Persistence and Competition: A Review involving Non-spatial and Spatial Modeling Environments

By

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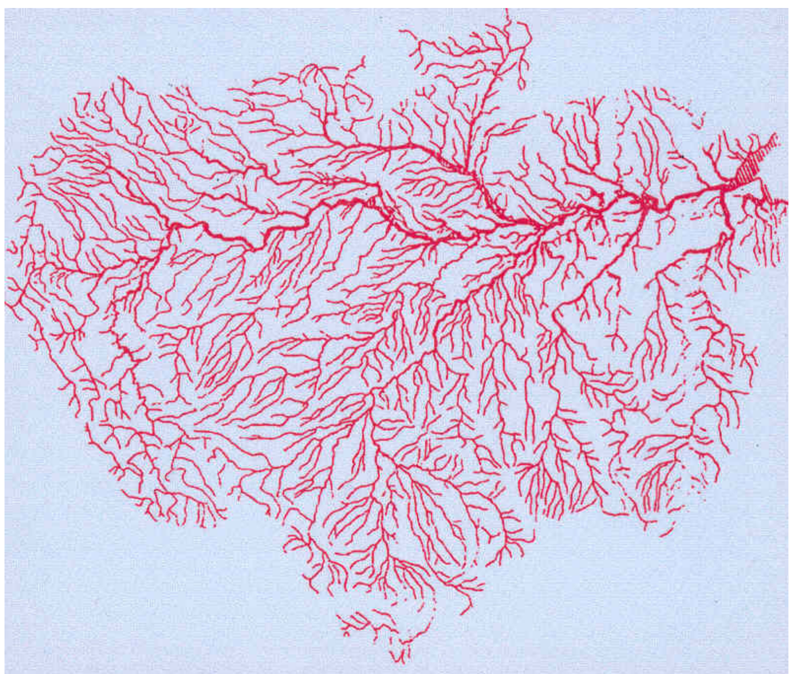


(Amazon River Basin, by Hideki Takayusu)

Talk Outline

The Beginnings: Single Population, Single Compartment

Mobility: Diffusion-Proliferation Modeling and “Patch” size

Populations in Advection-driven Environments: flow rate vs. reproduction rate

Persistence in River Networks

Competition between Two Species: Single Compartment and Competitive Exclusion

Two Species Competition in an Advection-driven Environment

Beginning Demographics

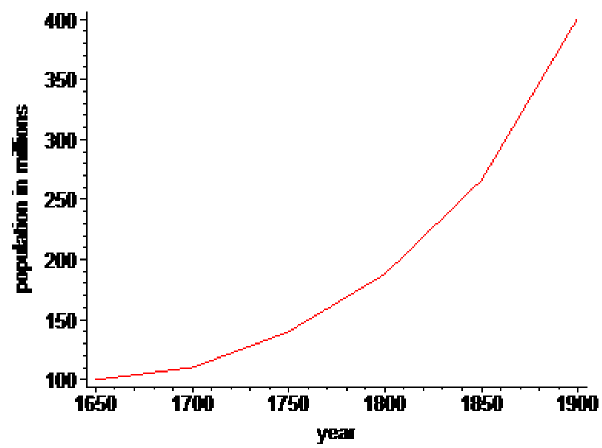
Thomas Robert Malthus: *An Essay on the Principle of Population as it Affects the future Improvement of Society* (1798-anonymously; 1803-signed)

population increases in geometric ratio, food only in arithmetic ratio.

Necessary for population to be limited by 'checks' of vice and misery….created controversy.

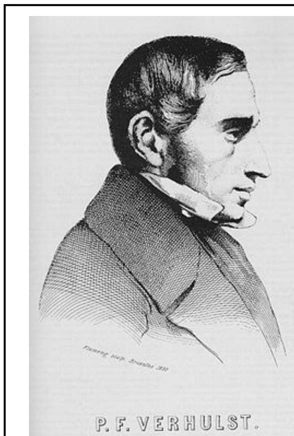
$$\frac{dN}{dt} = rN = (b-d)N$$

$N(t)$=*population density*



Observations Concerning the Increase of Mankind (1751, Circulated 1755)

Unrestrained population growth could double itself every 25 years or so



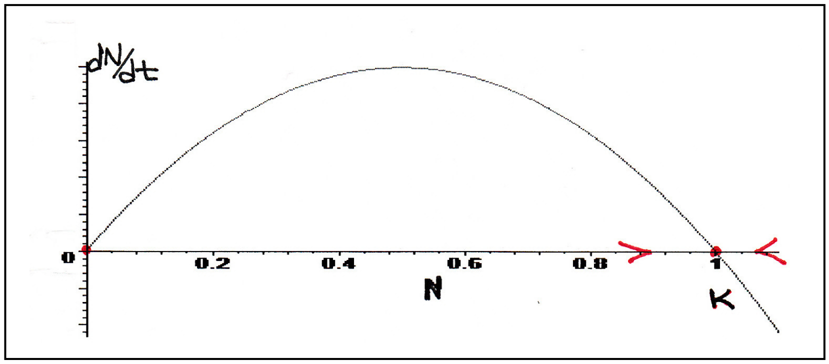
P.F. Verhulst, Mem. Acad. Roy. Bruxelles (1844)

