Qualitative studies of Lotka-Volterra competition system with advection

Qi Wang

Department of Applied Mathematics
Southwestern University of Finance and Economics
Chengdu, Sichuan

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Outline

Population dynamics of single species

- $u(t)$: total population at time t

Logistic growth: $u'(t) = u(a - bu)$, $u(0) = u_0 > 0$.

- a: carrying capacity
- b: crowing effect
- $u(t) \to \frac{a}{b}$ exponentially as $t \to \infty$

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Population growth model: $u'(t) = f(u, t)u$, $u(0) = u_0 > 0$.

Population dynamics of two competing species

$u(t)$: total population of focal species at time t
$v(t)$: total population of competing species at time t

$$\begin{cases} u_t = f(u,v), \ t > 0, \\ v_t = g(u,v), \ t > 0, \end{cases}$$

- f, g: growth rate

Population dynamics of two competing species

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- f, g: growth rate

Competition relationship (inter-specific competition)

- f: decreasing in v
- g: decreasing in u

Crowing effect (intra-specific competition)

- f: increasing in u for small u, decreasing for large u
- g: increasing in v for small v, decreasing for large v

Lotka-Volterra Competition model

$$\begin{cases} u_t = (a_1 - b_1 u - c_1 v)u, & t > 0, \\ v_t = (a_2 - b_2 u - c_2 v)v, & t > 0, \end{cases}$$

- $a_1, a_2 > 0$: carrying capacity
- $b_1, c_2 > 0$: intra-specific competition rate
- $b_2, c_1 > 0$: inter-specific competition rate

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Four equilibria

- $(0,0), (\frac{a_1}{b_1}, 0), (0, \frac{a_2}{c_2})$ and $(\bar{u}, \bar{v}) = \left(\frac{a_1 c_2 - a_2 c_1}{b_1 c_2 - b_2 c_1}, \frac{a_2 b_1 - a_1 b_2}{b_1 c_2 - b_2 c_1}\right)$

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$(\bar{u}, \bar{v})$ is positive if and only if one of the followings

- $\frac{c_1}{c_2} < \frac{a_1}{a_2} < \frac{b_1}{b_2}$:
- $\frac{b_1}{b_2} < \frac{a_1}{a_2} < \frac{c_1}{c_2}$:

Lotka-Volterra Competition model

$$\begin{cases} u_t = (a_1 - b_1 u - c_1 v)u, & t > 0, \\ v_t = (a_2 - b_2 u - c_2 v)v, & t > 0, \end{cases}$$

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Four equilibria

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$(\bar{u}, \bar{v})$ is positive if and only if one of the followings

- $\frac{c_1}{c_2} < \frac{a_1}{a_2} < \frac{b_1}{b_2}$: weak competition
- $\frac{b_1}{b_2} < \frac{a_1}{a_2} < \frac{c_1}{c_2}$: strong competition

Lotka-Volterra competition model with species dispersals

- Ω: bounded domain in $\mathbb{R}^N$, $N \geq 1$
- $u(x,t)$: population density at space-time location (x,t)
- $v(x,t)$: population density at space-time location (x,t)

Diffusive Lotka-Volterra Competition model

$$\begin{cases} u_t = D_1 \Delta u + (a_1 - b_1 u - c_1 v)u, & x \in \Omega,\ t > 0, \\ v_t = D_2 \Delta v + (a_2 - b_2 u - c_2 v)v, & x \in \Omega,\ t > 0, \\ \frac{\partial u}{\partial \mathbf{n}} = \frac{\partial v}{\partial \mathbf{n}} = 0, & x \in \partial\Omega,\ t > 0, \\ u(x,0) = u_0(x) \geq 0,\ v(x,0) = v_0(x) \geq 0, & x \in \Omega. \end{cases}$$

- Species disperse within an enclosed habitat (NBC)
- D_1, D_2: species dispersal rate (positive)
- No population pressure from inter-species (random dispersal)

Lotka-Volterra competition model with species dispersals

Diffusive Lotka-Volterra Competition model

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Large diffusion rates:

- **P. de Mottoni, F. Rothe**, 1979: No nonconstant steady states if both D_1 and D_2 are large;
- **J. Smoller**, 1984: Behave like the ODEs if both D_1 and D_2 are large;
- **Y. Lou, W.-M. Ni**, 1996: No nonconstant steady state if one of D_1 and D_2 is large;

Effect of diffusion rates

Weak competition case: completely understood

- (**E. Conway, D. Hoff, J. Smoller**, 1978; **P.De Mottoni**, 1979): In the weak competition case, $(\bar{u}, \bar{v})$ is asymptotically stable in the sense that for any solution $(u(x,t), v(x,t))$

$$\lim t \to \infty \|(u(\cdot,t), v(\cdot,t)) - (\bar{u}, \bar{v}))\|_\infty \leq Ce^{\mu t},$$

- $C > 0$: regardless of the initial conditions and the size of D_1 and D_2
- μ: principal eigenvalue of Neumann Laplacian

Effect of diffusion rates

Strong competition case: complicated with interesting phenomena

- **Kishimoto**, 1981: No nonconstant stable steady states, if is a rectangular parallelepiped in $\mathbb{R}^N$, $N \geq 1$.
- **Kishimoto, Weinberger**, 1985: No nonconstant stable steady states, if Ω is a convex domain in $\mathbb{R}^N$, $N \geq 1$.
- **Matano, Mimura**, 1983: Nonconstant positive steady state, if Ω is of dumbbell shape, with D_1 and D_2 being taken properly.
- **M. Mimura, S. Ei, Q. Fang**, 1991: Nonconstant positive steady state, if Ω is of dumbbell shape with a very narrow bar.
- **Y. Kan-on, E. Yanagida**, 1993: Nonconstant positive steady state, if the curvature of the boundary and the diffusion rates D_1 and D_2 are properly balanced.

