The effect of time delay on diffusive Lotka-Volterra competition models

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Winter Workshop on Competition Dynamics in Biology
Ohio State University
December 16, 2021

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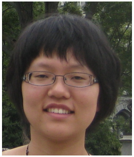
Collaborators

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- Chen, Shanshan, Shi, Junping, Global dynamics of the diffusive Lotka-Volterra competition model with stage structure. *Calc. Variations and Part. Differential Equations*, (2020) 59:33.
- Shi, Junping; Wang, Chuncheng; Wang, Hao, Spatial movement with diffusion and memory-based self-diffusion and cross-diffusion. *J. Differential Equations*. 305 (2021), 242-269.

Competition

- The competition for limited resource exists almost everywhere.
- In an intraspecific competition, members of the same species compete for limited resources.
- In an interspecific competition, members of different species compete for a shared resource.
- War is the extreme result of intraspecific competition in humans.
- It is important to know (or predict) the outcome of the competition.

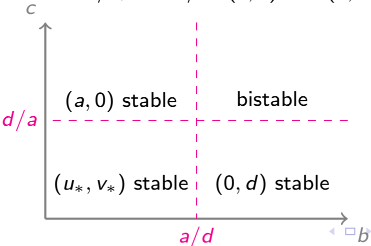
https://en.wikipedia.org/wiki/Intraspecific_competition

Lotka-Volterra competition model

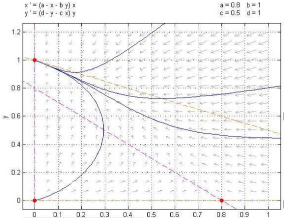
[Lotka, 1932], [Volterra, 1928] $u' = u(a - eu - bv), \quad v' = v(d - fv - cu)$.
a, d: growth or resource; e, f: intraspecific competition; b, c: interspecific competition.
Simplified to: $u' = u(a - u - bv), \quad v' = v(d - v - cu)$.

Trivial equilibrium: $(0, 0)$ (unstable)
Semi-trivial equilibrium: $(a, 0)$ (saddle if $c < d/a$, stable if $c > d/a$)
Semi-trivial equilibrium: $(0, d)$ (saddle if $b < a/d$, stable if $b > a/d$)
Coexistence equilibrium: $(u_*, v_*) = (\frac{d - ac}{1 - bc}, \frac{a - bd}{1 - bc})$
(stable when $c < d/a$ and $b < a/d$; saddle when $c > d/a$ and $b > a/d$)

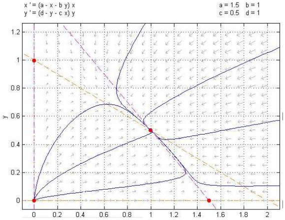
Case 1: u is superior than v $c > d/a$, $b < a/d$: $(a, 0)$ is globally asymptotically stable
Case 2: v is superior than u $c < d/a$, $b > a/d$: $(0, d)$ is globally asymptotically stable
Case 3: weak competition $c < d/a$, $b < a/d$: (u_*, v_*) is globally asymptotically stable
Case 4: strong competition $c > d/a$, $b > a/d$: $(a, 0)$ and $(0, d)$ are bistable



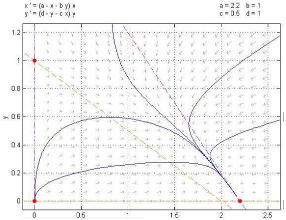
Lotka-Volterra competitive system: phase portraits



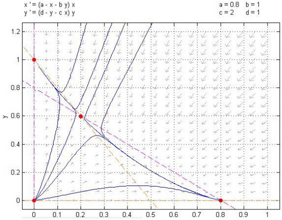
v sup.



weak comp.



u sup.



strong comp.

Reaction-diffusion Lotka-Volterra competition model

$$\begin{cases} U_t = d_1 \Delta U + U\left(m_1(x) - U - cV\right), & x \in \Omega,\ t > 0, \\ V_t = d_2 \Delta U + V\left(m_2(x) - bU - V\right), & x \in \Omega,\ t > 0, \\ U_\nu = V_\nu = 0, & x \in \partial\Omega,\ t > 0, \\ U(x,0) = U_0(x) \geq 0,\ V(x,0) = V_0(x) \geq 0, & x \in \Omega. \end{cases}$$

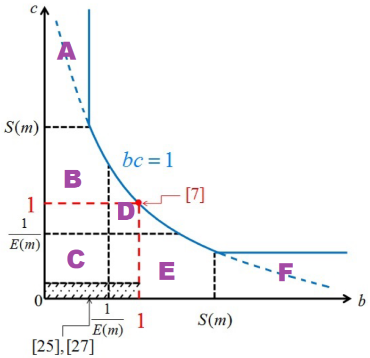
Semitrivial steady states $\left(\theta_1, 0\right) = \left(\theta_{d_1,m_1}, 0\right)$ and $\left(0, \theta_2\right) = \left(0, \theta_{d_2,m_2}\right)$, where θ_{d_i,m_i} satisfies the equation

$$\begin{cases} d_i \Delta\theta + m_i(x)\theta - \theta^2 = 0, & x \in \Omega, \\ \theta_\nu = 0, & x \in \partial\Omega. \end{cases}$$

1. [Brown, 1980, SIAP] [Lou-Ni, 1996, JDE] $m_1(x) = a, m_2(x) = d$ (constant): ODE dynamics holds (except bistable case)
2. [Dockery et.al, 1998, JMB]: $m_1(x) = m_2(x)$ (not constant) and $b = c = 1$: if $d_1 < d_2$, then $(\theta_1, 0)$ is globally asymptotically stable ("slower disperser wins")
3. [Lou, 2006, JDE] [He-Ni, 2016, CPAM]: $m_1(x), m_2(x)$ (not constant) and $bc < 1$ (weak competition): complete dynamics classified.
   Other work: [Lam-Ni, 2012, SIAP] [He-Ni, 2013, JDE] [He-Ni, 2016,2017, CVPDE]

