Coupled dynamics, quiescent phases, and distributed sojourn times

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Coupled System

$$f, g : \mathbb{R}^n \to \mathbb{R}^n$$

P, Q positive diagonal matrices

$$\begin{aligned} \dot{v} &= f(v) - Pv + Qw \\ \dot{w} &= g(w) + Pv - Qw \end{aligned}$$

diffusive coupling

Quiescent Phase

$g \equiv 0$

Compare the behavior of

$$\dot{u} = f(u) \qquad \text{“small”}$$

to the behavior of

$$\begin{aligned} \dot{v} &= f(v) - Pv + Qw \\ \dot{w} &= Pv - Qw \qquad \text{“large”} \end{aligned}$$

Equal rates

$$P = pI, \quad Q = qI$$

$n = 1$: Global existence of the small system implies global existence of the large system.
Compact global attractor of the small system implies compact global attractor of the large system.

$n \geq 1$: Similar results under the assumption that infinity is uniformly repelling.

Stationary points

Stationary points are "the same":
$\bar{u}$ stationary point of the small system
$\Rightarrow (\bar{u}, Q^{-1}P\bar{u})$ stationary point of the large system.

Jacobian matrix $A = f'(\bar{u})$

$$B = \begin{pmatrix} A - P & Q \\ P & -Q \end{pmatrix}$$

Equal rates: Stability of the small system
$\Rightarrow$ stability of the large system

General case: A Turing phenomenon!

Turing phenomenon

$$u_t = Du_{xx} + Au$$

A is called stable if all eigenvalues have negative real parts.
A is called strongly stable if for any nonnegative diagonal matrix D the matrix $A - D$ is stable.
A is called excitable if A is stable but not strongly stable.

Activator - inhibitor dynamics

$n = 2$

$$A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}$$

A stable: $\det A > 0$, $\operatorname{tr} A < 0$
A strongly stable: A stable and $a_{11} \leq 0$, $a_{22} \leq 0$
A excitable: A stable and $a_{11} > 0$

Furtheron assume that A is stable!

Turing versus quiescence

$n = 2$

Turing phenomenon: A real eigenvalue of $A - D$ passes through zero.

Quiescence: 0 is never an eigenvalue of B.
A complex-conjugate pair of eigenvalues of B passes through the imaginary axis.

For $n = 2$ the following are equivalent:

0) The matrix A is excitable.
i) For some D the matrix $A - D$ has an eigenvalue with positive real part.
ii) For some P, Q the matrix B is not stable.
iii) For some P, Q the matrix B has a real positive eigenvalue.
iv) For some P, Q the matrix B has a pair of purely imaginary eigenvalues.

Results for $n \geq 2$:

For some D the matrix $A - D$ has an eigenvalue with positive real part.
$\Rightarrow$ For some P, Q the matrix B has an eigenvalue with positive real part.
$\Rightarrow$ For some P, Q the matrix B has a pair of purely imaginary eigenvalues.

For some P, Q the matrix B has a real positive eigenvalue.
$\Leftrightarrow$ For some D the matrix $A - D$ has a real positive eigenvalue.

Biological message

Distinct rates may lead to Hopf bifurcations.

For example, if inhibitor goes quiescent at a high rate.

Equal rates: Quiescence stabilizes

$$B = \begin{pmatrix} A - pI & qI \\ pI & -qI \end{pmatrix}$$

Spectral mapping theorem applies:
μ eigenvalue of A, λ_1, λ_2 eigenvalues of B

$$\lambda^2 + \lambda(p + q - \mu) - \mu q = 0$$

$\Re\lambda_2 < 0$

Stability domain

$$\{\mu = \alpha + i\beta : \Re\lambda_1 < 0\}$$

The stability domain, depending on p and q, is larger than the left half plane.

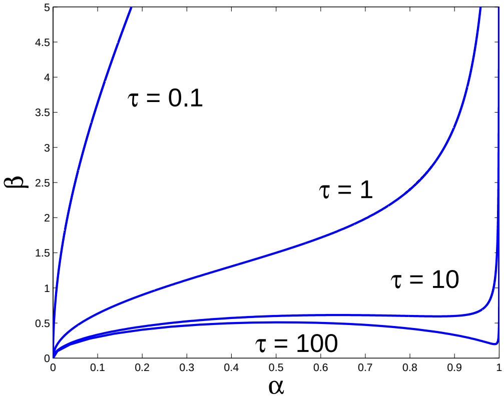

Figure: Stability boundary: The value of $p = 1$ is fixed, and $\tau = 1/q$. When $p\tau > 8$ then the curve is not monotone.

Periodic orbits

Observation: Periodic orbits shrink, i.e., the non-quiescent projection shrinks.

