Prey Taxis and Pattern Formation in a Predator-mediated Coexistence Model

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Talk Outline

1. Competing species, common predator dynamics
2. Taxis, prey-taxis (indirect and direct modeling)
3. Main model and existence result
4. Pattern formation: bifurcation of nontrivial steady states
5. Numerical simulation results
6. Conclusions from the study so far
7. More models and questions for the future

Competing species (u, v), common predator w

$$\begin{cases} \dot{u} = u(1 - u - a_1 v - b_1 w) \\ \dot{v} = v(r - a_2 u - rv - b_2 w) \\ \dot{w} = w(\mu - \epsilon w + c_2 u + c_2 v) \end{cases}$$

u, v subsystem $(\bar{u}_s, \bar{v}_s) = (\frac{r(1-a_1)}{r-a_1 a_2}, \frac{r-a_2}{r-a_1 a_2})$. Linearizing about $(\bar{u}_s, \bar{v}_s)$ $(u = \bar{u}_s + U, v = \bar{v}_s + V)$

$$\frac{d}{dt}\begin{bmatrix} U \\ V \end{bmatrix} = \begin{bmatrix} -\bar{u}_s & -a_1 \bar{u}_s \\ -a_2 \bar{v}_s & -r\bar{v}_s \end{bmatrix}\begin{bmatrix} U \\ V \end{bmatrix} = J_2 \begin{bmatrix} U \\ V \end{bmatrix}$$

Let $\begin{bmatrix} U \\ V \end{bmatrix} = e^{\lambda t}\vec{\Xi}$. Then $det(J_2 - \lambda \mathcal{I}) = \lambda^2 + a\lambda + b = 0$

$\Re(\lambda) < 0$ iff $a = -tr(J_2) > 0, b = det(J_2) > 0$

ODE competing species cases

- $a_1 < 1, a_2 < r$, then $(\bar{u}_s, \bar{v}_s)$ exists, and is stable;
- $a_1 > 1, a_2 > r$, then $(\bar{u}_s, \bar{v}_s)$ exists, and is unstable;
- $a_1 < 1, a_2 > r$, then $(\bar{u}_s, \bar{v}_s) \to (1, 0)$ as $t \to \infty$; that is, "u wins";
- $a_1 > 1, a_2 < r$, then $(\bar{u}_s, \bar{v}_s) \to (0, 1)$ as $t \to \infty$; that is, "v wins"

first case is coexistence; last two cases example of competitive exclusion principle

Three species ODE model ($c_j = b_j$)

We have the admissible set

$\mathcal{A} = \{(a_1, a_2, b_1, b_2, r, \epsilon, \mu) \in \mathbb{R}_+^6 \times \mathbb{R}\backslash\{0\} | \exists (u_s, v_s, w_s) \in \mathbb{R}_+^3, (u_s, v_s, w_s)$ is stable$\}$

Lemma

If $(a_1, a_2, b_1, b_2, r, \epsilon, \mu) \in \mathcal{A}$, then (u_s, v_s, w_s) is the globally stable positive coexistence solution to our (u, v, w) ODE system.

Haskell, Bell, 2019, DCDS, in process

(Scaled) diffusion model

Model:

$$u_t = d\triangle u + u(1 - u - a_1 v - b_1 w)$$

$$v_t = \eta d\triangle v + v(r(1 - v) - a_2 u - b_2 w)$$

$$w_t = \triangle w + w(\mu - \epsilon w + c_1 u + c_2 v)$$

on $\Omega \times (0, T)$, bounded $\Omega \subset \mathbb{R}^n$, smooth boundary, no-flux b.c.s, positive i.c.s

Example work: one predator, 2 competing prey

Feng '93, existence of semi-trivial and pos. steady states, Dirichlet b.c.s, super-/sub-solution technique

Caristi, et al '92, Neumann b.c.s, existence non-constant steady states, spatial-temporal oscillations-stable Hopf bifurcations

