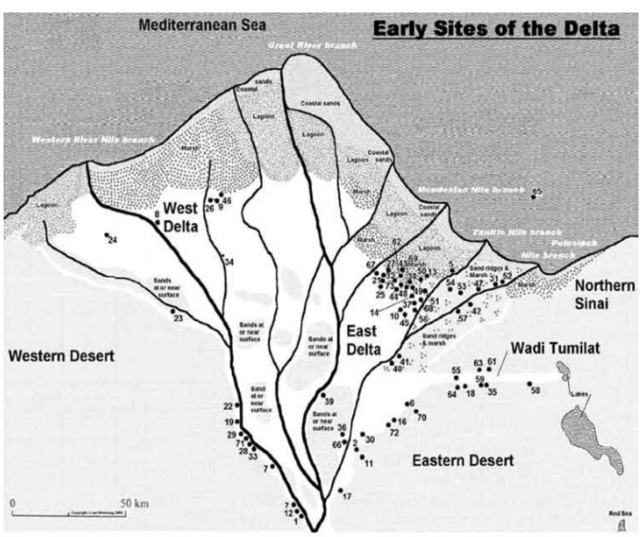
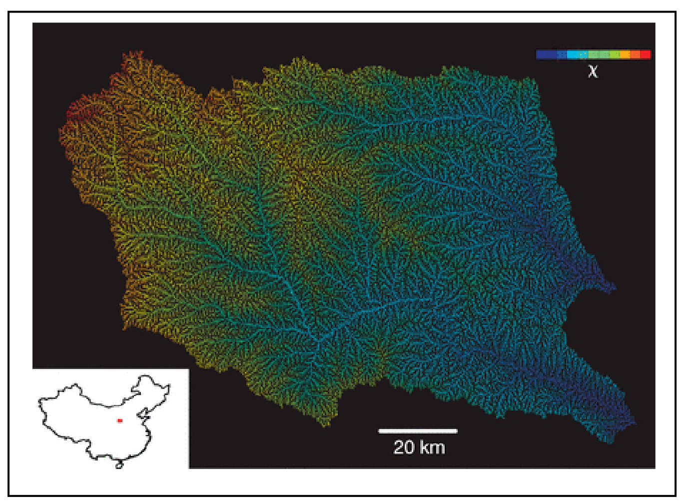


(Amazon river basin: courtesy of Hideki Takayusu)



(Early Nile Delta)



(Yanke & Qingjian rivers; Willett, et al, 2014)

Some Motivation

Query: How do populations persist in the face of downstream biased flow?

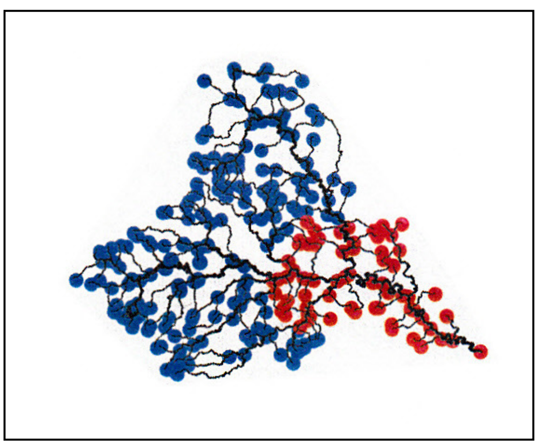
In an advection-driven environment this is the 'drift paradox' (Muller, 1954; Hershey, et al, 1993; …)

Query: How does advection-driven environment affect competition among species?

Species proliferation rate versus advection rate is important.

Query: Does a branching river network add new dynamical behavior and affect persistence?

Query: Can the study of populations (pathogens) in river networks help us to better understand the dynamics of water born infectious diseases, like cholera, typhoid fever, botulism, etc?



Sites with reported cases of cholera, Thukela river basin, South Africa (see Gatto, et al, 2012, PNAS)

Talk Outline

1. Persistence in a single population, single branch advection-driven environment

2. Persistence of a single population in a branched river system

3. Competition between populations in a single branch advection-driven environment

Advection-Driven Environments

Streams, rivers, estuaries

Coastlines with unidirectional currents, mountain slopes

Vertical water column in a lake

The gut

With a suitable change of coordinates, moving temperature isoclines

We think of stream/rivers

Well-mixed, vertically and transversally,

(only measure along length of stream)

Uniform cross-section (per branch)

Constant advection

Finite length stream

In an advection-driven environment, if a population does not have the ability in invade upstream, it will eventually be completely discharged. So a population-based transport mechanism is required

$\Rightarrow$ advection-diffusion dynamics

Single Population-Single Stream

(1) $N_t = DN_{xx} - QN_x + rNf(N)$, $0 < x < L, \quad t > 0$

Upstream terminus:

(2) $-DN_x(0,t) + QN(0,t) = 0$ (individuals cannot leave the domain)

Downstream terminus:

(3a) $N(L,t) = 0$ "hostile" b.c. (Speirs, Gurney, 2001; Sarhad, et al, 2012)

(3b) $N_x(L,t) = 0$ advection-only outflow : Danckwert b.c.