Classification of RD L-V dynamics

[He-Ni, 2016, CPAM] (Figure 1.1 from this paper)



A: $(0, \theta_2)$ g.a.s. for all $d_1, d_2 > 0$

B: $(0, \theta_2)$ g.a.s. for some (d_1, d_2), and (u_*, v_*) g.a.s. for other (d_1, d_2)

C: coexistence state (u_*, v_*) g.a.s. for all $d_1, d_2 > 0$

D: $(0, \theta_2)$ g.a.s. for some (d_1, d_2), $(\theta_1, 0)$ g.a.s. for some (d_1, d_2), and (u_*, v_*) g.a.s. for other (d_1, d_2)

E: $(\theta_1, 0)$ g.a.s. for some (d_1, d_2), and (u_*, v_*) g.a.s. for other (d_1, d_2)

F: $(\theta_1, 0)$ g.a.s. for all $d_1, d_2 > 0$

G: $b = c = 1$, degenerate case

[7]=[Dockery et.al, 1998, JMB]
[25]=[Lam-Ni, 2012, SIAP]
[27]=[Lou, 2006, JDE]

$$E(m) = \sup_{d>0} \frac{\int_\Omega \theta_{d,m}}{\int_\Omega m},$$

$$S(m) = \sup_{d>0} \sup_{\overline{\Omega}} \frac{m}{\theta_{d,m}}$$

Proof of classification

[He-Ni, 2016, CPAM]

$$\begin{cases} U_t = d_1 \Delta U + U\left(m(x) - U - cV\right), & x \in \Omega,\ t > 0, \\ V_t = d_2 \Delta U + V\left(m(x) - bU - V\right), & x \in \Omega,\ t > 0, \\ U_\nu = V_\nu = 0, & x \in \partial\Omega,\ t > 0, \\ U(x,0) = U_0(x) \geq 0,\ V(x,0) = V_0(x) \geq 0, & x \in \Omega. \end{cases}$$

1. Carefully analyze the stability of the two semi-trivial steady state solutions.
2. Every coexistence steady state is linearly stable (thus unique).
3. (monotone dynamical system theory) Either there is a unique co-existence steady state that is globally asymptotically stable; or there is no co-existence steady state and one of the two semi-trivial steady state is globally asymptotically stable.

Patch model: [Chen-Shi-Shuai-Wu, 2022, Nonlinearity] (tomorrow's talk by Wu)

$$\begin{cases} u_i' = \mu_u \sum (a_{ij} u_j - a_{ji} u_i) + u_i(p_i - u_i - cv_i), & i = 1, \dots, n,\ t > 0, \\ v_i' = \mu_v \sum (a_{ij} v_j - a_{ji} v_i) + v_i(q_i - bu_i - v_i), & i = 1, \dots, n,\ t > 0. \end{cases}$$

(A1) (weak competition) $b, c > 0$, and $0 < bc \leq 1$; $p_i, q_i > 0$ for all $i = 1, 2, ..., n$.
(A2) The weighted digraph $\mathcal{G}$ is strongly connected (L is irreducible).
(A3) The weighted digraph $\mathcal{G}$ is cycle-balanced.

Then a positive equilibrium $E = (u, v)$, if exists, is locally asymptotically stable except for the case $bc = 1$, hence a classification of the dynamics can also be acheived.

Effect of time delays

The birth and growth of the population may depend on the population in the past.

1. (Growth rate per capita depending on the past) [Hutchinson, 1948]

$$u'(t) = au(t)(1 - u(t-\tau)/K), \quad \text{or more general} \quad u'(t) = u(t)f(u(t-\tau))$$

   can occur in interspecific or intraspecific comeptiton

2. (Birth/recuitement rate depending on the past) [Gurney et.al, 1980, Nature]

$$u'(t) = au(t-\tau)e^{-bu(t-\tau)} - du(t), \quad \text{or more general} \quad u'(t) = f(u(t-\tau)) - du(t)$$

   can occur in intrinsic growth in compeition models

3. (Movement depending on memory) [Fagan et.al, 2013, Ecol. Lett.] [Fagan et.al, 2017, Am. Nat.] [Potts-Lewis, 2019, BMB] and many others [Shi-Wang-Wang-Yan, 2020, JDDE] [Shi-Wang-Wang, 2019, Nonlinearity] [Shi-Shi-Wang, 2021, JMB]

$$u_t(x,t) = D_1 \Delta u(x,t) + D_2 div(u(x,t)\nabla u(x,t-\tau)) + g(x,t,u(x,t)),$$

   can occur in the movement mode of compeition model

   Question: How do these time delays affect the reaction-diffusion competition dynamics?

Deriviation of model (I)

[Chen-Shi, 2020, CVPDE]
Model: [Metz-Diekmann, 1983] [Al-Omari-Gourley, 2002] [So-Wu-Zou, 2001]
Let $u(x,t,a)$ be the density of a species of age a at space x and time t, and let τ be the maturation period. And let $u_m(x,t) := \int_\tau^\infty u(x,t,a)da$ be the mature species.

$$\begin{cases} u_t + u_a = \tilde{d}\Delta u - \gamma u, & x \in \Omega,\ t > 0\ 0 < a < \tau, \\ u_\nu = 0, & x \in \partial\Omega,\ t > 0,\ 0 < a < \tau, \\ u(x,t,0) = m(x)u_m(x,t), & x \in \Omega,\ t > 0, \end{cases}$$

$$\begin{cases} (u_m)_t = d\Delta u_m + u(x,t,\tau) - u_m^2, & x \in \Omega,\ t > 0, \\ (u_m)_\nu = 0, & x \in \partial\Omega,\ t > 0. \end{cases}$$