System with advected species dispersal

In summary

- Introduction of diffusions into the Lotka-Volterra ODE competition model will not induce nonconstant steady states in almost all cases, at least when Ω is convex.
- Not entirely realistic to assume that species moves randomly
- Dispersal pressure from inter- and intra-species

$$\begin{cases} u_t = \nabla \cdot (D_1 \nabla u + \chi_1 \Phi_1(u,v) \nabla v) + f(u,v), & x \in \Omega,\ t > 0, \\ v_t = \nabla \cdot (D_2 \nabla v + \chi_2 \Phi_2(u,v) \nabla u) + g(u,v), & x \in \Omega,\ t > 0, \\ u(x,0) = u_0(x) \geq 0,\ v(x,0) = v_0(x) \geq 0, & x \in \Omega, \end{cases}$$

- f, g: Lotka-Volterra dynamics
- χ_1, χ_2: constant

System with advected species dispersal

$$\begin{cases} u_t = \nabla \cdot (D_1 \nabla u + \chi u \phi(v) \nabla v) + (a_1 - b_1 u - c_1 v) u, \\ \tau v_t = D_2 \Delta v + (a_2 - b_2 u - c_2 v) v, \\ \frac{\partial u}{\partial \mathbf{n}} = \frac{\partial v}{\partial \mathbf{n}} = 0, \\ u(x,0) = u_0(x) \geq 0, \ v(x,0) = v_0(x) \geq 0, \end{cases} \tag{1}$$

- Global existence
- Nonconstant steady states
- Transition-layered steady states
- Segregation phenomenon

Derivation of advective Lotka-Volterra competition model

$$\begin{cases} u_t = \nabla \cdot (D_1 \nabla u + \chi_1 \Phi_1(u,v) \nabla v) + f(u,v), & x \in \Omega,\ t > 0, \\ v_t = \nabla \cdot (D_2 \nabla v + \chi_2 \Phi_2(u,v) \nabla u) + g(u,v), & x \in \Omega,\ t > 0, \\ u(x,0) = u_0(x) \geq 0,\ v(x,0) = v_0(x) \geq 0, & x \in \Omega, \end{cases}$$

Conservation of total population of species u leads to the transport equation

$$u_t = -\nabla \cdot \mathbf{J} + f, \tag{2}$$

- $\mathbf{J}$: the total population flux
- f: the birth-death rate of the species

Derivation of advective Lotka-Volterra competition model

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- $\mathbf{J}$: the total population flux
- f: the birth-death rate of the species
- $\mathbf{J}$: superposition of the diffusion flux $\mathbf{J}_{\text{diffusion}}$ from random walks and the competition flux $\mathbf{J}_{\text{competition}}$ due to the interspecific population pressure

Derivation of advective Lotka-Volterra competition model

Total flux

- $\mathbf{J}$=$\mathbf{J}_{\text{diffusion}} + \mathbf{J}_{\text{competition}}$
- $\mathbf{J}_{\text{diffusion}} = -D_2 \nabla u$: Fick's law
- $\mathbf{J}_{\text{competition}} = -\chi_1 \Phi_1(u, v) \nabla v$: density dependent competition flux

Derivation of advective Lotka-Volterra competition model

Total flux

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$\chi_1 > 0$ if u escapes the habitat of v and $\chi_1 < 0$ if u invades the habitat of v

$$u_t = \nabla \cdot (D_1 \nabla u + \chi_1 \Phi_1(u, v) \nabla v) + f(u, v)$$

- Keller-Segel Chemotaxis model

SKT Lotka-Volterra competition model

Shigesada, Kawasaki and Teramoto proposed the following system in 1979

$$\begin{cases} u_t = \Delta[(D_1 + \rho_{11}u + \rho_{12}v)u] + (a_1 - b_1u - c_1v)u, & x \in \Omega,\ t > 0, \\ v_t = \Delta[(D_2 + \rho_{21}u + \rho_{22}v)v] + (a_2 - b_2u - c_2v)v, & x \in \Omega,\ t > 0, \\ \frac{\partial u}{\partial \mathbf{n}} = \frac{\partial v}{\partial \mathbf{n}} = 0, & x \in \partial\Omega,\ t > 0, \\ u(x,0) = u_0(x) \geq 0,\ v(x,0) = v_0(x) \geq 0, & x \in \Omega, \end{cases}$$

where $\rho_{i,j}$, $i, j = 1, 2$, are nonnegative constants.