Taxis

Taxis (Gr. *to arrange*) originally Keller, Segel '70, aggregation of slime mould (chemotaxis); limit of directionally biased random walk

"The purpose of taxis range from the movement toward food, and avoidance of noxious substances, to large scale aggregations for survival". Othmer, Stevens '97

many types: aerotaxis, haptotaxis, phototaxis, chemotaxis, etc.

prey-taxis: active movement of consumers in regions of higher resource density. Here prey-taxis acts either as a repulsive mechanism, or an attractive mechanism, to predator population.

direct taxis: non-random portion of predator's motion due to prey gradient

indirect taxis: predator's motion affected by the gradient of a chemical originating from the prey population, or due to the presence of the prey population

Two competing species, 1 predator, with prey-taxis

Indirect taxis model

$$u_t = d\triangle u + u(1 - u - a_1 v - b_1 w)$$

$$v_t = \eta d\triangle v + v(r(1 - v) - a_2 u - b_2 w)$$

$$w_t = \nabla \cdot (\nabla w + \chi w \nabla z) + w(\mu - \epsilon w + c_1 u + c_2 v)$$

$$z_t = d_z \triangle z + \rho u - \delta z$$

or direct taxis model (with no-flux boundary conditions)

$$\begin{aligned} u_t &= d\triangle u + u(1 - u - a_1 v - b_1 w) \quad \text{on } \Omega \times (0, T) \\ v_t &= \eta d\triangle v + v(r(1 - v) - a_2 u - b_2 w) \\ w_t &= \nabla \cdot (\nabla w + \chi w \nabla u) + w(\mu - \epsilon w + c_1 u + c_2 v) \end{aligned} \tag{1}$$

Note: generalist foragers

Global existence in 1D

$p > n \geq 1$; $W^{1,p}(\Omega, \mathbb{R}^n)$ is continuously embedded in $C(\Omega, \mathbb{R}^n)$.

$X \doteq \{y \in W^{1,p}(\Omega, \mathbb{R}^3) \mid \nu \cdot \nabla y_{|\partial\Omega} = 0\}$

Theorem

Suppose $(u_0, v_0, w_0) \in X$. *Then*

(i) *there exists a* $T = T_{max} \in (0, \infty]$, *depending on the initial conditions* (u_0, v_0, w_0), *such that problem (1) has a unique maximal classical solution* (u, v, w) *on* $\Omega \times [0, T_{max})$ *satisfying* $(u(\cdot, t), v(\cdot, t), w(\cdot, t)) \in C((0, T_{max}), X)$ *and* $(u, v, w) \in C^{2,1}((0, T_{max}) \times \overline{\Omega}, \mathbb{R}^3)$;

(ii) *if* $u_0, v_0, w_0 \geq 0$ *on* $\overline{\Omega}$, *then* $u, v, w \geq 0$ *on* $\Omega \times [0, T_{max})$;

(iii) *if* $||(u, v, w)(\cdot, t))||_{L^\infty(\Omega)}$ *is bounded for all* $t \in [0, T_{max})$, *then* $T_{max} = +\infty$; *that is,* (u, v, w) *is a global solution in time .*

Comment on existence

$z = (u, v, w)^T$; $z_t = \nabla \cdot (A(z)\nabla z) + F(z)$, where

$$A(z) = \begin{bmatrix} d & 0 & 0 \\ 0 & \eta d & 0 \\ \chi w & 0 & 1 \end{bmatrix}$$

positive eigenvalues, so normally parabolic

local theory (i) due to Amann ’90, ’93

for global theory (iii): energy arguments, Young, GLN inequalities, Moser-Alikakos iteration (Haskell, Bell, ’19)