Then $u(x,t,\tau) = e^{-\gamma\tau}\int_\Omega G(x,y,\tilde{d},\tau)m(y)u_m(y,t-\tau)dy$, where $G(x,y,\tilde{d},t)$ is the Green's function of diffusion equation. And

$$\begin{cases} (u_m)_t = d\Delta u_m + e^{-\gamma\tau}\int_\Omega G(x,y,\tilde{d},\tau)m(y)u_m(y,t-\tau)dy - u_m^2, & x \in \Omega,\ t > 0, \\ (u_m)_\nu = 0, & x \in \partial\Omega,\ t > 0. \end{cases}$$

Deriviation of model (II)

Two-species Lotka-Volterra competitive model:

$$\begin{cases} U_t = d_1\Delta U + e^{-\gamma_1\tau_1}\int_\Omega G(x,y,\tilde{d}_1,\tau_1)m_1(y)U(y,t-\tau_1)dy \\ \qquad -U^2 - cUV, & x\in\Omega,\ t>0, \\ V_t = d_2\Delta V + e^{-\gamma_2\tau_2}\int_\Omega G(x,y,\tilde{d}_2,\tau_2)m_2(y)V(y,t-\tau_2)dy \\ \qquad -bUV - V^2, & x\in\Omega,\ t>0, \\ U_\nu = V_\nu = 0, & x\in\partial\Omega,\ t>0, \\ U(x,t) = U_0(x,t)\geq 0, & x\in\Omega,\ t\in[-\tau_1,0], \\ V(x,t) = V_0(x,t)\geq 0, & x\in\Omega,\ t\in[-\tau_2,0]. \end{cases}$$

$G(x,y,\tilde{d}_i,\tau_i) = G(x,y,1,\tilde{d}_i\tau_i) \to \delta(x-y)$ as $\tilde{d}_i\tau_i \to 0$. When $\tilde{d}_1$ and $\tilde{d}_2$ (diffusion coefficients of the immature species) are small, the model is approximately

$$\begin{cases} U_t = d_1\Delta U + e^{-\gamma_1\tau_1}m_1(x)U(x,t-\tau_1) - U^2 - cUV, & x\in\Omega,\ t>0, \\ V_t = d_2\Delta V + e^{-\gamma_2\tau_2}m_2(x)V(x,t-\tau_2) - bUV - V^2, & x\in\Omega,\ t>0, \\ U_\nu = V_\nu = 0, & x\in\partial\Omega,\ t>0, \\ U(x,t) = U_0(x,t)\geq 0, & x\in\Omega,\ t\in[-\tau_1,0], \\ V(x,t) = V_0(x,t)\geq 0, & x\in\Omega,\ t\in[-\tau_2,0]. \end{cases} \tag{1}$$

Always assume: $m_i(x)\in C^\alpha(\overline{\Omega})$, for $\alpha\in(0,1)$, and $m_i(x) \geq 0$ on $\overline{\Omega}$ for $i=1,2$.

"No delay" model

$$\begin{cases} U_t = d_1 \Delta U + e^{-\gamma_1 \tau_1} m_1(x) U - U^2 - cUV, & x \in \Omega,\ t > 0, \\ V_t = d_2 \Delta V + e^{-\gamma_2 \tau_2} m_2(x) V - bUV - V^2, & x \in \Omega,\ t > 0, \\ U_\nu = V_\nu = 0, & x \in \partial\Omega,\ t > 0, \\ U(x,0) = U_0(x) \ge 0,\ V(x,0) = V_0(x) \ge 0, & x \in \Omega. \end{cases} \tag{2}$$

Semitrivial steady states $(\theta_1, 0) = (\theta_{d_1,\tau_1,\gamma_1,m_1}, 0)$ and $(0, \theta_2) = (0, \theta_{d_2,\tau_2,\gamma_2,m_2})$, where $\theta_{d_i,\tau_i,\gamma_i,m_i}$ satisfies the equation

$$\begin{cases} d_i \Delta \theta + e^{-\gamma_i \tau_i} m_i(x) \theta - \theta^2 = 0, & x \in \Omega, \\ \theta_\nu = 0, & x \in \partial\Omega. \end{cases}$$

$\Gamma = \{(d_1, d_2, \tau_1, \tau_2, \gamma_1, \gamma_2) \in \mathbb{R}^6 : d_1, d_2 > 0, \tau_1, \tau_2, \gamma_1, \gamma_2 \ge 0\}.$

$$\begin{aligned} S_u &:= \{(d_1, d_2, \tau_1, \tau_2, \gamma_1, \gamma_2) \in \Gamma : (\theta_1, 0) \text{ stable}\}, \\ S_v &:= \{(d_1, d_2, \tau_1, \tau_2, \gamma_1, \gamma_2) \in \Gamma : (0, \theta_2) \text{ stable}\}, \\ S_- &:= \{(d_1, d_2, \tau_1, \tau_2, \gamma_1, \gamma_2) \in \Gamma : (\theta_1, 0) \text{ and } (0, \theta_2) \text{ both unstable}\}, \\ S_{u,0} &:= \{(d_1, d_2, \tau_1, \tau_2, \gamma_1, \gamma_2) \in \Gamma : (\theta_1, 0) \text{ neutrally stable}\}, \\ S_{v,0} &:= \{(d_1, d_2, \tau_1, \tau_2, \gamma_1, \gamma_2) \in \Gamma : (0, \theta_2) \text{ neutrally stable}\}, \\ S_{0,0} &:= \{(d_1, d_2, \tau_1, \tau_2, \gamma_1, \gamma_2) \in \Gamma : (\theta_1, 0) \text{ and } (0, \theta_2) \text{ both neutrally stable}\}. \end{aligned}$$

"No delay" model dynamics

[He-Ni, 2016, CPAM]

Lemma 1. If $0 < bc \leq 1$, then for any $(d_1, d_2, \tau_1, \tau_2, \gamma_1, \gamma_2) \in \Gamma \setminus S_{0,0}$, every positive steady state of system (2) is linearly stable if exists.