- ρ_{11}, ρ_{22}: *self-diffusions*, the dispersal pressures due to the presence of conspecifics
- ρ_{12}, ρ_{21}: *cross-diffusions*, the dispersal pressures from the interspecific competitors.

SKT Lotka-Volterra competition model

Written into

$$\begin{cases} u_t = \nabla \cdot [(D_1 + 2\rho_{11} u + \rho_{12} v)\nabla u + \rho_{12} u \nabla v] + f(u,v), & x \in \Omega,\ t > \\ v_t = \nabla \cdot [(D_2 + \rho_{21} u + 2\rho_{22} v)\nabla v + \rho_{21} v \nabla u] + g(u,v), & x \in \Omega,\ t > \\ \frac{\partial u}{\partial \mathbf{n}} = \frac{\partial v}{\partial \mathbf{n}} = 0, & x \in \partial\Omega,\ t \\ u(x,0) = u_0(x) \geq 0,\ v(x,0) = v_0(x) \geq 0, & x \in \Omega. \end{cases}$$

- invading if $\rho_{12}, \rho_{21} < 0$
- negative diffusion rate
- systematic approach

Global existence and boundedness

$$\begin{cases} u_t = \nabla \cdot (D_1 \nabla u + \chi u \phi(v) \nabla v) + (a_1 - b_1 u - c_1 v) u, \\ \tau v_t = D_2 \Delta v + (a_2 - b_2 u - c_2 v) v, \\ \frac{\partial u}{\partial \mathbf{n}} = \frac{\partial v}{\partial \mathbf{n}} = 0, \\ u(x,0) = u_0(x) \geq 0, \ v(x,0) = v_0(x) \geq 0, \end{cases} \tag{3}$$

Theorem

Existence of uniformly bounded classical solutions

- *C, Gai, W, J. Yan, 2014: 1D; 2D if $\tau = 0$ and $\frac{b_1 D_2}{b_2 \chi}$ is large*
- *W, (preprint): 2D; ND, $N \geq 3$ $\phi(v)$ decays super-linearly*
- *Blow-up or global existence when N is large: Open problem*

Steady states in 1D

$$\begin{cases} (D_1 u' + \chi u \phi(v) v')' + (a_1 - b_1 u - c_1 v) u = 0, & x \in (0, L), \\ D_2 v'' + (a_2 - b_2 u - c_2 v) v = 0, & x \in (0, L), \\ u'(x) = v'(x) = 0, & x = 0, L. \end{cases} \tag{4}$$

1. Nonconstant positive steady states
2. Stability of the nonconstant positive solutions
3. Striking structures: Segregation phenomenon

Stability analysis of homogeneous equilibrium

$$\begin{cases} u_t = (D_1 u' + \chi u \phi(v) v')' + (a_1 - b_1 u - c_1 v)u, & x \in (0, L), t > 0, \\ v_t = D_2 v'' + (a_2 - b_2 u - c_2 v)v, & x \in (0, L), t > 0, \\ u(x, 0) = u_0(x), \ v(x, 0) = v_0(x), & x \in (0, L), \\ u'(x) = v'(x) = 0, & x = 0, L, t > 0. \end{cases}$$

