Quiescence, excitability, and heterogeneity in ecological models

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Gyllenberg + Webb 1989 (tumor growth)
Jäger, Krömker, Tang 1994 (chemostat)
Neubert, Klepac, van den Driessche 2002 *
KPH + Mark Lewis 2002 (travelling fronts),
Hillen 2003 (transport equations)
Pachepsky/Lutscher/Nisbet/Lewis 2005 (drift paradox)
Hillen + KPH 2005 (hyperbolic systems/transport equations)
T.Malik + H.L.Smith 2006 (microbial growth)
KPH 2007 (stability)
KPH + Hillen 2007 (Review)
Lydia Bilinsky + KPH 2009 (predator-prey)
KPH, Hillen, Lewis 2009 (Review: quiescence and ecology)
KPH + Lutscher 2012 (exit distributions)
KPH JoMB 2013 (ecology)
Quiescent phases

given system in $\mathbb{R}^n$

$$\dot{u} = f(u)$$ small system

system with quiescence in $\mathbb{R}^{2n}$

$$\dot{v} = f(v) - P v + Q w$$
$$\dot{w} = P v - Q w$$ extended system

$v$ active phase, $w$ quiescent phase

$P$, $Q$ positive diagonal matrices
To understand the effects of quiescent phases on dynamical systems and biological models in particular.

Suppose we know everything about the dynamics of the small system. What can we say about the extended system?

What about pattern formation, emergence of periodic orbits, or, on the contrary, stabilization?
Comparison: quiescence vs. diffusion

**Quiescence:** quiescent phases may stabilize against the onset of oscillations, but they also may cause oscillations if species go quiescent with different rates.

**Diffusion:** diffusion has a smoothing effect or may lead to pattern formation if species diffuse with different rates.
It’s all about non-negative diagonal matrices $D$, $P$, $Q$ and general matrices $A$. Distinguished commutative subalgebra of the matrix algebra. No invariance with respect to transformations of the dependent variables.
Definition: strong stability, excitability

\[ u_t = D\Delta u + Au \]

A matrix \( A \) is called stable if all eigenvalues have negative real parts,

strongly stable if the matrix \( A - D \) is stable for every \( D \),

excitable if \( A \) is stable but not strongly stable.
Dimension 2

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

excitable: \( \det A > 0, \ \text{tr} \ A < 0, \ a_{11}a_{22} < 0 \)

without lack of generality:

\[ a_{11} > 0, \quad a_{22} < 0. \]

Interpretation: activator and inhibitor.
Quiescence: second order equation

Model parameters can be estimated by observing only the active phase:

\[ (P + Q)^{-1} \ddot{\nu} + [I - (P + Q)^{-1} f'(\nu)] \dot{\nu} = (P + Q)^{-1} Q f(\nu) \]

For large \( P + Q \), the \( \dot{\nu} \) term acts like a damping term.
Limiting case

\[ P + Q \rightarrow \infty \]

\[ \dot{v} = (P + Q)^{-1} Q f(v) \]

Two very different cases!

Same rates: \( P = pI, \ Q = qI \)

\[ \dot{v} = \frac{q}{p + q} f(v) \]

The dynamics does not change.

General case: Different dynamics.

Lotka-Volterra stability, D-stability
General case: Stationary point

\( P, Q \) arbitrary positive diagonal matrices

small system: \( \bar{u}, f(\bar{u}) = 0 \)

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

large system: \( (\bar{u}, Q^{-1}P\bar{u}) \)

Jacobian matrix:

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

**Problem:** understand the stability changes in the transition from \( A \) to \( B \).
Special quiescence problem:

Equal rates:  \( P = pl, \quad Q = ql \)

\[
B = \begin{pmatrix}
A - pl & ql \\
pl & -ql
\end{pmatrix}
\]

To each eigenvalue \( \mu = \alpha + i\beta \) of \( A \) there are two eigenvalues \( \lambda_1, \lambda_2 \) of \( B \):

\[
\Re \lambda_2 \leq \Re \lambda_1
\]

\( \lambda_1 \) determines stability.

Quiescent phases stabilize complex eigenvalues with LARGE imaginary parts.
Figure: The stability boundary for $p = 1$ fixed, and various $\tau = 1/q$. When $p\tau > 8$ then the curve is not monotone.
Different rates: General $P, Q$

**Observation:** If the matrix $A$ is stable then, for any positive diagonal matrices $P, Q$, the matrix $B$ is non-singular.