Has been proved for a model problem.

Predator-prey system

MacArthur-Rosenzweig

$$\begin{aligned} \dot{u} &= au(1 - \frac{u}{K}) - b\frac{uv}{1+mu} \\ \dot{v} &= c\left(\frac{u}{1+mu} - \frac{B}{1+mB}\right)v \end{aligned}$$

Paradox of enrichment

with quiescence, general rates

$$
\begin{aligned}
\dot{u} &= au\left(1 - \frac{u}{K}\right) - b\frac{uv}{1+mu} - p_1 u + q_1 w \\
\dot{v} &= c\left(\frac{u}{1+mu} - \frac{B}{1+mB}\right) v - p_2 v + q_2 z \\
\dot{w} &= p_1 u - q_1 w \\
\dot{z} &= p_2 v - q_2 z
\end{aligned}
$$

Coexistence equilibrium

$a_{22} = 0$, hence $a_{11} = \operatorname{tr} A$

If the matrix is stable then it is not excitable.

Stability of the 4-dimensional system can be described in terms of $\det A$ and $\operatorname{tr} A$.

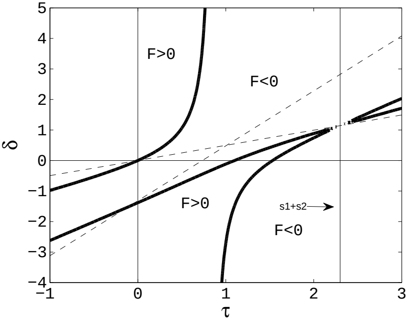

Figure: The τ, δ-plane with the null sets of the Hurwitz determinants. Quiescence leads to an enlarged stability domain. The domain gets larger when p_1, p_2 are increased.

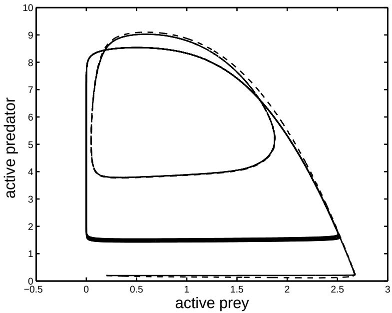

Figure: Phase plane for the MacArthur-Rosenzweig system (solid) and projection to the u, v-plane for the system with quiescence (dashed). Both systems have limit cycles. The projected limit cycle of the quiescent system is much smaller.

QUESTION

In the diffusive coupling model the sojourn times in the active and in the quiescent compartments are exponentially distributed.

What happens if we replace the exponential distributions by some other distributions?

The two-phase model

Coupling with arbitrary sojourn distributions

$$
\begin{aligned}
v_t + v_a + p(a)v &= m(a)F(t) \\
w_t + w_b + q(b)w &= n(b)G(t) \\
v(t,0) &= \int_0^\infty q(b)w(t,b)db + f(t) \\
w(t,0) &= \int_0^\infty p(a)v(t,a)da + g(t)
\end{aligned}
$$

$$
v(0,a) = v_0(a), \quad w(0,b) = w_0(b)
$$

Projection variables

recruitment rates

$$M(t) = v(t,0), \quad N(t) = w(t,0)$$

total population sizes

$$V(t) = \int_0^\infty v(t,a)da, \quad W(t) = \int_0^\infty w(t,b)db$$

Limiting system

M, N, V, W satisfy limiting equations

$$M(t) = \int_0^\infty e^{-\int_0^b q(\sigma)d\sigma} q(b)N(t-b)db$$
$$+ \int_0^\infty \int_0^b e^{-\int_s^b q(\sigma)d\sigma} q(b)n(s)G(t-b+s)dsdb + f(t)$$
$$N(t) = \int_0^\infty e^{-\int_0^a p(\sigma)d\sigma} p(a)M(t-a)da$$
$$+ \int_0^\infty \int_0^a e^{-\int_s^a p(\sigma)d\sigma} p(a)m(s)F(t-a+s)dsda + g(t)$$

The functions V, W satisfy

$$\begin{aligned}\dot{V}(t) &= M(t) - N(t) + F(t) + g(t) \\ \dot{W}(t) &= N(t) - M(t) + G(t) + f(t)\end{aligned}$$

Exponential distributions (Poisson case)

There is a limiting system for V, W that is independent of the functions M, N:

$$\begin{aligned} \dot{V} &= -pV + qW + F(t) + f(t) \\ \dot{W} &= -qW + pV + G(t) + g(t) \end{aligned}$$

Semi-Poisson case with quiescence

Particles enter w phase with rate p and leave it with rate $q(b)$. No production during w phase:

$$\begin{aligned}
v_t + v_a + pv &= m(a)F(t) \\
v(t,0) &= \int_0^\infty q(b)w(t,b)db + f(t) \\
w_t + w_b + q(b)w &= 0 \\
w(t,0) &= p\int_0^\infty v(t,a)da + g(t)
\end{aligned}$$

.