(Vasilyeva, Lutscher, 2010; Ballyk, Smith, 1998, …)

Linear (Malthusian) problem: (1),(2),(3b), $f(N) \equiv 1$

$$N(x,t) = e^{Qx/2D} \sum_{n\geq 1} B_n e^{-\lambda_n t} \left\{ \sin(\omega_n x) + \frac{2\omega_n D}{Q} \cos(\omega_n x) \right\}$$

$\omega_n := \dfrac{\sqrt{4D(r+\lambda_n) - Q^2}}{2D}$ an increasing sequence of solutions to

$$\tan(\omega L) = \frac{4QD\omega}{4D^2\omega^2 - Q^2}$$

Either the population goes extinct or population grows unboundedly if $\lambda < 0$. Boundary when lowest eigenvalue $\lambda_1 = 0$. Critical length is

$$L = L_{cr}(Q) = \frac{1}{\omega} \left\{ \arctan\left[\frac{Q\sqrt{4rD - Q^2}}{2rD - q^2} \right] + \pi\Theta(Q - 2\sqrt{rD}) \right\} , \quad \omega = \frac{\sqrt{4rD - Q^2}}{2D}$$

Observations:

$Q \to Q_{cr} := 2\sqrt{rD}$ *then* $L_{cr} \to \infty$ whole population washes out

So we want $Q^2 < Q_{cr}^2 \Leftrightarrow Q^2 / 4D < r$

Generally $f(N) < 1$ in the nonlinear case, so r is the maximum reproduction rate that must satisfy $Q^2 / 4D < r$.

$Q < Q_{cr}$ *and* $L < L_{cr} (< \infty)$, then $N(\cdot, t) \to 0$ *as* $t \to \infty$

$Q < Q_{cr}$ *and* $L > L_{cr}$, then $N(\cdot, t) \to \infty$ *as* $t \to \infty$

For persistence, linear model requires long enough domain.

Remark: In **non-advective** (diffusive) environment, a minimum domain (patch) size necessary for persistence has been known for a long time. With absorbing boundaries, the diffusion rate must be below a critical value for persistence (Gurney, Nisbet, 1975; Ludwig, et al, 1979). In RD systems with hostile b.c.s also had critical domain requirement, and loss of individuals is entirely due to diffusion. In advection-diffusion case it is due to advection.

Single Population-Nonlinear Proliferation

Logistic growth case: $f(N) = 1 - N/K$

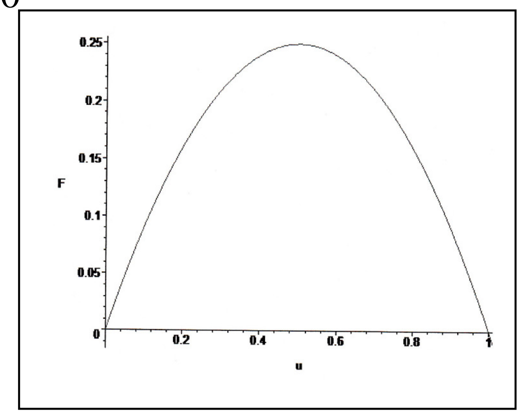
nondimensionalization: $u = N/K, \quad \tilde{x} = x\sqrt{\frac{r}{D}}, \quad \tilde{t} = rt, \quad q = \frac{Q}{\sqrt{rD}}, \quad \tilde{L} = L\sqrt{\frac{r}{D}}$

drop tilde notation

(1) $u_t = u_{xx} - qu_x + u(1-u) \quad in \quad 0 < x < L, \quad t > 0$

(2) $u_x(0,t) = qu(0,t)$

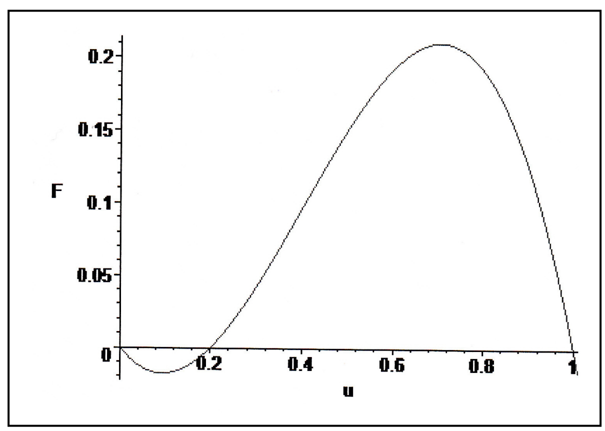
(3) $u_x(L,t) = 0$



Bistable growth case: $r_0 N f(N) = r_0 N(K-N)(N-B), 0 < B < K$

Allee mechanism

(1') $u_t = u_{xx} - qu_x + \kappa u(1-u)(u-\alpha)$



Steady State Solutions: logistic growth

(4) $u'' - qu' + u(1-u) = 0$ or $\begin{cases} u' = v \\ v' = qv - u(1-u) \end{cases}$