Consequence:
Turing instability: real eigenvalue passes through 0.
Quiescence instability: complex pair passes through imaginary axis.
Connecting quiescence and pattern formation

**Theorem:** Let $n = 2$. Let the matrix $A$ be strongly stable. Then the matrix $B$ is stable for any choice of the diagonal matrices $P, Q$. 
Proposition: Let $n = 2$ and let the matrix $A$ be stable. The following are equivalent:

i) The matrix $A$ is (Turing) excitable.

ii) The matrix $A$ is not Lotka-Volterra stable.

iii) For some $D$ the matrix $A - D$ has an eigenvalue with positive real part.

iv) For some $P, Q$ the matrix $B$ is not stable.

v) For some $P, Q$ the matrix $B$ has a real positive eigenvalue.

vi) For some $P, Q$ the matrix $B$ has a pair of purely imaginary eigenvalues.
Can stationary states of ecological models or epidemic models be excitable?

Trivial observation: Two-species competition models are never excitable!

What about predator-prey models?

R. May, S. Levin
Predator-prey models

\[ \dot{x} = g(x) - bh(x)y \]
\[ \dot{y} = ch(x)y - d(y)y \]

Jacobian matrix at coexistence point

\[ A = (a_{ij}) = \begin{pmatrix} g'(x) - bh'(x)y & -bh(x) \\ ch'(x)y & -d'(y)y \end{pmatrix} \]

If the predator mortality is constant then the matrix \( A \) is either strongly stable or unstable. The matrix is **never** excitable.
Modified MacArthur-Rosenzweig model (MMR)

\[
\begin{align*}
\dot{x} &= ax\left(1 - \frac{x}{K}\right) - b\frac{x}{1 + mx}y \\
\dot{y} &= c\frac{x}{1 + mx}y - (d_0 + ey)y
\end{align*}
\]

Multistability: either one node/focus or two of these with a saddle point in between. Both can undergo Hopf bifurcations.
Excitability

**Finding:** In the MMR model parameters can be chosen such that there is an excitable coexistence point.

**Consequence:** For the MMR with quiescent phases there are two routes to a Hopf bifurcation, either by increasing the carrying capacity of the prey (increasing predator mortality), or by changing the rates for the quiescent phases.
Epidemic models

\[
\begin{align*}
\dot{S} &= \mu - \mu S - \beta SI \\
\dot{I} &= -\mu I + \beta SI - \alpha(I)I
\end{align*}
\]

Standard case $\alpha$ constant: the coexistence point is not excitable.

$\alpha'(I) < 0$: recovery takes longer if prevalence is high due to lack of sufficient health care.

There are backward bifurcations and also choices of the parameters such that the Jacobian matrix is excitable.
Periodic orbits

Highly symmetric model problem in $\mathbb{R}^2$:

$$\dot{r} = rg(r), \quad \dot{\varphi} = 1$$

One periodic orbit of the small system may result in up to three periodic orbits of the large system in $\mathbb{R}^4$.

Numerical simulations with $P = pI$, $Q = qI$ show that periodic orbits (i.e., the projections) shrink.
Figure: MR model with quiescence (L. Bilinsky)
**Theorem:** If the given $\mathbb{R}^2$ periodic orbit is a **convex curve** then for large $p, q$ the projection of the $\mathbb{R}^4$ curve to the active plane lies inside the given curve.
Detour: The role of convexity?

Reaction-diffusion:
\[ \dot{u} = F(u), \quad u_t = D \Delta u + F(u) \]

Claim: “If the set \( M \in \mathbb{R}^n \) is positively invariant for the o.d.e. then it is positively invariant for the p.d.e.”

True if \( M \) is convex and \( D = dl \)
True if \( M \) is a generalized rectangle.
Observation in $\mathbb{R}^2$

$$\dot{x} = f(x, y)$$
$$\dot{y} = g(x, y)$$

Define “curvature”

$$C(x, y) = f^2 g_x + fg(g_y - f_x) - g^2 f_y$$

If $C > 0$ in some domain then every periodic orbit in the domain is convex.

Does convexity of a periodic orbit have some biological relevance?
MR model

\[
\dot{x} = ax \left(1 - \frac{x}{K}\right) - b \frac{x}{1 + mx} y
\]

\[
\dot{y} = c \frac{x}{1 + mx} y - dy
\]

Suppose \( K, m, c, d \) are such that the coexistence point is unstable. Then there is a critical value \( a_0 \) for such that the periodic orbit is a convex curve for all \( a < a_0 \).