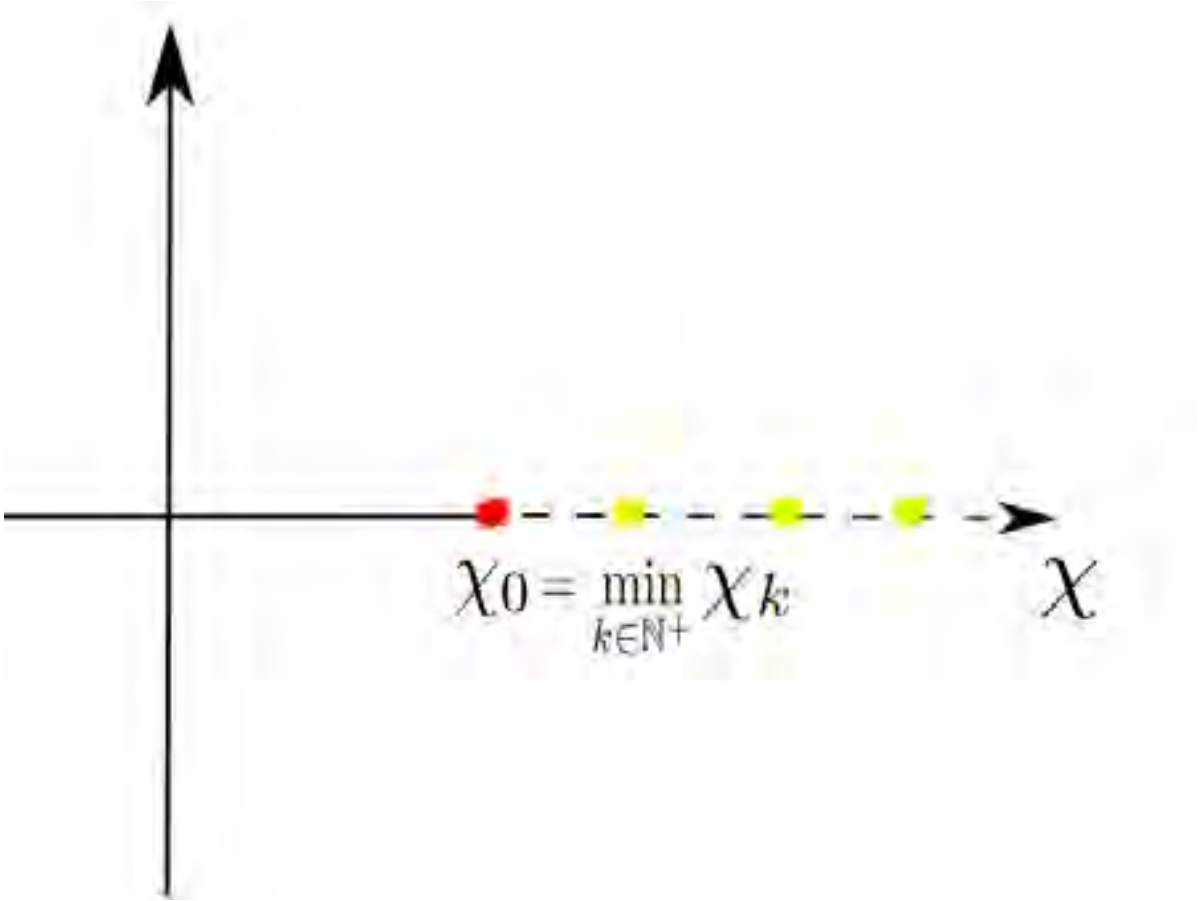
Theorem

$(\bar{u}, \bar{v})$ is unstable if

$$\chi > \chi_0 = \min_{k \in \mathbb{N}^+} \frac{\left(D_1 (\frac{k\pi}{L})^2 + b_1 \bar{u}\right)\left(D_2 (\frac{k\pi}{L})^2 + c_2 \bar{v}\right) - b_2 c_1 \bar{u}\bar{v}}{b_2 (\frac{k\pi}{L})^2 \phi(\bar{v}) \bar{u}\bar{v}}.$$

- *Holds in $\mathbb{R}^N$, $N \geq 2$ if replacing $(\frac{k\pi}{L})^2$ by k-th Laplacian eigenvalue*

Stability analysis of homogeneous equilibrium



Existence of nonconstant positive steady states

Crandall-Rabinowitz bifurcation theory.