(5) $v(0) = qu(0), \quad v(L) = 0$

Remark: Traveling wave solutions for Fisher's equation

$u_t = u_{xx} + u(1-u)$ (propagation of a favorable gene in 1D habitat)

(Fisher, 1937; KPP, 1937)

$u(x,t) = U(z), \quad z = x + ct, \quad c > 0 \Rightarrow U'' - cU' + U(1-U) = 0$

with $\lim_{z \to -\infty} U(z) = 0, \quad \lim_{z \to \infty} U(z) = 1 \qquad c \leftrightarrow q$

$(U, U') = (1,0)$ is a saddle point in phase plane

$(U, U') = (0,0)$ is an unstable node (for $U(z) > 0$) $\Leftrightarrow q \geq 2$ ($Q \geq Q_{cr} = 2\sqrt{rD}$)

Lemma 1: There are no non-trivial solutions to (4),(5) for $q \geq 2$.

So we want

$0 < q < 2 \Leftrightarrow 0 < Q < Q_{cr} \Leftrightarrow Q^2 / 4D < r$

Theorem 1 (Vasilyeva, Lutscher, 2010):

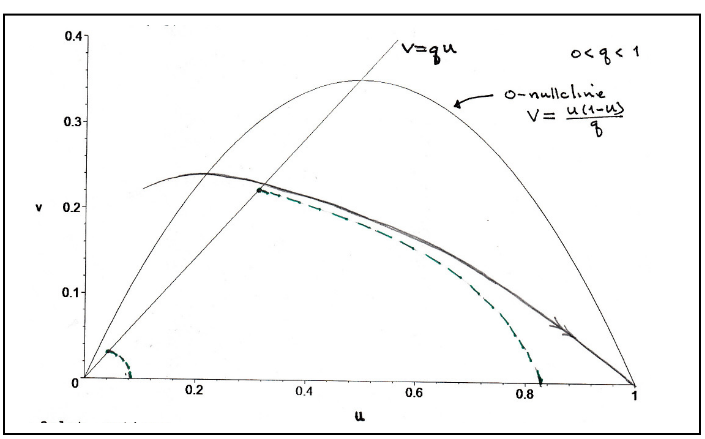
For $0 < q < 2$, $L > L_{cr}$, there is

a unique positive solution, $u^*(x)$, to (4), (5).

i) $u^*(x)$ is an increasing function of x. ii) $u^*(x)$ is linearly stable.

iii) $u^*(x)$ is a decreasing function of the advection speed; i.e.

$0 < q_1 < q_2 < 2 \rightarrow u(x;q_2) < u(x;q_1) \quad on \quad [0, L]$.



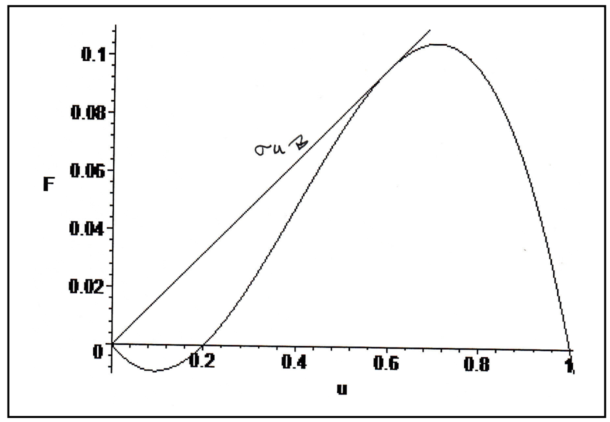
Bistable Proliferation Case

Consider

$u_t = Du_{xx} - qu_x + ru(1-u)(u-\alpha)$, with Danckwert b.c.s

Let $\sigma := \sup_{u>0}\{f(u)/u\}$ then for $u \geq 0 \quad f(u) \leq \sigma u$

For $f(u) = ru(1-u)(u-\alpha)$, $\sigma = \dfrac{r(1-\alpha)^2}{4}$



From a **comparison principle***, if $q \geq 2\sqrt{\sigma D} = \sqrt{rD}(1-\alpha)$, then the population will be washed out (non-persistence)

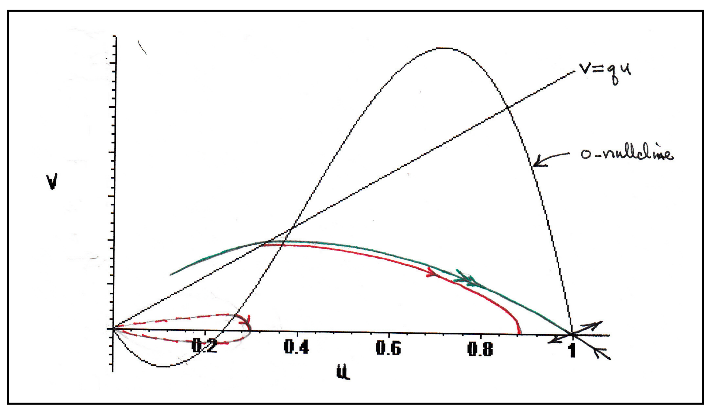
Lemma 2: For $0 < q < q_{bd} := 2\sqrt{rD}(1-\alpha)$

There exist $L > 0$ for which

$$\begin{cases} u' = v \\ v' = D^{-1}\left(qv - ru(1-u)(u-\alpha)\right) \end{cases}$$

$v(0) = qu(0), \quad v(L) = 0$

has a positive, increasing in solution $u^*(x)$.