Lemma 2. If $0 < bc \leq 1$, then we have the following mutually disjoint decomposition of Γ for (2):

$$\Gamma = (S_u \cup S_{u,0} \setminus S_{0,0}) \cup (S_v \cup S_{v,0} \setminus S_{0,0}) \cup S_- \cup S_{0,0}.$$

Moreover, the following statements hold for model (2):

(i) For any $(d_1, d_2, \tau_1, \tau_2, \gamma_1, \gamma_2) \in (S_u \cup S_{u,0}) \setminus S_{0,0}$, $\left(\theta_{d_1,\tau_1,\gamma_1,m_1}, 0\right)$ is globally asymptotically stable.

(ii) For any $(d_1, d_2, \tau_1, \tau_2, \gamma_1, \gamma_2) \in (S_v \cup S_{v,0}) \setminus S_{0,0}$, $\left(0, \theta_{d_2,\tau_2,\gamma_2,m_2}\right)$ is globally asymptotically stable.

(iii) For any $(d_1, d_2, \tau_1, \tau_2, \gamma_1, \gamma_2) \in S_-$, model (2) has a unique positive steady state, which is globally asymptotically stable.

(iv) For any $(d_1, d_2, \tau_1, \tau_2, \gamma_1, \gamma_2) \in S_{0,0}$, $\theta_{d_1,\tau_1,\gamma_1,m_1} \equiv c\theta_{d_2,\tau_2,\gamma_2,m_2}$, and model (2) has a compact global attractor consisting of a continuum of steady states

$$\{\left(\rho\theta_{d_1,\tau_1,\gamma_1,m_1}, (1-\rho)\theta_{d_1,\tau_1,\gamma_1,m_1}/c\right) : \rho \in (0,1)\}.$$

Linearized systems

Linearied eigenvalue equation of "delayed model" (1) at a positive steady state (u, v):

$$\begin{cases} \lambda\phi_1 = d_1\Delta\phi_1 + e^{-\gamma_1\tau_1-\lambda\tau_1}m_1(x)\phi_1 - (2u+cv)\phi_1 - cu\phi_2, & x \in \Omega, \\ \lambda\phi_2 = d_2\Delta\phi_2 + e^{-\gamma_2\tau_2-\lambda\tau_2}m_2(x)\phi_2 - (bu+2v)\phi_2 - bv\phi_1, & x \in \Omega, \\ (\phi_1)_\nu = (\phi_2)_\nu = 0, & x \in \partial\Omega. \end{cases}$$

With $\psi_1 = \phi_1$ and $\psi_2 = -\phi_2$, it is equivalent to

$$\begin{cases} \lambda\psi_1 = d_1\Delta\psi_1 + e^{-\gamma_1\tau_1-\lambda\tau_1}m_1(x)\psi_1 - (2u+cv)\psi_1 + cu\psi_2, & x \in \Omega, \\ \lambda\psi_2 = d_2\Delta\psi_2 + e^{-\gamma_2\tau_2-\lambda\tau_2}m_2(x)\psi_2 - (bu+2v)\psi_2 + bv\psi_1, & x \in \Omega, \\ (\psi_1)_\nu = (\psi_2)_\nu = 0, & x \in \partial\Omega. \end{cases} \tag{3}$$

Corresponding eigenvalue problem for "no delay' model" (2):

$$\begin{cases} \lambda\psi_1 = d_1\Delta\psi_1 + e^{-\gamma_1\tau_1}m_1(x)\psi_1 - (2u+cv)\psi_1 + cu\psi_2, & x \in \Omega, \\ \lambda\psi_2 = d_2\Delta\psi_2 + e^{-\gamma_2\tau_2}m_2(x)\psi_2 - (bu+2v)\psi_2 + bv\psi_1, & x \in \Omega, \\ (\psi_1)_\nu = (\psi_2)_\nu = 0, & x \in \partial\Omega. \end{cases} \tag{4}$$

Stability of steady states

Theorem 3. Assume that $d_1, d_2 > 0$, and $\tau_1, \tau_2, \gamma_1, \gamma_2 \geq 0$. Then there exists a principal eigenvalue $\tilde{\lambda}_1$ of (3) with an associated eigenfunction $(\psi_1, \psi_2) > (0, 0)$. Furthermore,

(i) $\tilde{\lambda}_1 = \sup\{\mathcal{R}e\lambda : \lambda$ is an eigenvalue of (3)$\}$,

(ii) $\tilde{\lambda}_1$ is simple and has the same sign as λ_1, the principal eigenvalue of (4),

(iii) any eigenvalue $\hat{\lambda}$ of (3) with $\hat{\lambda} \neq \tilde{\lambda}_1$ satisfies $\mathcal{R}e\hat{\lambda} < \tilde{\lambda}_1$.

Similar results also hold for the semitrivial steady states.

Proof.
1. $\tilde{\lambda}_1$ of (3) is for a linear delayed reaction-diffusion system, and λ_1 of (4) is for a linear reaction-diffusion system (with no delay).
2. Prove the solution operator $U(t)$ of the delayed system is positive, and eventually strongly positive.
3. Prove the supreme of the spectral set of the delayed equation is a spectral value, and it has the same sign as the no-delayed equation. [Kerscher-Nagel, 1984]
4. Prove the supreme of the spectral set is a principal eigenvalue with positive eigenfunction.