Scalar limiting equation

$$
\begin{aligned}
\dot{V}(t) &= p\left[\int_0^\infty L(b)V(t-b)db - V(t)\right] \\
&\quad + \int_0^\infty L(b)g(t-b)db + F(t) + f(t)
\end{aligned}
$$

Autonomous system

Delay equation

$$\dot{V}(t) = p\left[\int_0^\infty L(b)V(t-b)db - V(t)\right] + f(V(t))$$

Exponential distribution:

$$\dot{V}(t) = p\left[\int_0^\infty qe^{-qb}V(t-b)db - V(t)\right] + f(V(t))$$

equivalent with diffusive coupling system

Dirac distribution

Transition from v to w at constant rate p,
transition from w to v with fixed exit time $\tau > 0$

V satisfies the delay equation

$$\dot{V}(t) = p[V(t-\tau) - V(t)] + f(V(t))$$

Dynamical system (semi-Poisson case)

vector valued case

$$\dot{V}(t) = p\left[\int_0^\infty L(b)V(t-b)db - V(t)\right] + f(V(t))$$

Integral operator acts component wise.

Linearize at stationary point

$$\dot{U}(t) = p\left[\int_0^\infty L(b)U(t-b)db - U(t)\right] + AU(t)$$

Stability analysis

Ask for exponential solutions

$$A\bar{U} = \lambda \bar{U} - p\left[\int_0^\infty L(b)e^{-\lambda b}db - 1\right]\bar{U}$$

Spectral mapping property: μ an eigenvalue of the matrix A, λ a root of the equation

$$\lambda - p\left[\int_0^\infty L(b)e^{-\lambda b}db - 1\right] = \mu$$

Preservation of stability

$\mu = \alpha + i\beta$ eigenvalue of A
$\lambda = \xi + i\eta$ an eigenvalue corresponding to the delay equation
Relations between the real parts of the eigenvalues:

1. $\alpha \geq 0 \quad \Rightarrow \quad \xi \leq \alpha$
2. $\alpha \leq 0 \quad \Rightarrow \quad \xi \leq 0$
3. $\eta = 0 \quad \Rightarrow \quad \beta = 0$

Gamma distribution as an example

Standard notation

$$\frac{1}{\Gamma(k)\theta^k} x^{k-1} e^{-x/\theta}$$

$k > 0$ shape parameter

$\theta > 0$ scale parameter

Interpolating notation

$$L(b) = L(b; \kappa, n) = \frac{\kappa n (\kappa n b)^{n-1}}{\Gamma(n)} e^{-\kappa n b},$$

mean $\tau = 1/\kappa$
shape parameter n

$n = 1$: exponential distribution
$n \to \infty$: Dirac distribution at $\tau = 1/\kappa$

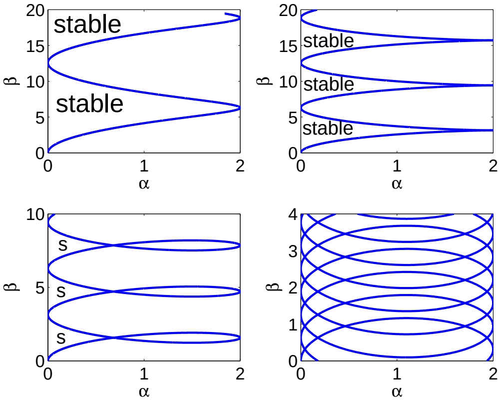

Figure: The stability boundary for the case of a delay τ. The value $p = 1$ is fixed; the value for τ varies: $\tau = 0.5$, $\tau = 1$, $\tau = 2.5$, $\tau = 5.5$.

Keeping the mean constant

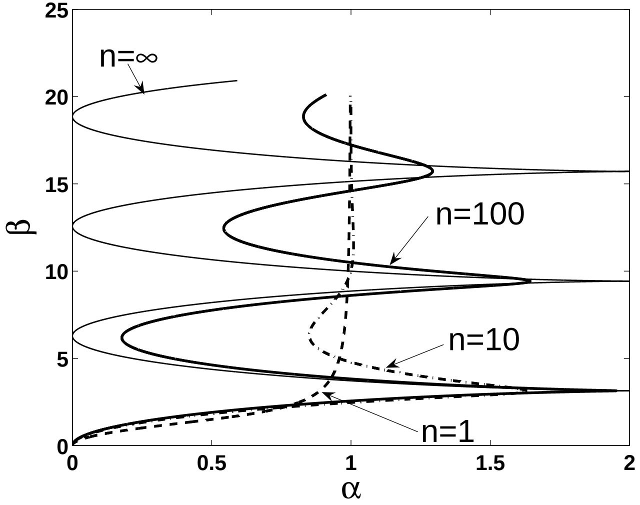

Figure: The stability boundary for the case $\tau = q = p = 1$ for different values of n.