*The comparison principle was developed for the tree graph case, but holds for single branches.

Persistence on a River Network

$\Omega = E \cup V$

$E = \{e_1, e_2, ..., e_N\}, V = \{v_1, v_2, ..., v_M\}$

$\partial\Omega = \{v \in V \mid index(v) = 1\} = \{\gamma_1, \gamma_2, ..., \gamma_m\}$

$V_r = V \setminus \partial\Omega = \{v \in V \mid index(v) > 2\}$

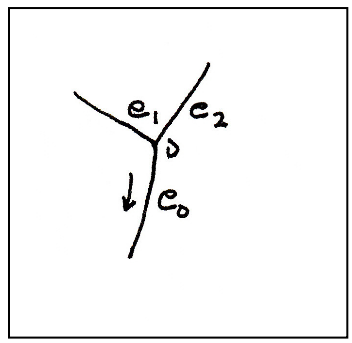
$\Omega =$ metric graph if every edge $e_j \in E$ is identified with an interval of the real line with positive length ℓ_j.

$\Omega =$ tree graph if there are no cycles.

(1) $u_t = Du_{xx} - qu_x + f(u)$ in $\{\Omega \setminus V\} \times (0, \infty)$. Let $f(u) = ru, \quad r > 0$.

Flux on e_j is $\varphi_j(\cdot, t) = A_j\left(-D_j \frac{\partial u_j}{\partial x} + q_j u_j\right)$, $A_j =$ cross-sectional area

Simplifying model assumptions: $D_j = D, \quad q_j = q, \quad all\_j$



Continuity at vertex v: $u_0 = u_1 = u_2, \quad t \geq 0$

Conservation at vertex v: $\varphi_0(v,t) = \varphi_1(v,t) + \varphi_2(v,t)$

At interior vertex v, incident sectional area difference is $B_v = A_0 - A_1 - A_2$.

Assume

(2) $B_v q = (A_0 - A_1 - A_2)q \geq 0$ for $v \in V_r = V \setminus \partial\Omega$

Upstream boundary vertex condition: $\varphi(\gamma, t) = 0, \quad \gamma \in \partial\Omega$

Hostile river ending at downstream vertex γ_d: $u(\gamma_d, t) = 0$

Reduction: $u(x,t) = e^{qx/2D} w(x,t) \Rightarrow$

(3) $w_t = Dw_{xx} + (r - \frac{q^2}{4D})w = 0$ in $\{\Omega \setminus V\} \times (0,\infty)$

(4) at $\gamma \in \partial\Omega \setminus \{\gamma_d\}$: $\varphi = A_j\left(-D\frac{\partial w}{\partial x} + \frac{q}{2}w\right) = 0$ $\quad (e_j \sim \gamma)$

(5) at γ_d : $w(\gamma_d, t) = 0$

(6) at $v \in V \setminus \partial\Omega$: $A_0\left(\frac{q}{2}w_0 - D\frac{\partial w_0}{\partial x}\right) = A_1\left(\frac{q}{2}w_1 - D\frac{\partial w_1}{\partial x}\right) + A_2\left(\frac{q}{2}w_2 - D\frac{\partial w_2}{\partial x}\right)$

plus continuity at $v \in V_r$

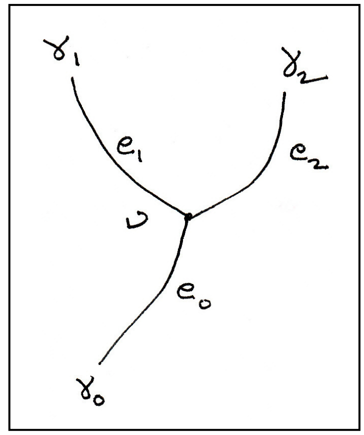
Remark: On $\Omega \setminus V$, set $r - q^2/4D = 0$, $L := D\frac{\partial^2}{\partial x^2} \Rightarrow$ $w_t = Lw$ is formally self-adjoint. With Ω a metric tree graph with finitely many edges, L can be shown self-adjoint with compact resolvent, so there is a spectrum $\{\lambda_j\}$, $\lambda_j \to -\infty$; and an ON basis $\{\varphi_j\}$of eigenfunctions. When

(2) $B_v q = (A_0 - A_1 - A_2)q \geq 0$ at each $v \in V \setminus \partial\Omega$

w equation satisfies a maximum principle. If $u(x,0)$ on Ω is continuous, non-negative, then $u(x,t) \geq 0$ for all $t > 0$.