Monotone dynamical system approach

Propostion 4. The stage structured model generates a monotone dynamical system:

$$\begin{cases} U_t = d_1 \Delta U + e^{-\gamma_1 \tau_1} m_1(x) U(x, t-\tau_1) - U^2 - cUV, & x \in \Omega, \ t > 0, \\ V_t = d_2 \Delta V + e^{-\gamma_2 \tau_2} m_2(x) V(x, t-\tau_2) - bUV - V^2, & x \in \Omega, \ t > 0, \\ U_\nu = V_\nu = 0, & x \in \partial\Omega, \ t > 0. \end{cases}$$

That is, let $(U_i(x,t), V_i(x,t))$ be the corresponding solution of model (1) with initial value $(U_{0,i}, V_{0,i})$ for $i = 1, 2$. Assume that

$$U_{0,1} \geq U_{0,2} \geq 0 \ \text{ for } \ x \in \overline{\Omega}, \ t \in [-\tau_1, 0],$$

$$0 \leq V_{0,1} \leq V_{0,2} \ \text{ for } \ x \in \overline{\Omega}, \ t \in [-\tau_2, 0].$$

Then

$$U_1(x,t) \geq U_2(x,t) \ \text{ and } \ V_1(x,t) \leq V_2(x,t) \ \text{ for } \ x \in \overline{\Omega}, \ t \geq 0.$$

Note: The following system (delays in intraspecific competition) is not monotone:

$$\begin{cases} U_t = d_1 \Delta U + U[m_1(x) - U(x, t-\tau_1) - cV], & x \in \Omega, \ t > 0, \\ V_t = d_2 \Delta V + V[m_2(x) - bU - V(x, t-\tau_2)], & x \in \Omega, \ t > 0, \\ U_\nu = V_\nu = 0, & x \in \partial\Omega, \ t > 0. \end{cases}$$

Main result

Theorem 5. If $0 < bc \leq 1$, then we have the following mutually disjoint decomposition of Γ for (1): $\Gamma = (S_u \cup S_{u,0} \setminus S_{0,0}) \cup (S_v \cup S_{v,0} \setminus S_{0,0}) \cup S_- \cup S_{0,0}$.
Moreover, the following statements hold for model (1):

(i) For any $(d_1, d_2, \tau_1, \tau_2, \gamma_1, \gamma_2) \in (S_u \cup S_{u,0}) \setminus S_{0,0}$, $\left(\theta_{d_1,\tau_1,\gamma_1,m_1}, 0\right)$ is g.a.s.

(ii) For any $(d_1, d_2, \tau_1, \tau_2, \gamma_1, \gamma_2) \in (S_v \cup S_{v,0}) \setminus S_{0,0}$, $\left(0, \theta_{d_2,\tau_2,\gamma_2,m_2}\right)$ is g.a.s.

(iii) For any $(d_1, d_2, \tau_1, \tau_2, \gamma_1, \gamma_2) \in S_-$, model (2) has a unique positive steady state, which is g.a.s.

(iv) For any $(d_1, d_2, \tau_1, \tau_2, \gamma_1, \gamma_2) \in S_{0,0}$, $\theta_{d_1,\tau_1,\gamma_1,m_1} \equiv c\theta_{d_2,\tau_2,\gamma_2,m_2}$, and model (1) has a compact global attractor consisting of a continuum of steady states

$$\left\{\left(\rho\theta_{d_1,\tau_1,\gamma_1,m_1}, (1-\rho)\theta_{d_1,\tau_1,\gamma_1,m_1}/c\right) : \rho \in (0,1)\right\}.$$

The asymptotic dynamics of

$$\begin{cases} U_t = d_1\Delta U + e^{-\gamma_1\tau_1} m_1(x)U(x, t-\tau_1) - U^2 - cUV, & x \in \Omega,\ t > 0, \\ V_t = d_2\Delta V + e^{-\gamma_2\tau_2} m_2(x)V(x, t-\tau_2) - bUV - V^2, & x \in \Omega,\ t > 0, \\ U_\nu = V_\nu = 0, & x \in \partial\Omega,\ t > 0. \end{cases}$$

and

$$\begin{cases} U_t = d_1\Delta U + e^{-\gamma_1\tau_1} m_1(x)U - U^2 - cUV, & x \in \Omega,\ t > 0, \\ V_t = d_2\Delta V + e^{-\gamma_2\tau_2} m_2(x)V - bUV - V^2, & x \in \Omega,\ t > 0, \\ U_\nu = V_\nu = 0, & x \in \partial\Omega,\ t > 0. \end{cases}$$

are identical. But the delays τ_1, τ_2 alter the steady states and they could change the outcome of the competition.

Example (A)

$$\begin{cases} U_t = d\Delta U + e^{-\gamma\tau_1} m(x) U(x, t-\tau_1) - U^2 - UV, & x \in \Omega,\ t > 0, \\ V_t = d\Delta V + e^{-\gamma\tau_2} m(x) V(x, t-\tau_2) - UV - V^2, & x \in \Omega,\ t > 0, \\ U_\nu = V_\nu = 0, & x \in \partial\Omega,\ t > 0, \\ U(x,t) = U_0(x,t) \geq 0, & x \in \Omega,\ t \in [-\tau_1, 0], \\ V(x,t) = V_0(x,t) \geq 0, & x \in \Omega,\ t \in [-\tau_2, 0]. \end{cases} \tag{5}$$

Theorem 6. Assume that $m(x) \in C^\alpha(\overline{\Omega})$ $(\alpha \in (0,1))$, $m(x) > 0$ on $\overline{\Omega}$, and $d, \gamma, \tau_1, \tau_2 > 0$. Then

(*i*) If $\tau_1 > \tau_2$, then $(0, \theta_{\tau_2})$ is globally asymptotically stable.

(*ii*) If $\tau_1 < \tau_2$, then $(\theta_{\tau_1}, 0)$ is globally asymptotically stable.