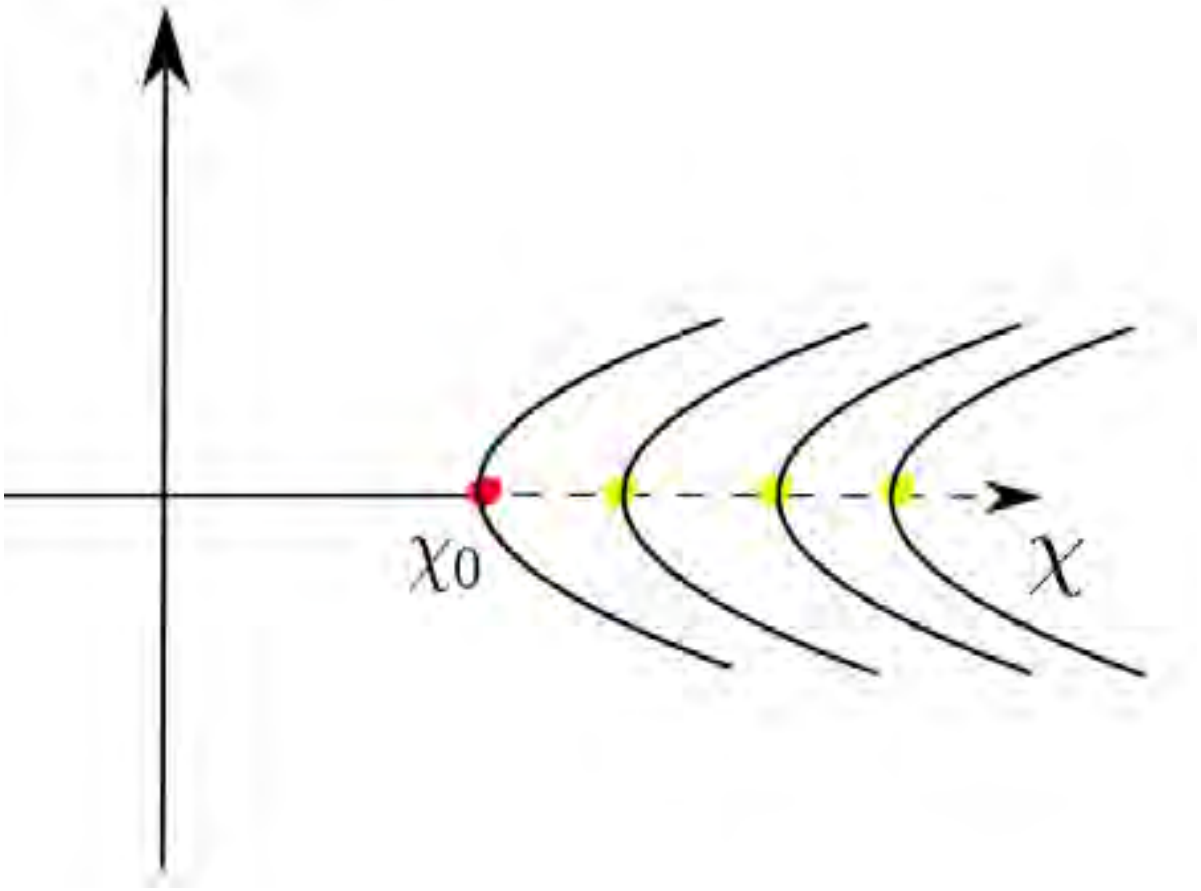
Theorem

Denote $\chi_k = \frac{\left(D_1(\frac{k\pi}{L})^2+b_1\bar{u}\right)\left(D_2(\frac{k\pi}{L})^2+c_2\bar{v}\right)-b_2c_1\bar{u}\bar{v}}{b_2(\frac{k\pi}{L})^2\phi(\bar{v})\bar{u}\bar{v}}$*, and assume that* $\chi_i \neq \chi_j$, $\forall i \neq j \in \mathbb{N}^+$*. Then Bifurcation occurs at* $(\bar{u}, \bar{v}, \chi_k)$ *for each* $k \in \mathbb{N}^+$*, hence there exists nonconstant positive steady state* $(u_k(s,x), v_k(s,x), \chi_k(s))$ *around* $(\bar{u}, \bar{v}, \chi_k)$ *such that,*

$$\begin{cases} \chi_k(s) = \chi_k + O(s), \\ (u_k(s,x), v_k(s,x)) = (\bar{u}, \bar{v}) + s(Q_k, 1)\cos\frac{k\pi x}{L} + o(s) \end{cases}$$

with $Q_k = -\frac{D_2(\frac{k\pi}{L})^2+c_2\bar{v}}{b_2\bar{v}}$*; moreover, all nontrivial steady states near the bifurcation point* $(\bar{u}, \bar{v}, \chi_k)$ *must stay on the curve* $\Gamma_k(s) = (u_k(s), v_k(s), \chi_k(s))$*,* $s \in (-\delta, \delta)$*.*