Theorem (Sarhad, Carlson, Anderson, 2012): Suppose w satisfies (3)-(6), with (2) holding. Then, if $r - q^2/4D <$ $|\lambda_1|$, the population will not persist. (In particular, it will not persist if $r - q^2/4D \leq 0$.) If $r - q^2/4D \geq$ $|\lambda_1|$ a continuous positive initial population will persist.

Steady state problem on the star graph:



$$\ddot{u}_j - q\dot{u}_j + ru_j = 0, \quad j = 0,1,2 \quad e_j = (0, l_j)$$

$$\dot{u}_1(0) = qu_1(0), \quad \dot{u}_2(0) = qu_2(0) \ , \ \dot{u}_0(l_0) = 0$$

$$\text{at } v: \begin{cases} u_0(0) = u_1(l_1) = u_2(l_2)(= \bar{u}) \\ (-\dot{u}_0(0) + qu_0(0))A_0 = (-\dot{u}_1(l_1) + qu_1(l_1))A_1 + (-\dot{u}_2(l_2) + qu_2(l_2))A_2 \end{cases}$$

Assume $r > \dfrac{q^2}{4}$; let $\omega := \sqrt{r - q^2/4}$ and $u_j(x) = e^{qx/2} U_j(x) \Rightarrow$

$$\ddot{U}_j + \omega^2 U_j = 0, \quad j = 0,1,2$$

$$\dot{U}_1(0) = \frac{q}{2} U_1(0), \quad \dot{U}_2(0) = \frac{q}{2} U_2(0), \quad \dot{U}_0(l_0) = -\frac{q}{2} U_0(l_0)$$

$$\text{and at } v: \begin{cases} U_0(0) = e^{ql_1/2} U_1(l_1) = e^{ql_2/2} U_2(l_2)(= \bar{U}) \\ A_0 \dot{U}_0(0) = A_1 e^{ql_1/2} \dot{U}_1(l_1) + A_2 e^{ql_2/2} \dot{U}_2(l_2) + \frac{q}{2} \bar{U}\left(A_0 + e^{ql_1/2} A_1 + e^{ql_2/2} A_2\right) \end{cases}$$

Thus,

$$U_0(x) = \cos \omega x + \frac{\omega \sin \omega l_0 - (q/2)\cos \omega l_0}{\omega \cos \omega l_0 + (q/2)\sin \omega l_0} \sin \omega x$$

$$U_1(x) = \frac{q e^{-ql_1/2}}{q \sin \omega l_1 + 2\omega \cos \omega l_1} \left[\sin \omega x + \frac{2\omega}{q} \cos \omega x \right]$$

$$U_2(x) = \frac{q e^{-ql_2/2}}{q \sin \omega l_2 + 2\omega \cos \omega l_2} \left[\sin \omega x + \frac{2\omega}{q} \cos \omega x \right]$$

Then,

Theorem: For $r > \frac{q^2}{4}$, there is a unique positive steady state solution, $U^*(x)$, up to multiplicative constant, as long as $0 < l_j < L^*$, $j = 0,1,2$, where L^* is the smallest positive zero of $\sin \omega l + \frac{2\omega}{q} \cos \omega l = 0$, that is,

$$L^* = \frac{1}{\omega} \arctan(-2\omega / q) > 0 \quad ,$$

and such that the following holds:

$$A_0\left(\Phi(l_0) + \tfrac{q}{2\omega}\right) + A_1\left(\Phi(l_1) + \tfrac{q}{2\omega} e^{ql_1/2}\right) + A_2\left(\Phi(l_2) + \tfrac{q}{2\omega} e^{ql_2/2}\right) = 0 \quad ,$$

where

$$\Phi = \Phi(l) := \frac{q \cos \omega l - 2\omega \sin \omega l}{q \sin \omega l + 2\omega \cos \omega l} \quad .$$

Weakly-Mixed River (Speirs & Gurney, 2001)

Uniform channel, depth d, z variable, downward from surface ($0 < z < d$)

$q = q(z) = v_s[1-(z/d)^2]$ is horizontal flow velocity, v_s = surface velocity

- In many streams, rivers estuaries, rates of hydrodynamic mixing is orders of magnitude lower in the vertical vs. horizontal direction
- Individual motion may be more successful in decoupling individual motion from vertical water movement than from horizontal movement. If $D = D_x$ is horizontal component of diffusivity and D_z is vertical component, $D_z = 0$ (the limiting no vertical dispersal) implies members of a lineage will live out their lives at one depth. This gives rise to a sequence of decoupled advection-diffusion equations of the type discussed earlier.
- If persistence requires $q < 2\sqrt{rD}$ then lower discharge rates may allow persistence near the bottom when v_s is above critical.

Speirs & Gurney, 2001 applied persistence conditions to plankton and insects in small streams in SE England.