Pattern formation

Linearize about constant steady state (u_s, v_s, w_s):

$$\frac{\partial}{\partial t}\begin{bmatrix} U \\ V \\ W \end{bmatrix} = \begin{bmatrix} d & 0 & 0 \\ 0 & \eta d & 0 \\ \chi w_s & 0 & 1 \end{bmatrix} \triangle \begin{bmatrix} U \\ V \\ W \end{bmatrix} + \begin{bmatrix} -u_s & -a_1 u_s & -b_1 u_s \\ -a_2 v_s & -r v_s & -b_2 v_s \\ b_1 w_s & b_2 w_s & -\epsilon w_s \end{bmatrix} \begin{bmatrix} U \\ V \\ W \end{bmatrix}$$

$(U, V, W)^T = e^{\lambda t + i\vec{k}\cdot\vec{x}}\Xi$, $k = |\vec{k}| \rightarrow$ Jacobian $J_k \rightarrow$ dispersion relation

$$det(J_k) = \lambda^3 + a(k^2)\lambda^2 + b(k^2, \chi)\lambda + c(k^2, \chi) = 0$$

(u_s, v_s, w_s) is stable iff $\Re(\lambda) < 0$ iff $a > 0, c > 0, ab - c > 0$

(u_s, v_s, w_s) is unstable if either $c < 0$ or $ab - c < 0$

Global stability of the coexistence state

$(0,0,0)$ is a lower solution to system (1)

Having L^∞ norms on u, v, w being bounded, we have a constant upper solution

$$\mathcal{H} \doteq \{(u,v,w) \in \mathbb{R}^3 \mid 0 \le u, v \le 1, 0 \le w \le M\}$$

is positive, invariant set

By a Lyopunov method we have

Theorem

Assume $(u_0, v_0, w_0) \in \mathcal{H}$. *If* $r > (a_1 + a_2)^2/4, \chi^2 < 4du_s/w_s$ *hold, then* (u_s, v_s, w_s) *is globally asymptotically stable.*

Bifurcation result

$\exists\ \chi_c(k^2) > 0$ s.t. $c < 0$ iff $\chi > \chi_c(k^2)$

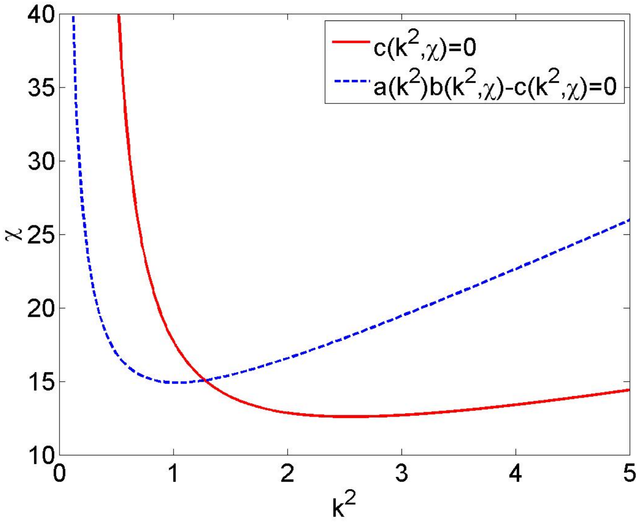
$\exists\ \chi_h(k^2) > 0$ s.t. $ab - c < 0$ iff $\chi > \chi_h(k^2)$

$\chi > \chi_0 \doteq \min_{k>0}\{\chi_c(k^2), \chi_h(k^2)\}$ does not guarantee pattern formation since Ω is bounded (wave numbers are discrete). For $\Omega = (0, L)$

Theorem

Assume $(a_1, a_2, b_1, b_2, r, \epsilon, \mu) \in \mathcal{A}$. *When* $\chi = 0$, (u_s, v_s, w_s) *is locally stable. Let* $\chi_m > \chi_c$ *be the first value of* χ *s.t. either* $k_1 L/\pi$ *or* $k_2 L/\pi$ *is an integer. Then* χ_m *is a bifurcation number and* $\chi > \chi_m$ *is a nec. and suff. condition for pattern formation of system (1).*

χ versus k^2



Dispersion relation

$\lambda^3 + a(k^2)\lambda^2 + b(k^2,\chi)\lambda + c(k^2,\chi) = 0$, with $a(k^2) > 0$