(*iii*) If $\tau_1 = \tau_2$, then model (5) has a compact global attractor consisting of a continuum of steady states $\{(\rho\theta_{\tau_1}, (1-\rho)\theta_{\tau_1}) : \rho \in (0,1)\}$.

The species with shorter maturation time will prevail if all other conditions (dispersal, growth) are identical. Faster maturer wins!

Example (B)

$$
\begin{cases}
U_t = d_1 \Delta U + e^{-\gamma_1 \tau_1} m_1(x) U(x, t - \tau_1) - U^2 - cUV, & x \in \Omega,\ t > 0, \\
V_t = d_2 \Delta V + m_2(x) V - bUV - V^2, & x \in \Omega,\ t > 0, \\
U_\nu = V_\nu = 0, & x \in \partial\Omega,\ t > 0, \\
U(x, t) = U_0(x, t) \geq 0, & x \in \Omega,\ t \in [-\tau_1, 0], \\
V(x, t) = V_0(x, t) \geq 0, & x \in \Omega,\ t = 0.
\end{cases} \tag{6}
$$

Semitrivial steady states: $(\theta_1, 0) = \left(\theta_{d_1, \tau_1, \gamma_1, m_1}, 0\right)$ and $(0, \theta_2) = \left(0, \theta_{d_2, 0, 0, m_2}\right)$.

$$
\tilde{S}_p := \{(d_1, d_2) : (d_1, d_2, 0, 0, 0, 0) \in S_p\} \text{ for } p = u, v, -,
$$
$$
\tilde{S}_{p,0} := \{(d_1, d_2) : (d_1, d_2, 0, 0, 0, 0) \in S_{p,0}\} \text{ for } p = u, v, 0,
$$

where S_u, S_v, S_-, $S_{u,0}$, $S_{v,0}$ and $S_{0,0}$ are defined as before.

If $bc \leq 1$, then $\left(\mathbb{R}^+\right)^2$ has the following mutually disjoint decomposition:

$$
\left(\mathbb{R}^+\right)^2 = (\tilde{S}_u \cup \tilde{S}_{u,0} \setminus \tilde{S}_{0,0}) \cup (\tilde{S}_v \cup \tilde{S}_{v,0} \setminus \tilde{S}_{0,0}) \cup \tilde{S}_- \cup \tilde{S}_{0,0}.
$$

Example (B)

Theorem 7. Suppose that $bc \leq 1$.

(i) If $(d_1, d_2) \in (\tilde{S}_v \cup \tilde{S}_{v,0}) \cup \tilde{S}_{0,0}$, then $(0, \theta_2)$ is g.a.s. for any $\gamma_1\tau_1 > 0$.

(ii) If $(d_1, d_2) \in \tilde{S}_- \cup \left(\tilde{S}_{u,0} \setminus \tilde{S}_{0,0}\right)$, then there exists $\tilde{\delta} \in (0,1)$ such that $(0, \theta_2)$ is g.a.s. for $\gamma_1\tau_1 \geq -\ln\tilde{\delta}$, and for $0 < \gamma_1\tau_1 < -\ln\tilde{\delta}$, there exists a unique positive steady state which is g.a.s.

(iii) If $(d_1, d_2) \in \tilde{S}_u$, then there exist $0 < \delta_1 \leq \delta_2 < 1$ such that

$$\mu_1\left(d_1, e^{-\gamma_1\tau_1} m_1 - c\theta_{d_2,0,0,m_2}\right) = 0 \;\text{ for }\; \gamma_1\tau_1 = -\ln\delta_1,$$
$$\mu_1\left(d_2, m_2 - b\theta_{d_1,\tau_1,\gamma_1,m_1}\right) = 0 \;\text{ for }\; \gamma_1\tau_1 = -\ln\delta_2.$$

Moreover,
(A) if $\delta_1 < \delta_2$, then $(\theta_1, 0)$ is g.a.s for $0 < \gamma_1\tau_1 \leq -\ln\delta_2$, $(0, \theta_2)$ is g.a.s. for $\gamma_1\tau_1 \geq -\ln\delta_1$, and for $-\ln\delta_2 < \gamma_1\tau_1 < -\ln\delta_1$, there exists a unique positive steady state, which is g.a.s.;
(B) if $\delta_1 = \delta_2$, then $(\theta_1, 0)$ is g.a.s. for $0 < \gamma_1\tau_1 < -\ln\delta_1$, $(0, \theta_2)$ is g.a.s. for $\gamma_1\tau_1 > -\ln\delta_1$, and for $\gamma_1\tau_1 = -\ln\delta_1$, system (6) has a compact global attractor consisting of a continuum of steady states.

previous partial result [Yan-Guo, 2018, DCDSB]

Example (C)

Delays in interspecific competition

$$\begin{cases} U_t = d_1 \Delta U + U\left[m_1(x) - U - cV(x, t-\tau_2)\right], & x \in \Omega,\ t > 0, \\ V_t = d_2 \Delta U + V\left[m_2(x) - bU(x, t-\tau_1) - V\right], & x \in \Omega,\ t > 0, \\ U_\nu = V_\nu = 0, & x \in \partial\Omega,\ t > 0, \\ U(x,t) = U_0(x,t) \geq 0,\ \ x \in \Omega,\ t \in [-\tau_1, 0], \\ V(x,t) = V_0(x,t) \geq 0,\ \ x \in \Omega,\ t \in [-\tau_2, 0]. \end{cases} \tag{7}$$

Different system but same method.

Theorem 8. If $0 < bc \leq 1$, then the global asymptotic dynamics of model (7) for $\tau_1, \tau_2 > 0$ is the same as that for $\tau_1 = \tau_2 = 0$.