- ✓ Absence of planktonic organisms in Broadstone Stream: relatively short,

  Shallow: organisms would have to exist throughout water column

  Significant advection: average advection exceeds critical value for realistic growth rate and diffusivity, hence expect washout.

- ✓ Stoneflies do exist. Nymphs are benthic (i.e. bottom dwellers)

  They experience effective advection speed that is reduced by 4 orders of magnitude, implying advection below the critical value

Competition in Advection-Driven Environments

(1) $$\begin{cases} u_t = u_{xx} - qu_x + u(1-u-a_{12}v) & 0<x<L, t>0 \\ v_t = v_{xx} - qv_x + v(r - a_{21}u - v) \end{cases}$$

(2) $$-u_x(0,t) + qu(0,t) = 0 = -v_x(0,t) + qv(0,t), \quad u_x(L,t) = v_x(L,t) = 0$$

Steady state solutions: $v = 0 \to 0 = u'' - qu' + u(1-u) \quad \to \quad u = \bar{u}(x)$

Similarly, $v = \bar{v}(x) \quad solves \quad v'' - qv' + v(r-v) = 0$

Invasion analysis: single species states are $(\bar{u}(x), 0), \quad (0, \bar{v}(x))$

Linearize (1) about these single species states:
$u = e^{qx/2}n(x,t), \quad v = \bar{v}(x) + e^{qx/2}m(x,t) \to$ linearizing about $(0,\bar{v}(x))$

(3) $$n_t = n_{xx} + (1 - a_{12}\bar{v}(x) - \frac{q^2}{4})n \quad n_x(0,t) = \frac{q}{2}n(0,t), \quad n_x(L,t) = -\frac{q}{2}n(L,t)$$

Similarly, linearizing (1) about $(\bar{u}(x),0)$ gives

(4) $$m_t = m_{xx} + (r - a_{21}\bar{u}(x) - \frac{q^2}{4})m \ , \ m_x(0,t) = \frac{q}{2}m(0,t), \quad m_x(L,t) = -\frac{q}{2}m(L,t)$$

Each species will invade the other species state exactly when the *zero equilibrium state* of (3) (for invasion of the first species), or (4) (invasion of the second species) is unstable. If
$n = e^{\sigma_1 t}n^*(x), \quad m = e^{\sigma_2 t}m^*(x)$, then

(5) $$\ddot{n}^* + (1 - a_{12}\bar{v}(x) - \frac{q^2}{4})n^* = \sigma_1 n^*, \quad \dot{n}^*(0) - \frac{q}{2}n^*(0) = 0 = \dot{n}^*(L) + \frac{q}{2}n^*(L)$$

(6) $$\ddot{m}^* + (r - a_{21}\bar{u}(x) - \frac{q^2}{4})m^* = \sigma_2 m^*, \quad \dot{m}^*(0) - \frac{q}{2}m^*(0) = 0 = \dot{m}^*(L) + \frac{q}{2}m^*(L)$$

Invasion of species 1: (variational principle: Cantrell, Cosner, 2003)

$$A = \left\{ h \in W^{1,2}([0,L]) : \| h \|_2^2 = \int_0^L h^2 dx = 1 \right\}$$

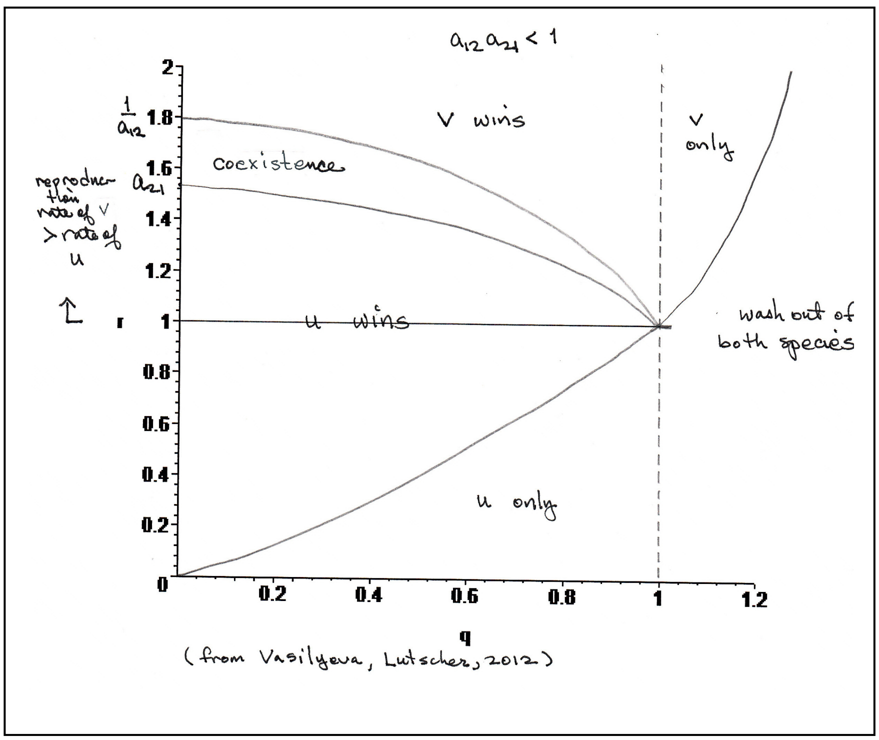
$$\Gamma(a_{21},q) := \min_{h\in A}\{\int_0^L [(h'(x))^2 + a_{21}\bar{u}(x)h(x)^2]dx + \frac{q}{2}(h(0)^2 + h(L)^2)\}$$