$\chi = \chi_c(k^2)$ iff $c = 0 \to \lambda(\lambda^2 + a\lambda + b) = 0 \to$
$\lambda = 0, \frac{1}{2}(-a \pm \sqrt{a^2 - 4b})$

for real negative evs, need $0 < b(k^2, \chi_c(k^2)) < a^2(k^2)/4$

$\chi = \chi_h(k^2)$ iff $ab - c = 0 \to (\lambda + a)(\lambda^2 + b) = 0 \to$
$\lambda = -a < 0, \pm\sqrt{-b} = \pm i\sqrt{b(k^2, \chi_h(k^2))}$

For a possible Hopf bifurcation, $b(k^2, \chi_h(k^2)) > 0$. With $\chi_0 \doteq \min_{k>0}\{\chi_c(k^2), \chi_h(k^2)\}$, then (u_s, v_s, w_s) is linearly asymptotically stable if $\chi < \chi_0$, and unstable if $\chi > \chi_0$.

Numerical simulation

1. Mainly used Discontinuous Galerkin method on 1D space domain using FEniCS software platform.
2. Initial simulations checked against a finite difference method and a continuous FEM program.
3. Search method for parameters in $\mathcal{A}$ but no systematic parameter sensitivity analysis done.
4. Initial conditions $u_0 = u_s + \varepsilon \sin(\frac{n\pi x}{L} + \phi)$, $\varepsilon = 10\%$ of u_s, $n = 1, 2$ usually, ϕ random.

Case 1: u "wins"

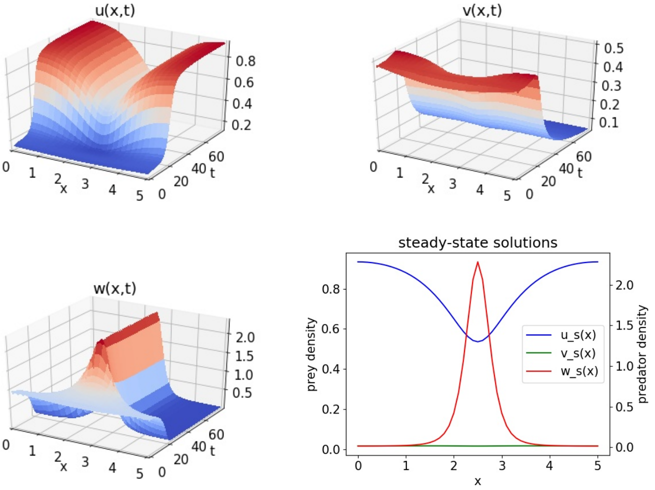


Figure: $(u_s, v_s, w_s) = (0.15, 0.48, 0.97)$

Case 2: v “wins”

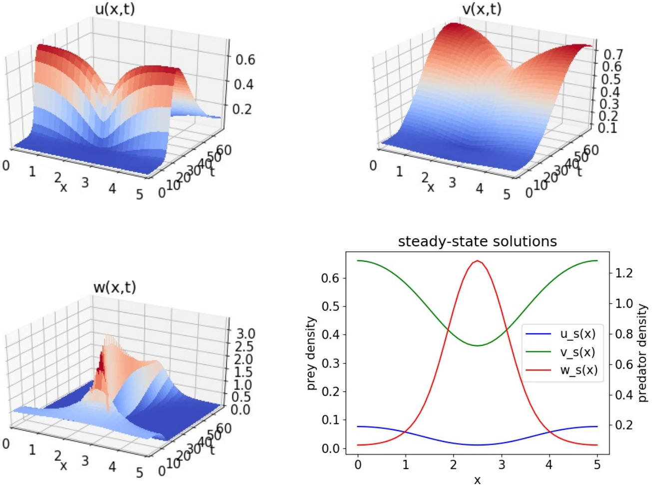
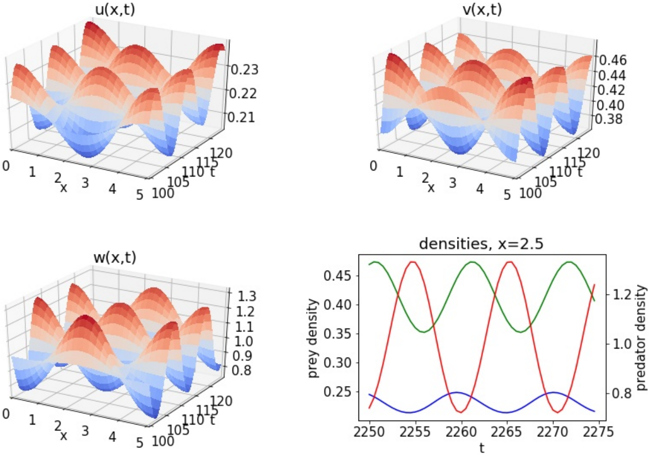