Note: [Chen-Shi-Wei, 2011, CMA] The result does not hold for similar predator-prey system (with m_1, m_2 constants):

$$\begin{cases} U_t = d_1 \Delta U + U\left[m_1 - U - cV(x, t-\tau_2)\right], & x \in \Omega,\ t > 0, \\ V_t = d_2 \Delta U + V\left[m_2 + bU(x, t-\tau_1) - V\right], & x \in \Omega,\ t > 0, \\ U_\nu = V_\nu = 0, & x \in \partial\Omega,\ t > 0, \end{cases}$$

Hopf bifurcation may occur when $\tau_1 + \tau_2$ is large.

Spatial movement model

Suppose that Ω is a bounded, connected open region in $\mathbf{R}^N$, and $u_i(x,t)$ is the population density of the i-th biological species for location $x \in \Omega$ and time $t \geq 0$.

Continuity equation:

$$\frac{\partial u_i}{\partial t} = \nabla \cdot \mathbf{J}_i + f_i(u_1, u_2, \cdots, u_k),$$

where $\mathbf{J}_i(x,t)$ is the population flux of the i-th biological species for $i = 1, 2, 3, \cdots, k$, and f_i depicts the effect of interaction between species on the i-th species.

Fick's law $\rightarrow$ Diffusion Equation

$$\mathbf{J}_i(x,t) = -D_i \nabla u_i(x,t) \quad \rightarrow \quad \frac{\partial u_i(x,t)}{\partial t} = D_i \Delta u_i(x,t).$$

Fick's law + Advection $\rightarrow$ Advection-Diffusion Equation

$$\mathbf{J}_i(x,t) = -D_i \nabla u_i(x,t) - \mathbf{v_i}(x,t) \cdot u_i(x,t) \quad \rightarrow \quad \frac{\partial u_i(x,t)}{\partial t} = D_i \Delta u_i(x,t) + \nabla \cdot (\mathbf{v_i}(x,t) \cdot u_i(x,t)).$$

Here $D_i > 0$ is the diffusion coefficient of u_i, and $\mathbf{v_i}(x,t)$ is a vector field indicating the fluid flow velocity.

Self-diffusion, cross-diffusion and taxis

[Shigesada-Kawasaki-Teramoto, 1979, JTB] Two-species model

$$\frac{\partial u_1}{\partial t} = \nabla \cdot \mathbf{J}_1 + f_1(u_1, u_2), \quad \frac{\partial u_2}{\partial t} = \nabla \cdot \mathbf{J}_2 + f_2(u_1, u_2).$$

Self-diffusion: additional diffusion depending on its own density
Cross-diffusion: additional diffusion depending on other's density

$$\begin{aligned}\mathbf{J}_1(x,t) &= -\nabla[u_1(x,t)\cdot(D_1 + D_{11}u_1(x,t) + D_{12}u_2(x,t))],\\ \mathbf{J}_2(x,t) &= -\nabla[u_2(x,t)\cdot(D_2 + D_{21}u_1(x,t) + D_{22}u_2(x,t))].\end{aligned}$$

[Keller-Segel, 1970, JTB]
Self-taxis: advection depending on its own density
Cross-taxis: advection depending on other's density (chemotaxis, prey-taxis, or predator-taxis)

$$\begin{aligned}\mathbf{J}_1(x,t) &= -D_1\nabla u_1(x,t) - u_1(x,t)[D_{11}\nabla u_1(x,t) + D_{12}\nabla u_2(x,t)],\\ \mathbf{J}_2(x,t) &= -D_2\nabla u_2(x,t) - u_2(x,t)[D_{21}\nabla u_1(x,t) + D_{22}\nabla u_2(x,t)].\end{aligned}$$

Cross-diffusion: $-\nabla[D_{12}u_1u_2] = -D_{12}(u_1\nabla u_2 + u_2\nabla u_1)$
Cross-taxis: $-D_{12}u_1\nabla u_2$

Memory-based self-taxis and cross-taxis

[Shi-Wang-Wang, 2021, JDE]
Delayed self-taxis: advection depending on its own density in the past
Delayed cross-taxis: advection depending on other's density in the past (delayed chemotaxis, prey-taxis, or predator-taxis)

$$\mathbf{J}_1(x,t) = -D_1\nabla u_1(x,t) - u_1(x,t)[D_{11}\nabla u_1(x,t-\tau) + D_{12}\nabla u_2(x,t-\tau)],$$
$$\mathbf{J}_2(x,t) = -D_2\nabla u_2(x,t) - u_2(x,t)[D_{21}\nabla u_1(x,t-\tau) + D_{22}\nabla u_2(x,t-\tau)].$$

Two-species reaction-diffusion system with delayed self-taxis and cross-taxis:

$$\begin{cases} \dfrac{\partial u}{\partial t} = D_1\Delta u + D_{11}\nabla\cdot(u\nabla u_\tau) + D_{12}\nabla\cdot(u\nabla v_\tau) + f(u,v), & x\in\Omega,\ t>0,\\ \dfrac{\partial v}{\partial t} = D_2\Delta v + D_{21}\nabla\cdot(v\nabla u_\tau) + D_{22}\nabla\cdot(v\nabla v_\tau) + g(u,v), & x\in\Omega,\ t>0,\\ \dfrac{\partial u}{\partial \nu} = 0, \quad \dfrac{\partial v}{\partial \nu} = 0, & x\in\partial\Omega,\ t>0,\\ u(x,t) = \phi_1(x,t), \quad v(x,t) = \phi_2(x,t), & x\in\Omega,\ t\in[-\tau,0], \end{cases} \tag{8}$$

where $u_\tau = u(x,t-\tau)$, $v_\tau = v(x,t-\tau)$.