The principle eigenvalue is $\sigma_2^* = r - \frac{q^2}{4} - \Gamma(a_{21},q)$

Invasion condition: $r > \frac{q^2}{4} + \Gamma(a_{21},q)$. The stability boundary condition between invasion and extinction of species 2 is

$$\sigma_2^* = 0 \Leftrightarrow r = \frac{q^2}{4} + \Gamma(a_{21},q)$$

For example, if $a_{12}a_{21} < 1$ a bifurcation diagram can be computed:



Spatial Implicit Approximation

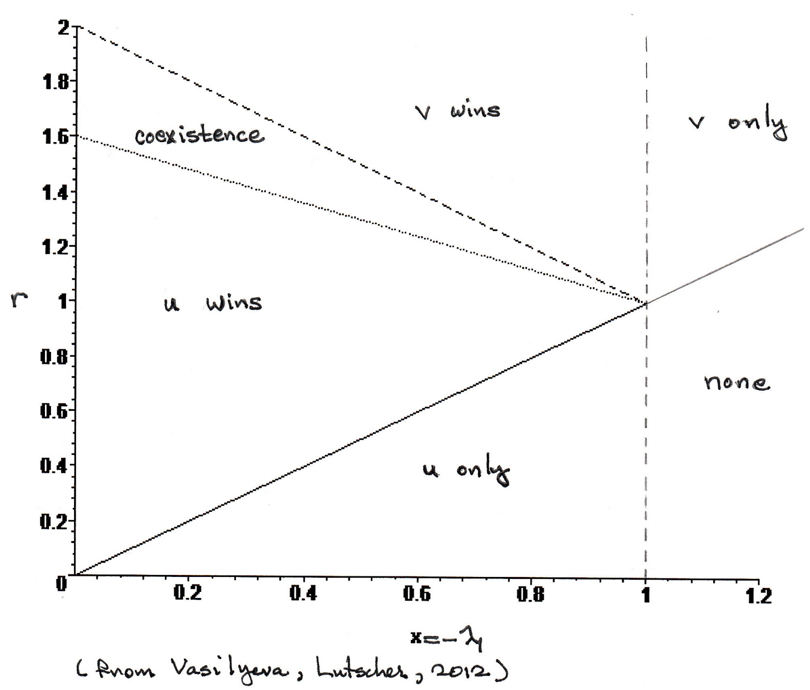
(Vasilyeva, Lutscher, 2012; van Kirk, Lewis, 1997; Strohm, Tyson, 2011)

In the absence of population growth the advection-diffusion operator, along with Danckwert b.c.s, leads to a net loss of individuals from the domain. Thus, Vasilyeva and Lutscher replaced the advection-diffusion operator with a 1st-order decay term that induces the same loss rate as the spatial movement operator.

The principle/dominant eigenvalue λ_1 is negative inverse of the resident time of individuals in domain $[0, L]$. So spatial movement is replace by $(\lambda_1(q)u, \lambda_1(q)v)$ that should implicitly capture loss due to spatial movement at the same rate. Hence

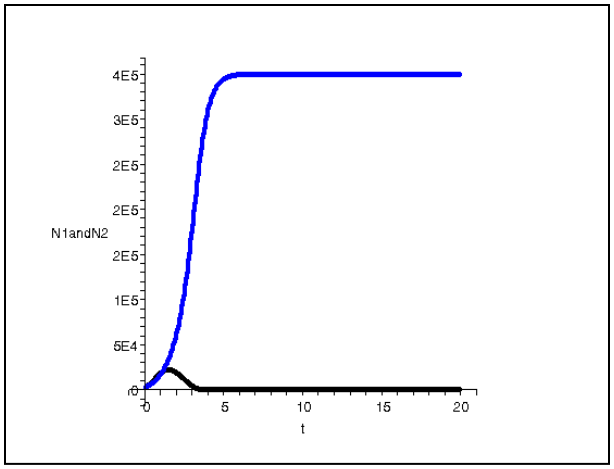
$$\begin{cases} \dot{u} = \lambda_1 u + u(1 - u - a_{12}v) \\ \dot{v} = \lambda_1 v + v(r - a_{21}u - v) \end{cases}$$