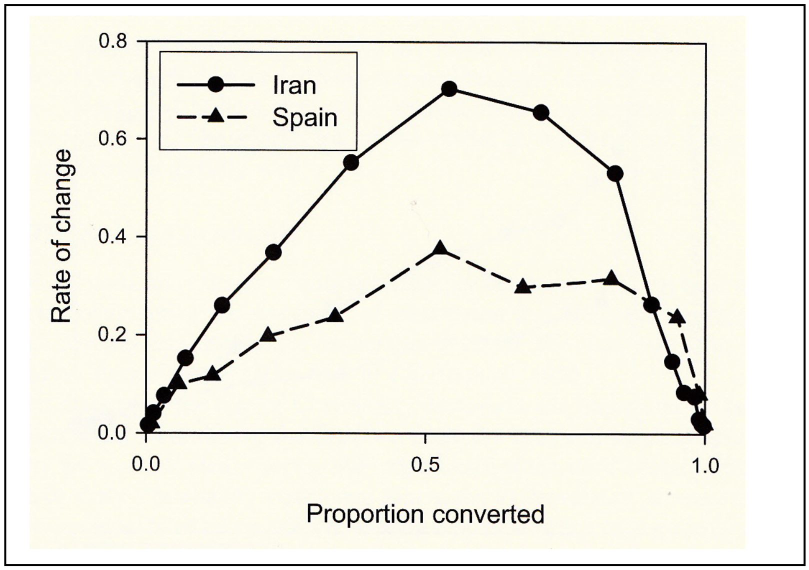
Rate of population growth is proportional to product of existing population and the difference between the total available resources and resources used by the present population

$$\frac{dN}{dt} = rN(K-N)$$

K = *Carrying Capacity*

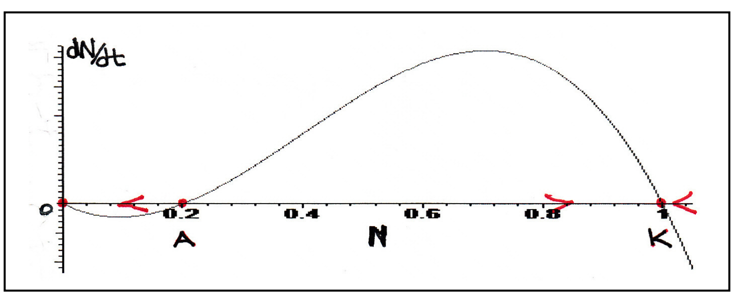
Verhulst (logistic):

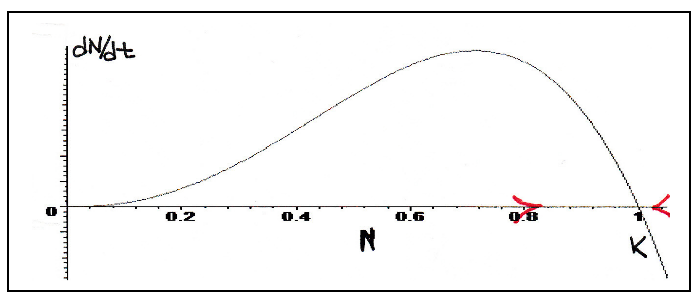




(from Turchin, Historical Dynamics)

Allee effect: maximum intrinsic growth at an intermediate density. Associated with overall individual fitness.





Strong Allee effect: **bistable case**

Weak Allee effect

$$\frac{dN}{dt} = rN(1 - N/K)(N/A - 1)$$

John Graunt: *Natural and Political Observations Made Upon the Bills of Mortality* (1662)

"…that London…is perhaps to a Head too big for the Body and possably to strong; that this head grows three times as fast as the Body to which it belongs…"

The Diseases, and Casualties this year being 1632.

Abortive, and Stilborn	445	Grief	11
Affrighted	1	Jaundies	43
Aged	628	Jawfaln	8
Ague	43	Impostume	74
Apoplex, and Meagrom	17	Kil'd by several accidents	46
Bit with a mad dog	1	King's Evil	38
Bleeding	3	Lethargie	2
Bloody flux, scowring, and flux	348	Livergrown	87
Brused, Issues, sores, and ulcers,	28	Lunatique	5
Burnt, and Scalded	5	Made away themselves	15
Burst, and Rupture	9	Measles	80
Cancer, and Wolf	10	Murthered	7
Canker	1	Over-laid, and starved at nurse	7
Childbed	171	Palsie	25
Chrisomes, and Infants	2268	Piles	1
Cold, and Cough	55	Plague	8
Colick, Stone, and Strangury	56	Planet	13
Consumption	1797	Pleurisie, and Spleen	36
Convulsion	241	Purples, and spotted Feaver	38
Cut of the Stone	5	Quinsie	7
Dead in the street, and starved	6	Rising of the Lights	98
Dropsie, and Swelling	267	Sciatica	1
Drowned	34	Scurvey, and Itch	9
Executed, and prest to death	18	Suddenly	62
Falling Sickness	7	Surfet	86
Fever	1108	Swine Pox	6
Fistula	13	Teeth	470
Flocks, and small Pox	531	Thrush, and Sore mouth	40
French Pox	12	Tympany	13
Gangrene	5	Tissick	34
Gout	4	Vomiting	1
		Worms	27

Christened { Males....4994, Females..4590, In all....9584 } Buried { Males....4932, Females..4603, In all....9535 } Whereof, of the Plague. 8

Increased in the Burials in the 122 Parishes, and at the Pest-house this year........ 993

Decreased of the Plague in the 122 Parishes, and at the Pest-house this year........ 266

The number of burials in London generally exceeded the number of baptisms throughout the 18th Century. For each thousand burials there was the following number of baptismal in successive twenty-year periods: 1680-1700, **681**; 1700-1720, **721**; 1720-1740, **649**; 1740-1760, **638**; 1761-1765 (4 years) **644**.