Existence of nonconstant positive steady states



Stability of bifurcating steady states

Theorem

Suppose that $\chi_{k_0} = \min_{k\in\mathbb{N}^+} \chi_k$*, then*
(i). $(u_k(s,x), v_k(s,x))$*,* $s \in (-\delta, \delta)$*, is unstable around* $(\bar{u}, \bar{v}, \chi_k)$ *for all positive integers* $k \neq k_0$*;*
(ii). $\chi'_{k_0}(0) = 0$*;* $(u_{k_0}(s,x), v_{k_0}(s,x))$ *is stable* $(\bar{u}, \bar{v}, \chi_{k_0})$ *if* $\chi''_{k_0}(0) > 0$ *and is unstable if* $\chi''_{k_0}(0) < 0$*.*

Stability of bifurcating steady states

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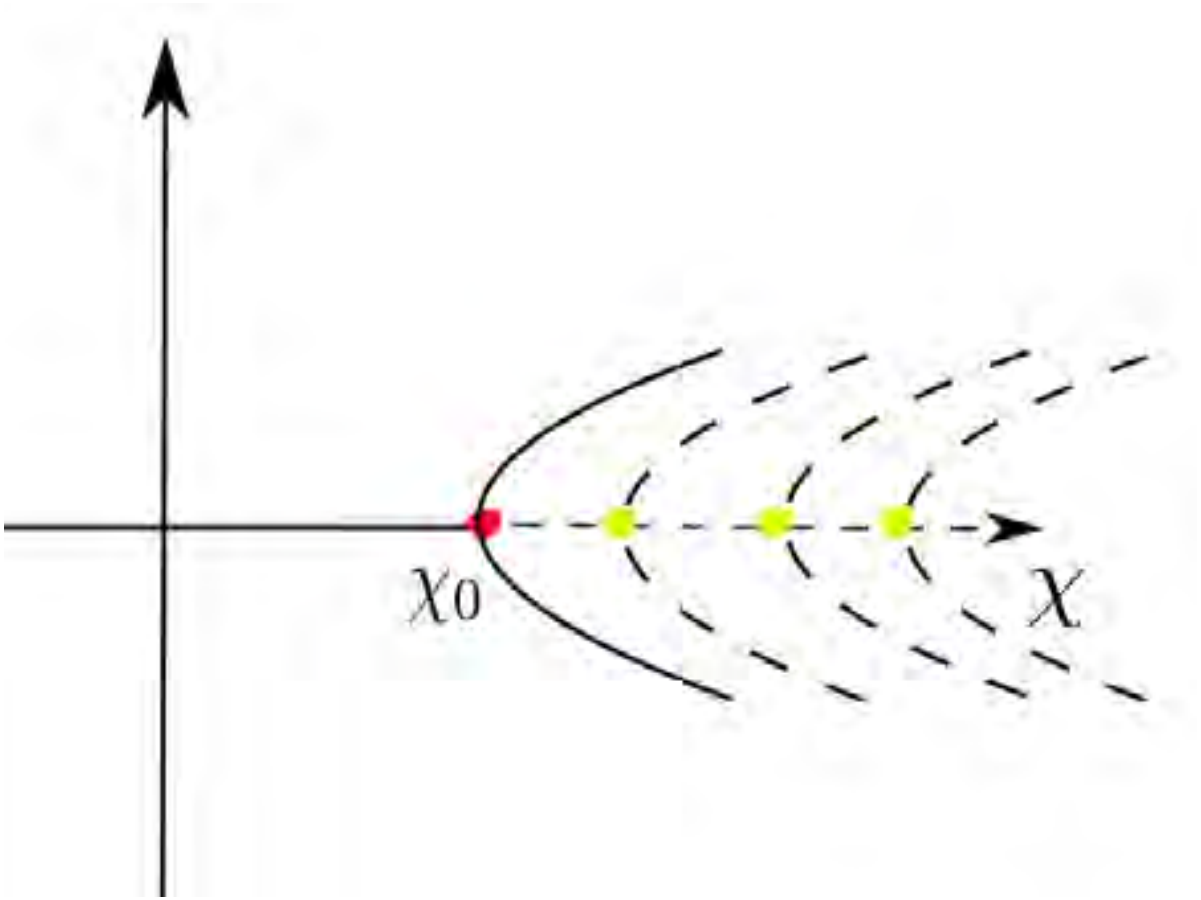
- pitch-fork bifurcation
- turning direction: stability
- local bifurcation