Quasimonotone behavior

Scalar equation

Appropriate assumptions on the kernel

Assume two solutions u, v exist in $(-infty, T]$, with $T > 0$, and $u(s) \leq v(s)$ for $s \leq 0$.
Then $u(t) \leq v(t)$ for $0 \leq t \leq T$.

Proposition: Assume that the ordinary differential equation $\dot{V} = f(V)$ has a compact global attractor $[c, d]$. Then every limit element of the delay equation satisfies $c \leq V(t) \leq d$.

Fisher equation with quiescence

(Lewis & Schmitz, KPH & Lewis, Zhao)
Standard reaction diffusion with quiescent compartment

$$
\begin{aligned}
v_t &= Dv_{xx} + f(v) - pv + qw \\
w_t &= pv - qw
\end{aligned}
$$

Splitting of reaction and diffusion

$$
\begin{aligned}
v_t &= Dv_{xx} - \mu v - pv + qw \\
w_t &= f(w) + pv - qw
\end{aligned}
$$

speeds of fronts and spread numbers

General case

$$u_t = p(L * u - u) + f(u) + Du_{xx}$$

$$[L * u](t, x) = \int_0^\infty L(b)u(t - b, x)db$$

Dirac case (a delayed Fisher equation)

$$u_t(t, x) = pu(t - \tau, x) - pu(t, x) + f(u(t, x)) + Du_{xx}(t, x)$$

Individuals stay quiescent for a time interval of exact length τ.

Formal treatment

Assumptions on f: $f(0) = f(1) = 0$,
$f'(0) > 0 > f'(1)$, $f(u) > 0$ for $0 < u < 1$,
$f(u) \leq f'(0)u$.
Traveling fronts with $u = 0$ at the leading edge.

Cooperative system. Theory of Lewis-Li-Weinberger for ordinary differential equations.

Similarity solution $u(t,x) = u(x-ct) = u(\xi)$,

$$-c\dot{u}(\xi) = pL * u(\xi - c\,\cdot) - pu(\xi) + f(u(\xi)) + D\ddot{u}(\xi).$$

Linearize at $u = 0$ and put $f'(0) = a > 0$,

$$-c\dot{u}(\xi) = pL * u(\xi - c\,\cdot) - pu(\xi) + au(\xi) + D\ddot{u}(\xi).$$

At the leading edge: exponential decay with exponent $\nu > 0$.

Set $u(\xi) = \exp\{-\nu\xi\}$ and get the characteristic equation

$$\phi(\nu, c) \equiv c\nu + p(1 - E(c\nu)) - D\nu^2 - a = 0,$$

where

$$E(z) = \int_0^\infty L(b) e^{-zb} db$$

The minimum

Suppose the function $E(z) \geq 0$ satisfies $E(0) = 1$, $E'(z) < 0$, $E''(z) > 0$, and $zE(z) \leq E^*$ for all $z \geq 0$.
Then the characteristic equation defines a positive function $c = c(\nu)$, for $\nu \in (0, \infty)$, that has a **unique** point ν where $c'(\nu) = 0$. At this point is the minimum of the function $c(\nu)$.
This minimum is (should be) the spread number.

Expansion

$f'(0) = a$

$$c = 2\sqrt{Da}\left(1 - p\frac{1 - E(2a)}{2a}\right) + o(p).$$

Gamma distribution: $E(z)$ is the moment generating function of L evaluated at $-z$, i.e.

$$E(\nu c) = \left(1 + \frac{\nu c}{\kappa n}\right)^{-n}.$$

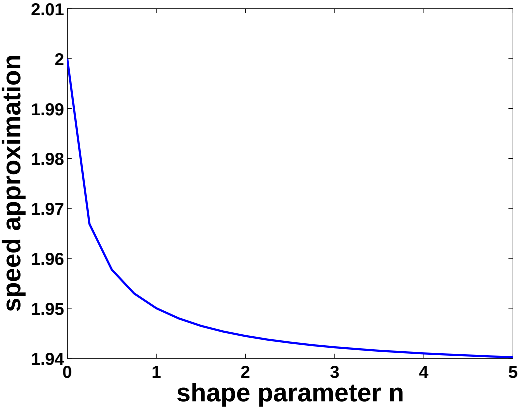

Figure: The speed of propagation as a function of the shape parameter n of the Gamma distribution is decreasing.