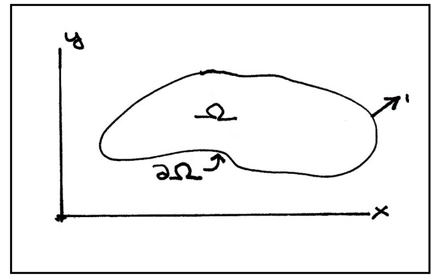
(Source: Montroll and Badger, Intro to Quantitative Aspects of Social Phenomena)

So we need to next consider population mobility…

Mobility through Diffusion

Case 1: Malthusian (linear): $N_t = D\Delta N + rN \quad in \quad \Omega \subset \Re^2$

$$a_1 N + a_2 \nu \cdot \nabla N = 0 \quad on \quad \partial\Omega$$



For operator $-\Delta$, spectrum is discrete, nondecreasing

Sequence of eigenvalues $\{\lambda_n\}$,

$N(x,t) = \sum a_n e^{(r-\lambda_n D)t} \varphi_n(x)$ so population goes extinct (or grows unboundedly) if $r - \lambda_1 D < 0$ (resp. $r - \lambda_1 D > 0$).

For fixed *r, D*, a monotonicity theorem ($\tilde{\Omega} \subset \Omega \Rightarrow \lambda_1(\tilde{\Omega}) > \lambda_1(\Omega)$) implies there is a **critical size of patch** such that $\lambda_1(\Omega_{cr}) = r/D$. For $\Omega \supset \Omega_{cr}$, $\lambda_1(\Omega) < r/D$.

Case 2: Verhulst (logistic): $N_t = D\Delta N + \rho N(1 - N/K) \quad in \quad \Omega$

Consider 1D case, nondimensionalize:

$u = N/K, \quad \tilde{x} = x/L, \quad \tilde{t} = tD/L^2, \quad r = L^2 \rho / D$; drop tilde notation

Fisher's Equation:

(Fisher, 1937; KPP, 1937)

$$\boxed{u_t = u_{xx} + ru(1-u)}$$

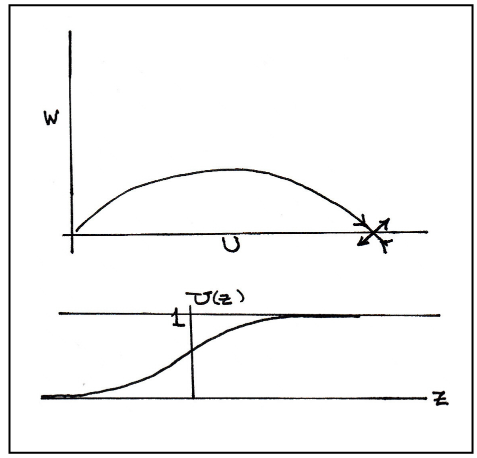
For spread of a favorable gene in a 1D habitat

Diversion:

Diffusion: **Traveling wave (front) solutions**

Case 2 continued (Logistic): $u_t = u_{xx} + ru(1-u)$

$u(x,t) = U(z), \quad z = x + \theta \cdot t$



$\theta U' = U'' + rU(1-U)$ or $\begin{cases} U' = w \\ w' = \theta w - rU(1-U) \end{cases}$

$\theta > 2\sqrt{r} \leftrightarrow r < \theta^2/4$

node-saddle heteroclinic orbit (TWS)

$0 < \theta < 2\sqrt{r}$ focus-saddle heteroclinic orbit

Case 3: Bistable: $u_t = u_{xx} + ru(1-u)(u-\alpha)$, $\alpha \in (0, \frac{1}{2})$

Again let $u(x,t) = U(z), \quad z = x + \theta \cdot t$;

There exists a unique saddle-saddle heteroclinic solution from $(U, w) = (0,0)$ to $(U, w) = (1,0)$ given by

$$U(z) = \frac{1}{1 + e^{-z/\sqrt{2r}}}, \quad \theta = \theta^* = \sqrt{2r}\left(\frac{1}{2} - \alpha\right)$$

Single Population-Single Stream

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

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.