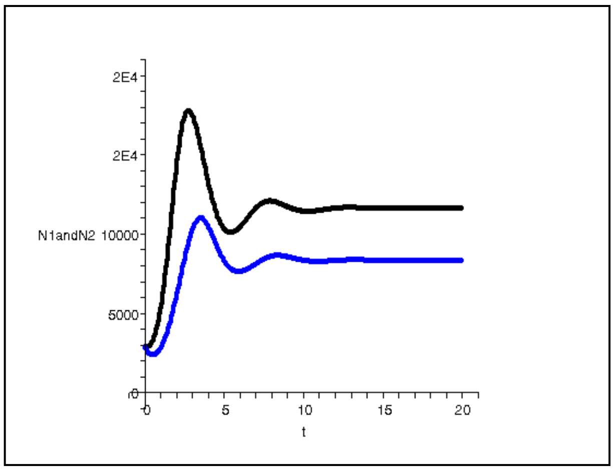
From phase plane analysis (here $a_{12} = 0.5, a_{21} = 1.6$, i.e. case $a_{12}a_{21} < 1$)

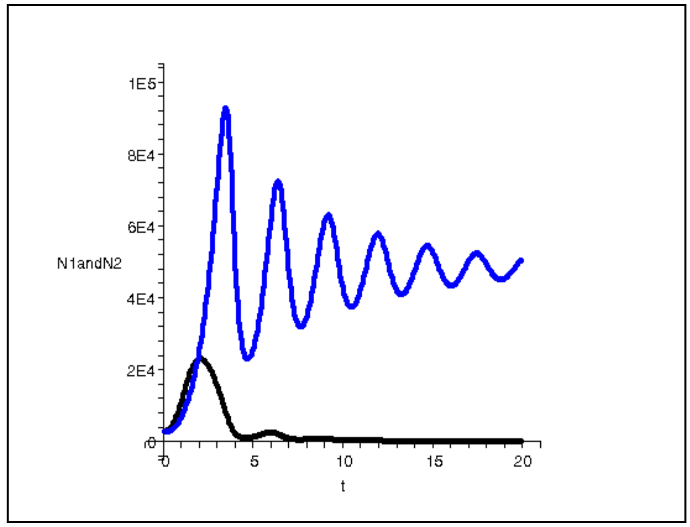


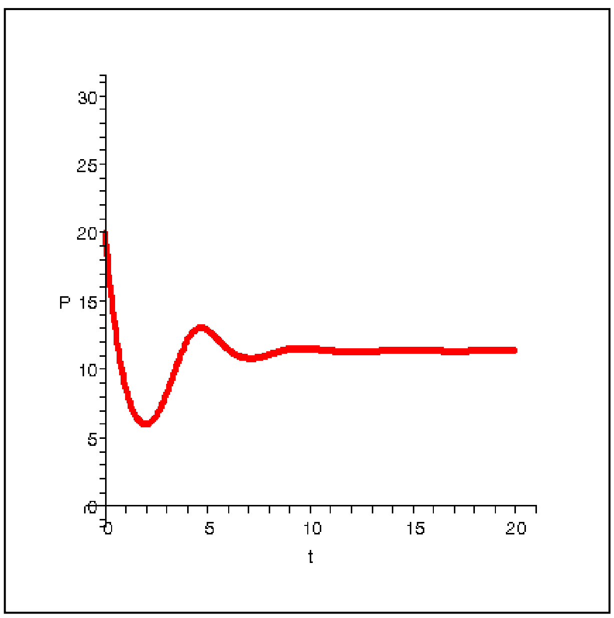
(from Vasilyeva, Lutscher, 2012)

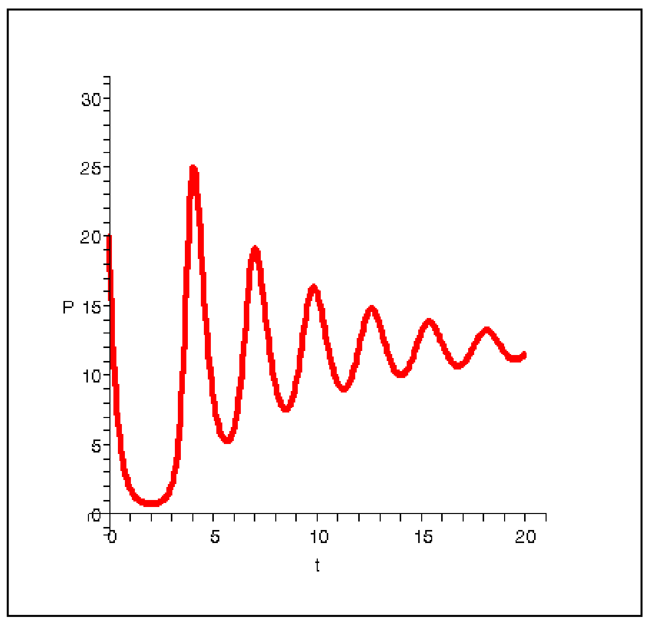
Competitive exclusion principle: two species in competition stabilized by introduction of a common predator. Harvesting the predator destabilizes the trophic level. How would the picture change in an advection-driven environment?











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under the title

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