Stability of bifurcating steady states



Wavemode selection mechanism

- $(\bar{u}, \bar{v})$ loses its stability to $(Q_{k_0}, 1)\cos\frac{k_0\pi x}{L}$ as χ surpasses $\chi_0 = \min_{k\in\mathbb{N}^+}\chi_k$
- $\chi_k \approx \frac{D_1 D_2(\frac{k\pi}{L})^2}{b_2\phi(\bar{v})\bar{u}\bar{v}}$, $k_0 = 1$ if L is small
- k_0 increases if L increases
- small domain only supports monotone stable solutions, while large domain supports non-monotone stable solutions.

Wavemode selection mechanism

Domain size L	3	5	7	9	11
k_0	1	2	2	3	3
χ_k	9.9418	10.392	9.9120	9.9418	9.9647
Domain size L	13	15	17	19	21
k_0	4	5	5	6	6
χ_k	9.8872	9.9418	9.8937	9.8956	9.9120

Table: Stable wavemode numbers and their bifurcation values. $D_1 = 1, D_2 = 0.1, a_1 = a_2 = 0.5, b_1 = 2, b_2 = 1$ and $c_1 = 0.5, c_2 = 1$. We see that larger domains support bigger wavemode number.

Wavemode selection mechanism

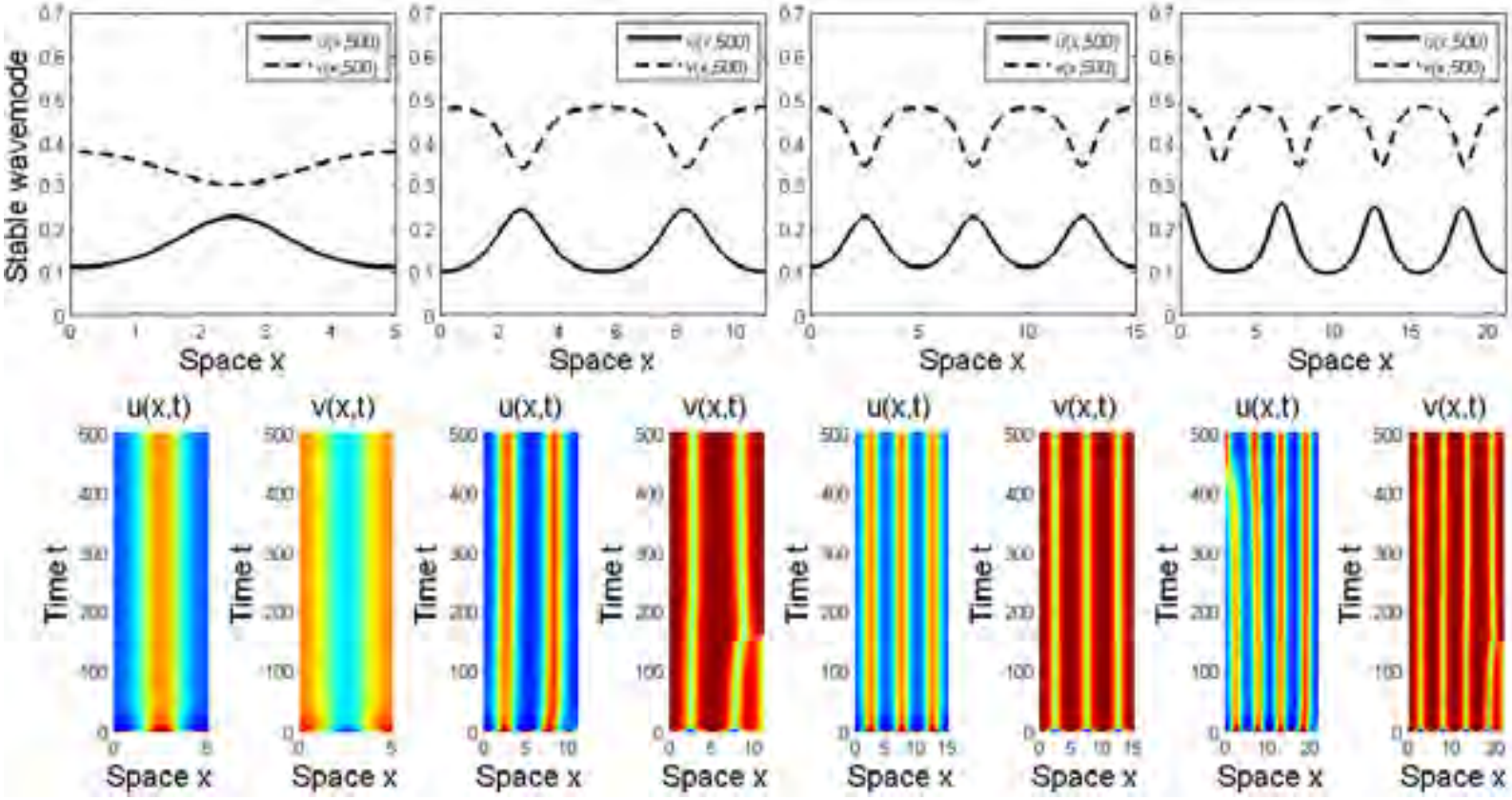


Figure: Stable wave mode in the form of cos $\frac{k_0 \pi x}{L}$, where k_0 is given in Table 1. χ is chosen to be slightly larger than χ_0 and the rest system parameters are chosen to be the same as in Table 1. Initial data are small perturbations of $(\bar{u}, \bar{v})$.

Wavemode selection mechanism

- $\Omega = (0, L) \times (0, L)$, the wavemode is $\cos \frac{m\pi x}{L} \cos \frac{n\pi y}{L}$

Domain size L	1	3	5	7
(m_0, n_0)	(1,1)	(1,1)	(1,1)	(1,2), (2,1)
$\chi_{m_0 n_0}$	42.2066	11.2318	9.9210	9.9022
Domain size L	11	13	15	17
(m_0, n_0)	(1,4), (4,1)	(2,4), (4,2)	(1,5), (5,1)	(3,5), (5,3)
$\chi_{m_0 n_0}$	9.8979	9.8889	9.8876	9.8869

Table: List of bifurcation values χ_{mn} over $\Omega = (0, L) \times (0, L)$ for different values of L. System parameters are chosen to be $D_1 = 1, D_2 = 0.1, a_1 = a_2 = 0.5, b_1 = 2, b_2 = 1, c_1 = 0.5, c_2 = 1$

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Wavemode selection mechanism