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

Case 1: Linear (Malthusian) problem: (1),(2),(3b), $f(N) = rN$

$$N(x,t) = e^{Qx/2D} \sum_{n\geq 1} B_n e^{-\lambda_n t} \left\{ \sin(\omega_n x) + \frac{2\omega_n D}{Q} \cos(\omega_n x) \right\} \qquad \omega_n := \frac{\sqrt{4D(r+\lambda_n) - Q^2}}{2D}$$

Population goes extinct or population grows unboundedly. Boundary when lowest eigenvalue $\lambda_1 = 0$. Critical length is

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

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

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

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

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

Single Population-Nonlinear Proliferation

Case 2: Logistic growth case: $f(N) = rN(1 - N/K)$

Nondimensionalize again:

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

(5) $\quad u_x(0,t) = qu(0,t), \quad u_x(L,t) = 0$

Steady State Solutions:

(6) $\quad u'' - qu' + ru(1-u) = 0$ or $\begin{cases} u' = w \\ w' = qw - ru(1-u) \end{cases}$

(7) $\quad w(0) = qu(0), \quad w(L) = 0$

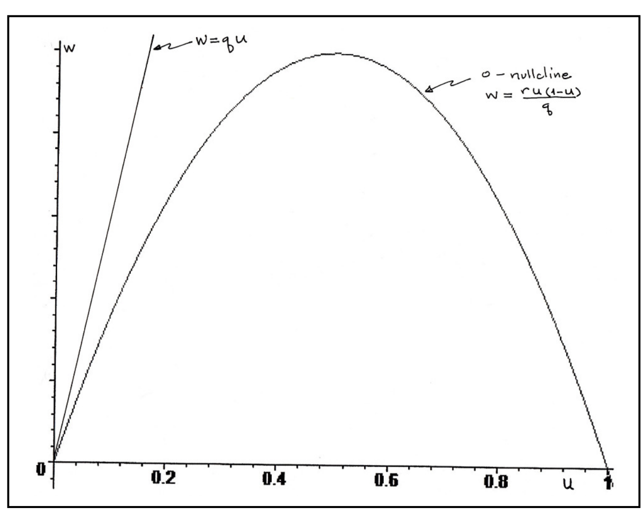
Remark: (6) is same equation as TWS equation for Fisher's equation

Lemma 1: There are no non-trivial solutions to (6), (7) for $q \geq 2\sqrt{r} = q_{cr}$.

(follows from $\dfrac{dw}{du} = q - \dfrac{ru(1-u)}{w} < q$)

So we want

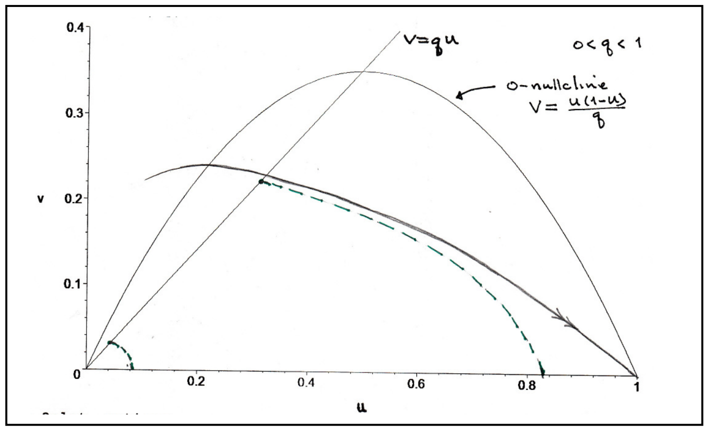
$0 < q < 2\sqrt{r} \Leftrightarrow 0 < Q < Q_{cr} \Leftrightarrow Q^2/4D < r$



Single Population-Single Stream continued:

Theorem 1 (Vasilyeva, Lutscher, 2010):

For $0 < q < 2\sqrt{r}$, $L > L_{cr}$, there is a unique positive solution, $u^*(x)$ to (4), (5), and $u^*(x)$ is stable.



Case 3: Bistable growth : $f(N) = rN(1 - N/K)(N - A)$; nondim'l form

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

(9) $\quad u_x(0,t) = qu(0,t), \quad u_x(L,t) = 0$

If $q \ge q_{bd} := \sqrt{r}(1-\alpha)$, then the population will be washed out (non-persistence).

Theorem 2: For $0 < q < q_{bd}$ there exist $L > 0$ for which (8), (9) has a positive, increasing steady state solution $u^*(x)$, and $u^*(x)$ is stable.

Weakly-Mixed River (Speirs & Gurney, 2001)

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

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

- In many streams, rivers estuaries, rates of hydrodynamic mixing is orders of magnitude lower in the vertical vs. horizontal direction
- If $D = D_x$ is horizontal component of diffusivity, 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 q_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

Persistence on a River Network

$\Omega = E \cup V$

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

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

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

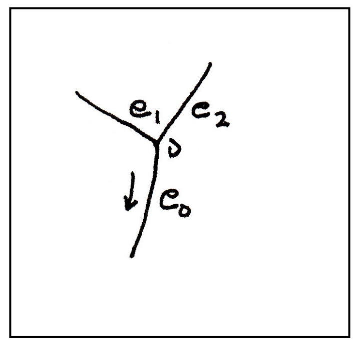
$\Omega =$ metric graph if it is a directed graph such that every edge $e_j \in E$ is identified with an interval of the real line with positive length ℓ_j.