End of Detour
More general scenario: Spatial heterogeneity

Claim
“stabilization by quiescence” is a special case of
“stabilization by heterogeneity”
Idea:

interpret “phases” as “sites”!

2 sites

\[ \begin{align*}
\dot{v} &= f(v) - pv + qw \\
\dot{w} &= \kappa f(w) + pv - qw
\end{align*} \]

m sites

\[ \begin{align*}
\dot{v}_k^{(i)} &= \kappa_i f_k^{(i)} (v^{(i)}) + \sum_j \gamma_{ij} v_k^{(j)}, \quad k = 1, \ldots, n. \\
v_k^{(i)} &= \text{density of } k\text{th species at site } i.
\end{align*} \]
Matrix notation

\[ \dot{V} = AVK + V\Gamma \]

\( V = (v_{ij}) \) with \( m \) columns and \( n \) rows.

A column represents all species at one site. 
A acts from the left, \( K \) and \( \Gamma \) act from the right.

Eigenvalue problem:

\[ \lambda V = AVK + V\Gamma \]

For each eigenvalue \( \mu \) of \( A \) there are \( m \) eigenvalues \( \lambda \).
Heterogeneity stabilizes!

**Proposition:** Suppose that at least two of the $\kappa_j$ are distinct. Let $\mu = i\beta$ be a purely imaginary eigenvalue of $A$ with $\beta \neq 0$. Then all corresponding eigenvalues $\lambda_j$ have negative real parts.

Neubert, Klepac, van den Driessche 2002
Proposition: Suppose that the $\kappa_j$ are pairwise distinct. Suppose $\mu = \alpha + i\beta$ with $\beta > 0$ large. Then the eigenvalue $\lambda_j$ corresponding to $\kappa_j$ satisfies

$$\lambda_j = \gamma_{jj} + \alpha \kappa_j + i\beta \kappa_j + o(1)$$

for $\beta \to \infty$. We have $\gamma_{jj} < 0$.

For $\alpha$ no too large and $\beta$ large the eigenvalue is in the left half plane.
Continuously many sites

\[ \nu_t = \kappa(x)f(\nu) + D\Delta \nu \]

with no-flux boundary condition.

Constant stationary solution: \( f(\bar{\nu}) = 0 \).

Linearized equation

\[ \nu_t = \kappa(x)A\nu + D\Delta \nu \]

same boundary condition.
Eigenvalue problem

\[ D \Delta v + \kappa(x) A v = \lambda v. \]

separation of variables \( v(x) = u(x) \hat{v} \)

\[ A \hat{v} = \mu \hat{v}, \quad \mu = \alpha + i \beta, \]

\[ D \Delta u + \kappa(x) (\alpha + i \beta) u = (\xi + i \eta) u. \]

Eigenvalue problem with a complex parameter.
Suppose that $\kappa(x)$ is not a constant. If $\alpha = 0$ and $\beta > 0$ then $u$ is not a constant and $\xi < 0$.

Inhomogeneity stabilizes purely imaginary eigenvalues.
Other distributions: non-exponential

Frithjof Lutscher

Semi-Poisson system

$$\nu_t + \nu_a + p\nu = m(a)F(t),$$

$$v(t, 0) = \int_0^\infty q(b)w(t, b)db + f(t)$$

$$w_t + w_b + q(b)w = 0$$

$$w(t, 0) = p\int_0^\infty v(t, a)da + g(t)$$

can be reduced to an integral equation for the function

$$V(t) = \int_0^\infty v(t, a)da.$$
\[
\dot{V}(t) = p \left[ \int_0^\infty L(b)V(t-b)db - V(t) \right] \\
+ \int_0^\infty L(b)g(t-b)db + F(t) + f(t)
\]

with

\[
L(b) = \exp\left\{ - \int_0^b q(s)ds \right\} q(b)
\]

Replace \( F(t) \rightarrow F(V(t)) \), \( f(t) \rightarrow f(V(t)) \), \( g(t) \rightarrow g(V(t)) \), get autonomous system.
Dirac case: Equation with constant delay. Vector valued case: $P$ is a diagonal matrix, $\tau$ is a vector (replacing $Q^{-1}$):

$$\dot{u}(t) = P(u(t - \tau) - u(t)) + f(u(t))$$

Stabilization of temporal patterns occurs if all $p_i$ and all $\tau_i$ are the same. In the general case there are two routes to Hopf bifurcation. However: Stabilization is not uniform.
Figure: The stability boundary for switching with fixed delay. The value of $p = 1$ is fixed; the value for $\tau$ varies.
GOOD LUCK, ODO!