L-V competition model with memory-based movement

[Wang-Shi-Wang, 2021, JDE]

$$\begin{cases} u_t = D_1\Delta u + D_{11}\nabla\cdot(u\nabla u_\tau) + D_{12}\nabla\cdot(u\nabla v_\tau) + u(1-u-\alpha v), & x\in\partial\Omega,\ t>0,\\ v_t = D_2\Delta v + D_{21}\nabla\cdot(v\nabla u_\tau) + D_{22}\nabla\cdot(v\nabla v_\tau) + \gamma v(1-v-\beta u), & x\in\partial\Omega,\ t>0,\\ \partial_\nu u = \partial_\nu v = 0, & x\in\partial\Omega,\ t>0. \end{cases}$$

where $u_\tau = u(x,t-\tau)$, $v_\tau = v(x,t-\tau)$.

Theorem 9. Assume that $0<\alpha,\beta<1$, then there is a coexistence equilibrium $E^* = (u^*, v^*)$ where $u^* = \dfrac{1-\alpha}{1-\alpha\beta}$ and $v^* = \dfrac{1-\beta}{1-\alpha\beta}$.

1. (self-taxis) Suppose that $D_{12}=D_{21}=D_{22}=0$ and $D_{11}\neq 0$. Then (u^*,v^*) is locally asymptotically stable provided that $|D_{11}|u^* < D_1$, and it is unstable (with dim(unstable manifold)$=\infty$) if $|D_{11}|u^* > D_1$.
2. (cross-taxis) Suppose that $D_{11}=D_{22}=D_{21}=0$. If $D_{12}>0$, then (u^*,v^*) becomes unstable through steady state bifurcations when D_{12} increases (regardless of τ); and if $D_{12}<0$, then (u^*,v^*) may become unstable through Hopf bifurcations when τ increases.

Note: When $D_{11}=D_{22}=D_{21}=D_{12}=0$, the constant equilibrium $E^*=(u^*,v^*)$ is globally asymptotically stable. We cannot prove the global stability when (u^*,v^*) is locally asymptotically stable.

"Checkerboard" pattern for large memory-based self-taxis

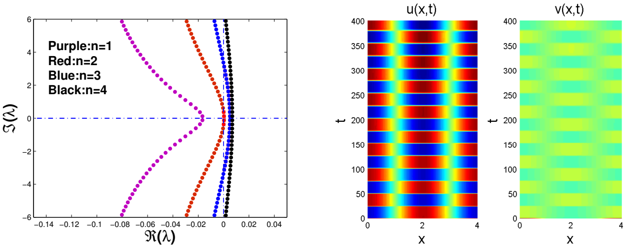


Figure: The roots of characteristic equations with $n = 1, 2, 3, 4$ (left), and "periodic" pattern (right). Here $D_1 = D_2 = 1$, $D_{12} = D_{21} = D_{22} = 0$, $\alpha = \beta = 0.5$, $\gamma = 1$, $r = 25$, and $D_{11} = 1.9 > 1/u^*$.

Scalar model with similar patterns: [Shi-Wang-Wang-Yan, 2020, JDDE]

Nonhomogeneous steady state with positive cross-taxis

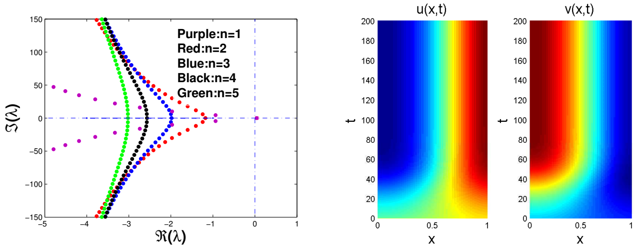


Figure: Left: The roots of characteristic equations with $n = 1, 2, 3, 4, 5$. Right: Convergence to a spatially nonhomogeneous steady state. Here $D_1 = 1$, $D_2 = 0.1$, $\alpha = \beta = 0.5$, $\gamma = 1$, $D_{11} = D_{22} = D_{21} = 0$, $D_{12} = 8.5 > 0$ and $r = 1$.

Similar pattern: [Mimura-Kawasaki, 1980, JMB] for cross-diffusion

Nonhomogeneous periodic solutions with negative memory-based cross-taxis

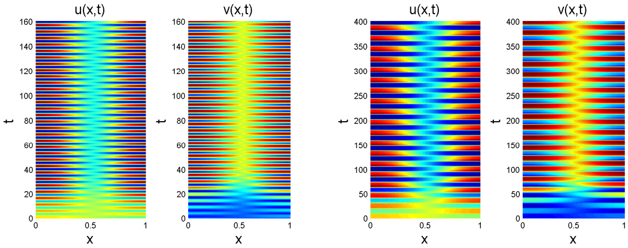


Figure: Periodic solutions for $r = 2.5 > r_1^0$ (left) and $r = 10$ (Right). Here $D_1 = 1$, $D_2 = 0.1$, $\alpha = \beta = 0.5$, $\gamma = 1$, $D_{11} = D_{22} = D_{21} = 0$ and $D_{12} = -12$.

Conclusions

- When the stage structure is added to the reaction-diffusion Lotka-Volterra competition system, times delays and maturation decays appear in the model. We show that the maturation decay terms could change the existence and stability of steady states which change the outcome of competition, but the time delays do not change asymptotic dynamics of the competition. Here the delays are "harmless" and do not induce oscillations as other delay models. When the two species are identical, the species with shorter maturation time wins the competition.
- Time delays in interspecific competitions will also not alter the outcome of the competition, but time delays in intraspecific competition may induce oscillatory patterns.
- For a competition model in the weak competition regime, if u is a timid competitor who will move downward the past (i.e., $D_{12} > 0$), then the constant coexistence steady state will become spatially inhomogeneous through Turing bifurcation, as the memory-based diffusion rate D_{12} increases; while if u is an aggressive competitor (i.e., $D_{12} < 0$), then Hopf bifurcation happens and a stable spatially nonhomogeneous time-periodic solution appears for the memory period τ at the right hand of a critical value.


Thank You!