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

(10) $\quad u_t = Du_{xx} - qu_x + f(u) \quad$ in $\quad \{\Omega \setminus V\} \times (0, \infty)$

Flux on e_j: $\varphi_j(\cdot, t) = A_j\left(-D_j \dfrac{\partial u_j}{\partial x} + q_j u_j\right)$, $A_j =$ 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: $\varphi_0(v,t) = \varphi_1(v,t) + \varphi_2(v,t)$

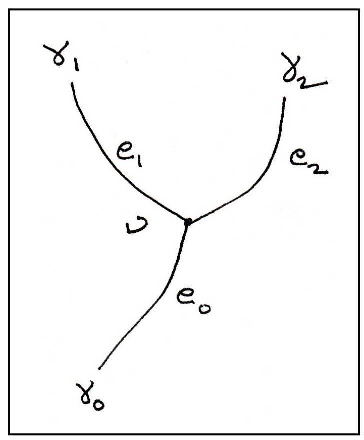
Upstream boundary vertex condition: $\varphi(\gamma, t) = 0, \quad \gamma \in \partial\Omega$

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

Case 1: $f(u) = ru$

(12) Let $(A_0 - A_1 - A_2) \geq 0$ at each $v \in V \setminus \partial\Omega$

Theorem (Sarhad, Carlson, Anderson, 2012): 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:

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

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

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

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

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

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

and at v: $\begin{cases} U_0(0) = e^{ql_1/2}U_1(l_1) = e^{ql_2/2}U_2(l_2)(=\overline{U}) \\ A_0\dot{U}_0(0) = A_1e^{ql_1/2}\dot{U}_1(l_1) + A_2e^{ql_2/2}\dot{U}_2(l_2) + \frac{q}{2}\overline{U}\left(A_0 + e^{ql_1/2}A_1 + e^{ql_2/2}A_2\right) \end{cases}$

Thus,

$$U_0(x) = \cos\omega x + \frac{\omega\sin\omega l_0 - (q/2)\cos\omega l_0}{\omega\cos\omega l_0 + (q/2)\sin\omega l_0}\sin\omega x$$
$$U_1(x) = \frac{qe^{-ql_1/2}}{q\sin\omega l_1 + 2\omega\cos\omega l_1}\left[\sin\omega x + \frac{2\omega}{q}\cos\omega x\right]$$
$$U_2(x) = \frac{qe^{-ql_2/2}}{q\sin\omega l_2 + 2\omega\cos\omega l_2}\left[\sin\omega x + \frac{2\omega}{q}\cos\omega x\right]$$

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,

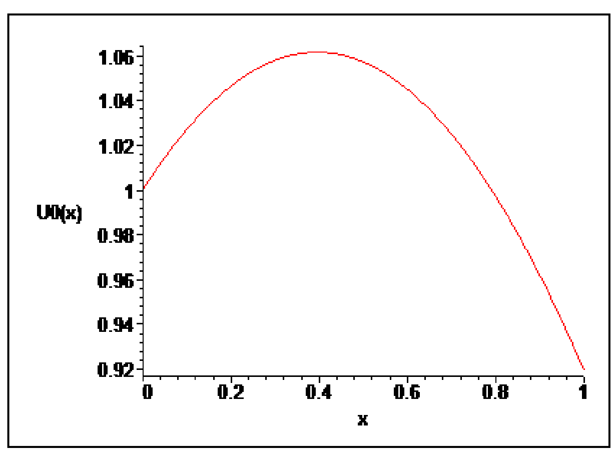
$$L^* = \frac{1}{\omega}\arctan(-2\omega/q) > 0 \quad ,$$

and such that the following holds:

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

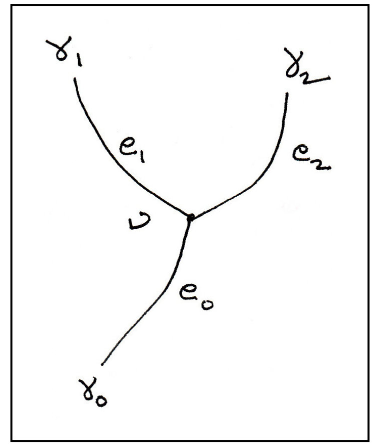
where

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



Steady State Solution on Star Graph with Logistic Proliferation

$$\begin{cases} \dot{u}_j = w_j \\ \dot{w}_j = q w_j - u_j(1-u_j) \end{cases} \qquad 0 < q < 2$$



$$w_1(0) = q u_1(0), \quad w_2(0) = q u_2(0), \quad w_0(l_0) = 0$$

At v: $u_0(0) = u_1(l_1) = u_2(l_2) \quad (= \bar{u})$

If we assume $A_0 = A_1 + A_2$ then

$$A_0 w_0(0) = A_1 w_1(l_1) + A_2 w_2(l_2)$$

If $A_1 = A_2$ then $2 w_0(0) = w_1(l_1) + w_2(l_2)$

If we also assume $l_1 = l_2$, then $w_0(0) = w_1(l_1) = w_2(l_1)$, and there exists a unique positive solution to the problem.