Figure: $(u_s, v_s, w_s) = (0.02, 0.10, 0.63)$

Case 3 (v wins): spatial temporal patterns



Some Conclusions

1. First work incorporating prey-taxis for single competing prey in a predator-prey environment. Taxis “breaks” symmetry of species behavior
2. Strong (repulsive) prey taxis can destabilize homogeneous coexistence steady state and foster spatial-temporal patterns. But the strong mechanism associated with the stronger competitor can thwart coexistence
3. When weaker competitor has defense mechanism, predator-mediated coexistence arises between competing prey. They also provide defense for stronger competitor in sense prey species coexist out of phase from predator population
4. Thwarting predator-mediated coexistence does not appear to occur for case of (attractive, i.e. $\chi < 0$) prey-taxis

Generalized model

$$u_t = d_1 \triangle u + f(u,v,w) \qquad \text{in } \Omega \times (0,T)$$

$$v_t = d_2 \triangle v + g(u,,w)$$

$$w_t = \nabla \cdot (d_3 \nabla w + \chi \phi(u,w) \nabla u + \xi \theta(v,w) \nabla v) + h(u,v,w)$$

no-flux b.c.s, non-negative i.c.s u_0, v_0, w_0, where

A_1: $\exists$ pos. coexistence constant steady state (u_s, v_s, w_s): $\hat{f} \doteq f(u_s, v_s, w_s) = 0 = \hat{g} = \hat{h}$

A_2: $\hat{f}_u, \hat{g}_v, \hat{h}_w < 0$ (limited carrying capacity)

A_3: $\hat{f}_v, \hat{f}_w, \hat{g}_u, \hat{g}_w < 0$, $\hat{h}_u, \hat{h}_v > 0$ (2 competing prey, 1 pred.)

Pattern formation and omnivory

Trophic level: comprised of organisms in food chain that share the same nutritional relationship to primary sources of energy

An omnivore is an organism that feeds on two or more trophic levels

Example:

$$u_t = d_1 \triangle u + u(1 - u/K - a_1 v - b_1 w)$$

$$v_t = \nabla \cdot (d_2 \nabla v - \chi v \nabla u) + v(r(1 - v) + a_2 u - b_2 w)$$

$$w_t = \nabla \cdot (d_3 \nabla w - \xi w \nabla v) + w(r_1(1 - w/K_w) + e_1 b_1 u + e_2 b_2 v)$$

Omnivory if $b_1 > 0$, pure food chain if $b_1 = 0$. Pattern differences?

Other project ideas

- Worm-bacteria modeling (both attractive & toxic chemotaxis)
- Dinoflagellate-copepod-shrimp modeling (bioluminescence 'defense' mechanism)
- Predacious mite, spider mite modeling (indirect source taxis)
- Population level pursuit-evasion modeling (both have biased mobility)
- Predator-prey modeling with both direct and indirect taxis
- Age model (predator changes diet with age)
- Classifying patterns in food webs

Thank you for your attention

Figure: AfterMath, my (cruising) home