Competition between Two Species: Single Compartment

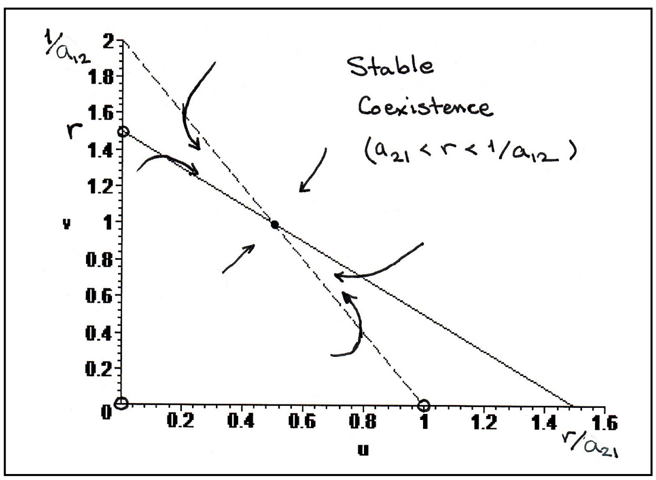
$$\begin{cases} \dot{u} = u(1 - u - a_{12}v) \\ \dot{v} = v(r - a_{21}u - v) \end{cases}$$

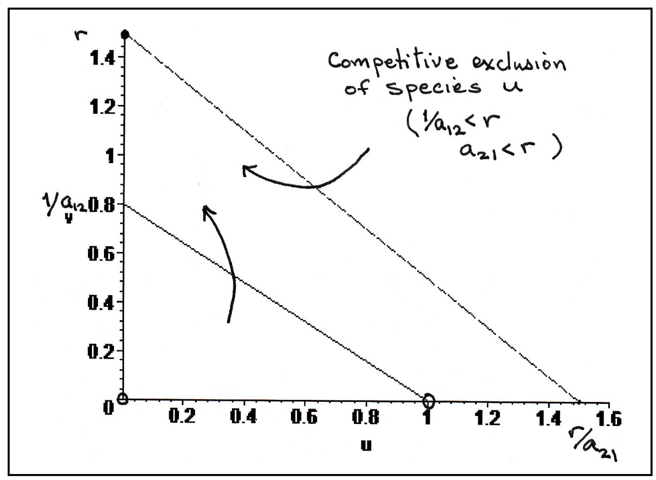
Summary: 1. If $ra_{12} < 1$ *and* $r < a_{21}$, then species u wins

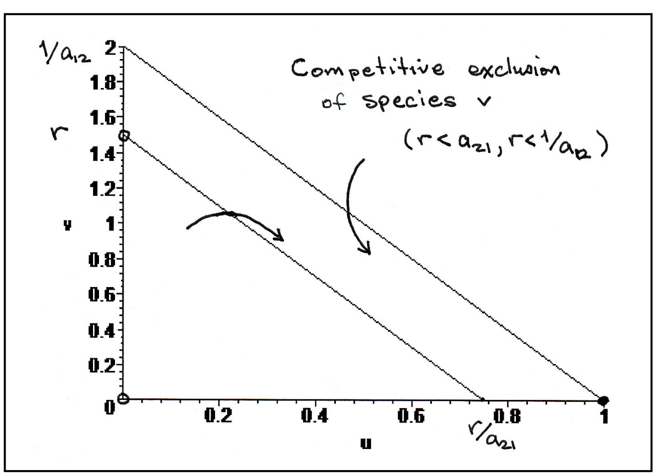
2. If $ra_{12} > 1$ *and* $r > a_{21}$, then species v wins

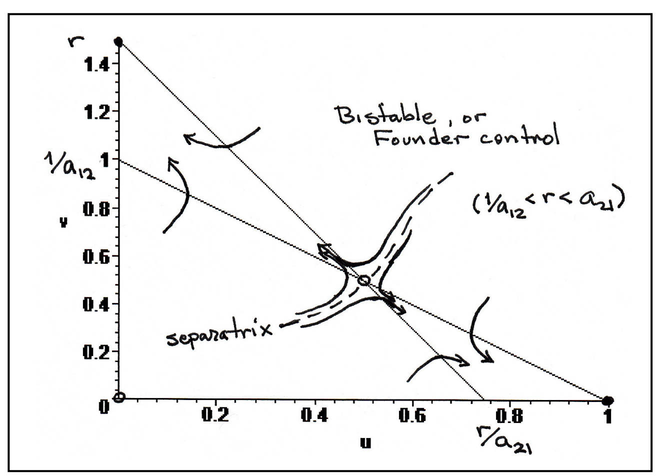
3. If $ra_{12} < 1$ *and* $r > a_{21}$, both species coexist

4. If $ra_{12} > 1$ *and* $r < a_{21}$, we have bistable situation





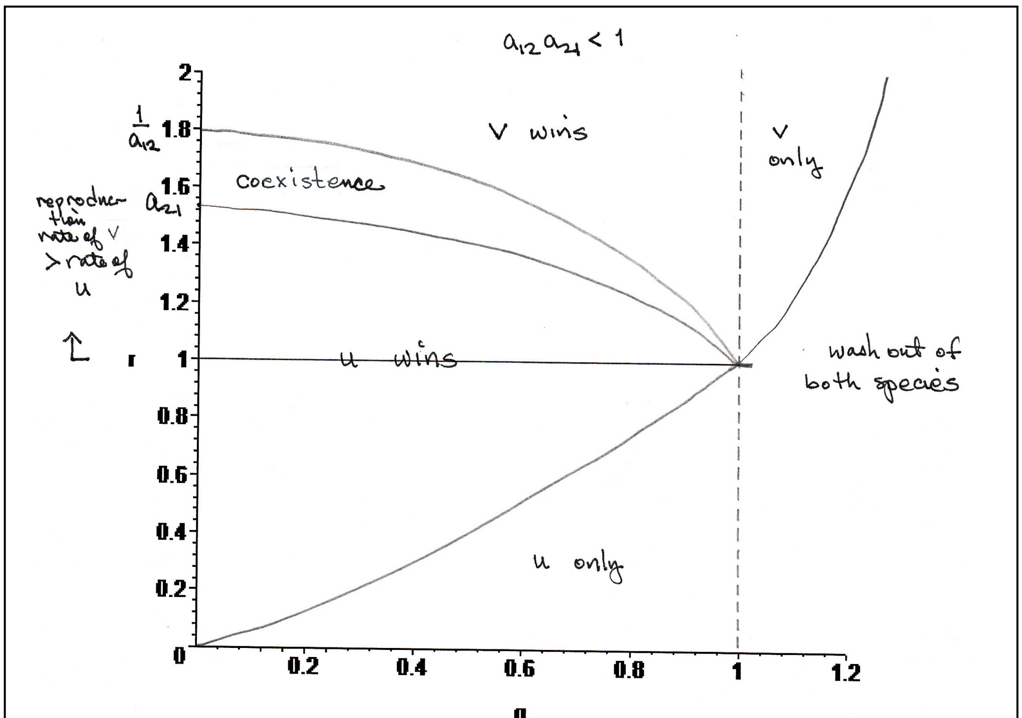




Competition in Advection-Driven Environments

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

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



(from Vasilyeva, Lutscher, 2012)

Spatial Implicit Approximation

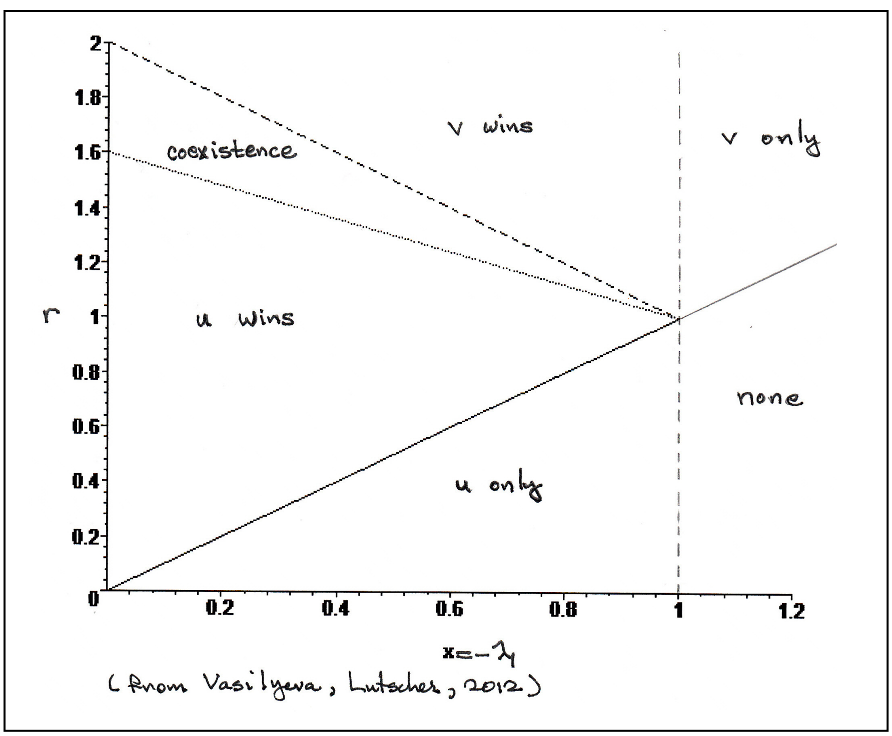
(Vasilyeva, Lutscher, 2012; van Kirk, Lewis, 1997; Strohm, Tyson, 2011)

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 replaced by $(\lambda_1(q)u, \lambda_1(q)v)$ that should implicitly capture loss due to spatial movement at the same rate. Hence

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

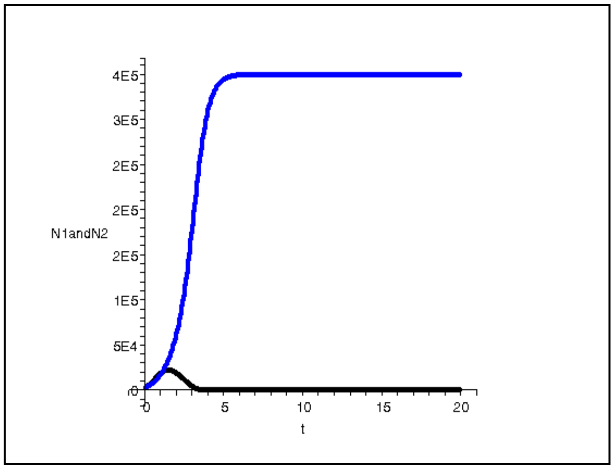
From phase plane analysis (here $a_{12}=0.5, a_{21}=1.6$, i.e. case $a_{12}a_{21}<1$)



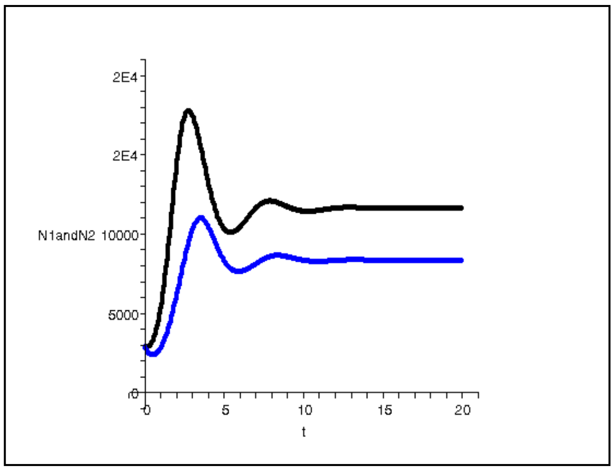
Going Forward…

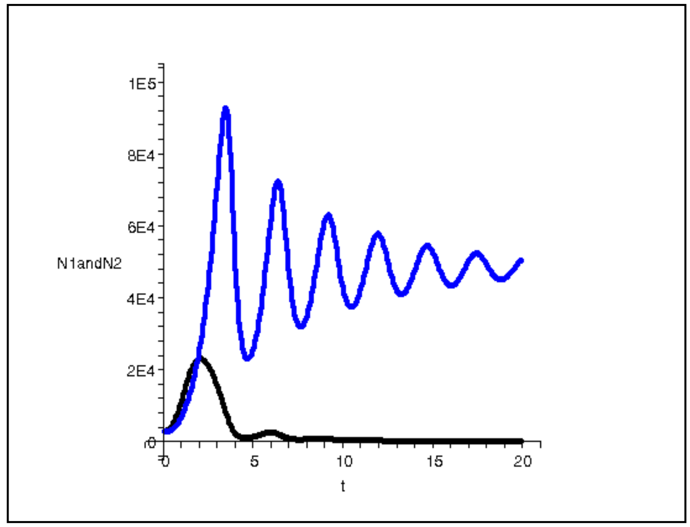
- Investigate competition between species with different diffusivities in an advection-driven environment
- Investigate competition in the presence of predation in an advection-driven environment
- Generalize motility beyond simple diffusion
- Expand invasion analysis to networks
- Compare results with different boundary conditions
- Investigate more aspects of partial-vertical mixing
- Include more aspects of variable flow speed downstream (period $q(t)$ for tidal effects, e.g.)
- Bring more fluid dynamics modeling into the stream model

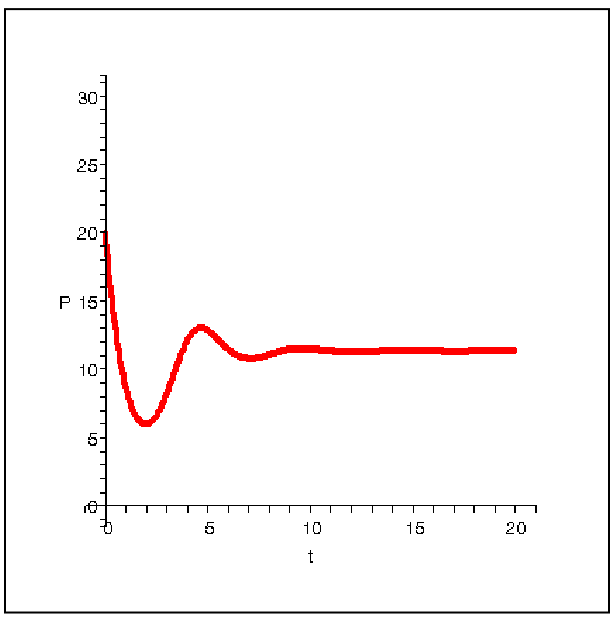
Questions driven by more biological observations

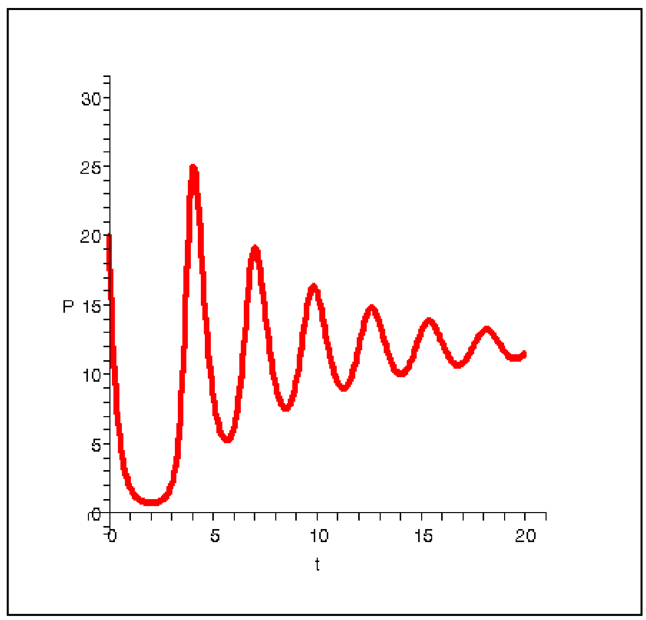


Competitive exclusion principle: two species in competition stabilized by introduction of a common predator. Harvesting the predator destabilizes the trophic level. How would the picture change in an advection-driven environment?









Thanks for Listening

AfterMath