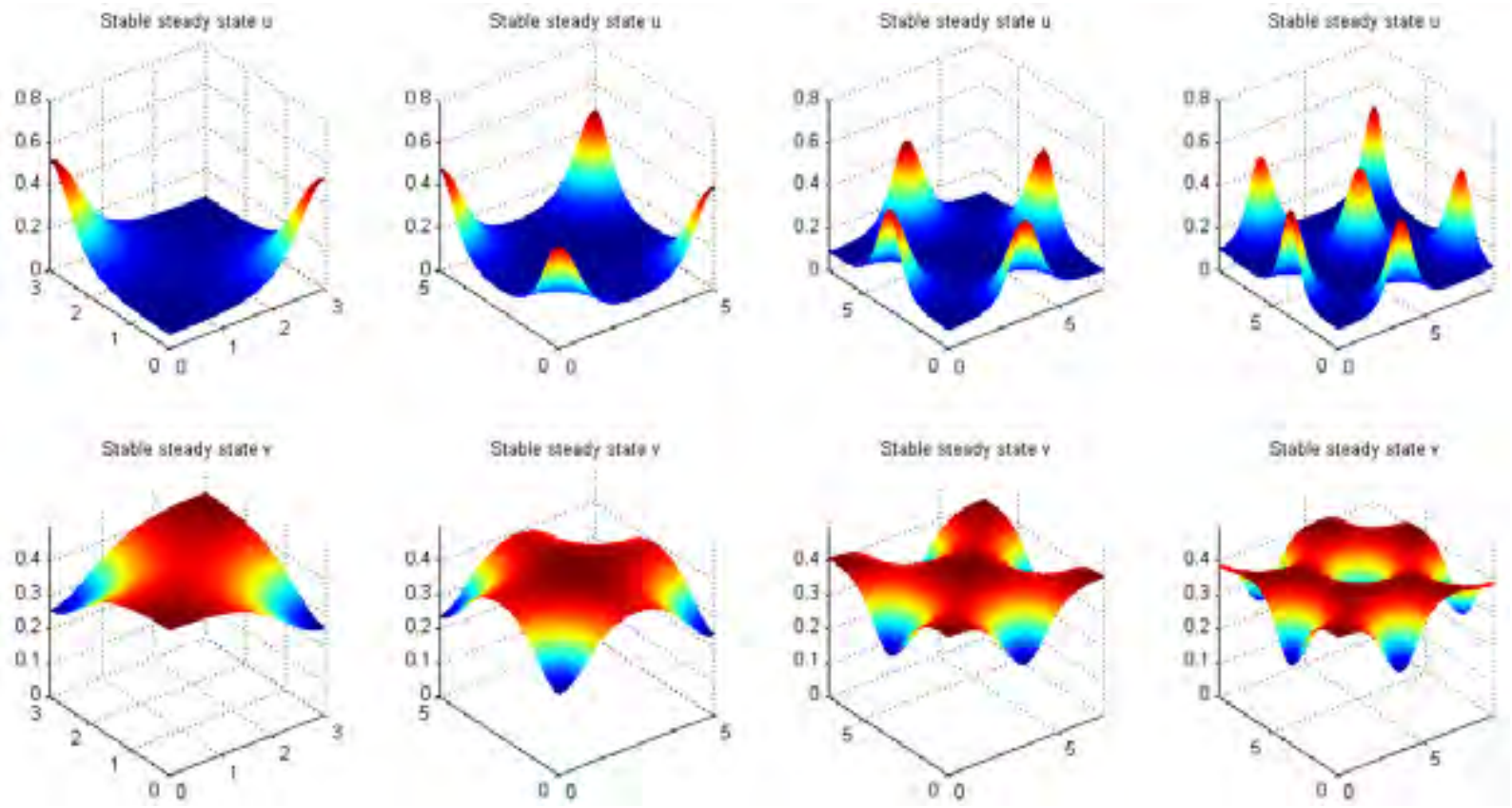

Figure: Stable patterns of u and v corresponding to the stable wavemode $\cos\frac{m_0\pi x}{L}\cos\frac{n_0\pi y}{L}$. System parameters are chosen to be the same as in Table 2 and χ is slightly larger than $\chi_{m_0 n_0}$. Initial data are small perturbations of $(\bar{u}, \bar{v})$.

Transition-layer solutions

$$\begin{cases} (D_1 u' + \chi u \phi(v) v')' + (a_1 - b_1 u - c_1 v) u = 0, & x \in (0, L), \\ D_2 v'' + (a_2 - b_2 u - c_2 v) v = 0, & x \in (0, L), \\ u'(x) = v'(x) = 0, & x = 0, L. \end{cases}$$

- Bifurcating solution: small amplitude solutions
- Existence of positive solutions with striking properties
- Segregation phenomenon
- Large advection rate and small diffusion rate

Transition-layer solutions

Let $r = \frac{\chi}{D_1}$, $D_2 = \epsilon$, $\phi(v) \equiv 1$ and $b_1 \to 0$ as $\epsilon \to 0$.

$$\begin{cases} D_1(u' + ruv')' + (a_1 - b_1 u - c_1 v)u = 0, & x \in (0, L), \\ \epsilon v'' + (a_2 - b_2 u - c_2 v)v = 0, & x \in (0, L), \\ u'(x) = v'(x) = 0, & x = 0, L. \end{cases}$$

Transition-layer solutions

Let $r = \frac{\chi}{D_1}$, $D_2 = \epsilon$, $\phi(v) \equiv 1$ and $b_1 \to 0$ as $\epsilon \to 0$.

$$\begin{cases} D_1(u' + ruv')' + (a_1 - b_1 u - c_1 v)u = 0, & x \in (0, L), \\ \epsilon v'' + (a_2 - b_2 u - c_2 v)v = 0, & x \in (0, L), \\ u'(x) = v'(x) = 0, & x = 0, L. \end{cases}$$

Theorem

Let $r = \frac{\chi}{D_1} \in (\frac{c_1}{a_1} \ln \frac{a_2 c_1}{a_2 c_1 - a_1 c_2}, \infty)$ be fixed. For any $\epsilon > 0$ being small, we can find $\bar{D} > 0$ large such that if $D_1 > \bar{D}$, there always exists a nonconstant positive solution (u, v). Moreover, as $D_1 \to \infty$, $(u(x), v(x))$ converges to $(\lambda_\epsilon e^{-r v_\epsilon(x)}, v_\epsilon(x))$ uniformly in $[0, L]$, where λ_ϵ is a positive constant and $\lambda_\epsilon \to \frac{(a_2 - c_2 \bar{v}_2) e^{r \bar{v}_2}}{b_2}$ as $\epsilon \to 0$; $v_\epsilon(x)$ is a positive function of x and $v_\epsilon(x) \to \bar{v}_2$ compact uniformly on $[0, x_0)$ and $v_\epsilon(x) \to 0$ compact uniformly on $(x_0, L]$, where $x_0 = \frac{a_1 L}{a_1 - (a_1 - c_1 \bar{v}_2) e^{-r \bar{v}_2}}$.

Transition-layer solutions

- both u and v have interior transition layer and they segregate
- x_0 hence $\bar{v}$ are arbitrarily given (infinitely many transition layers)
- x_0 decreases as $\bar{v}$

Transition-layer solutions

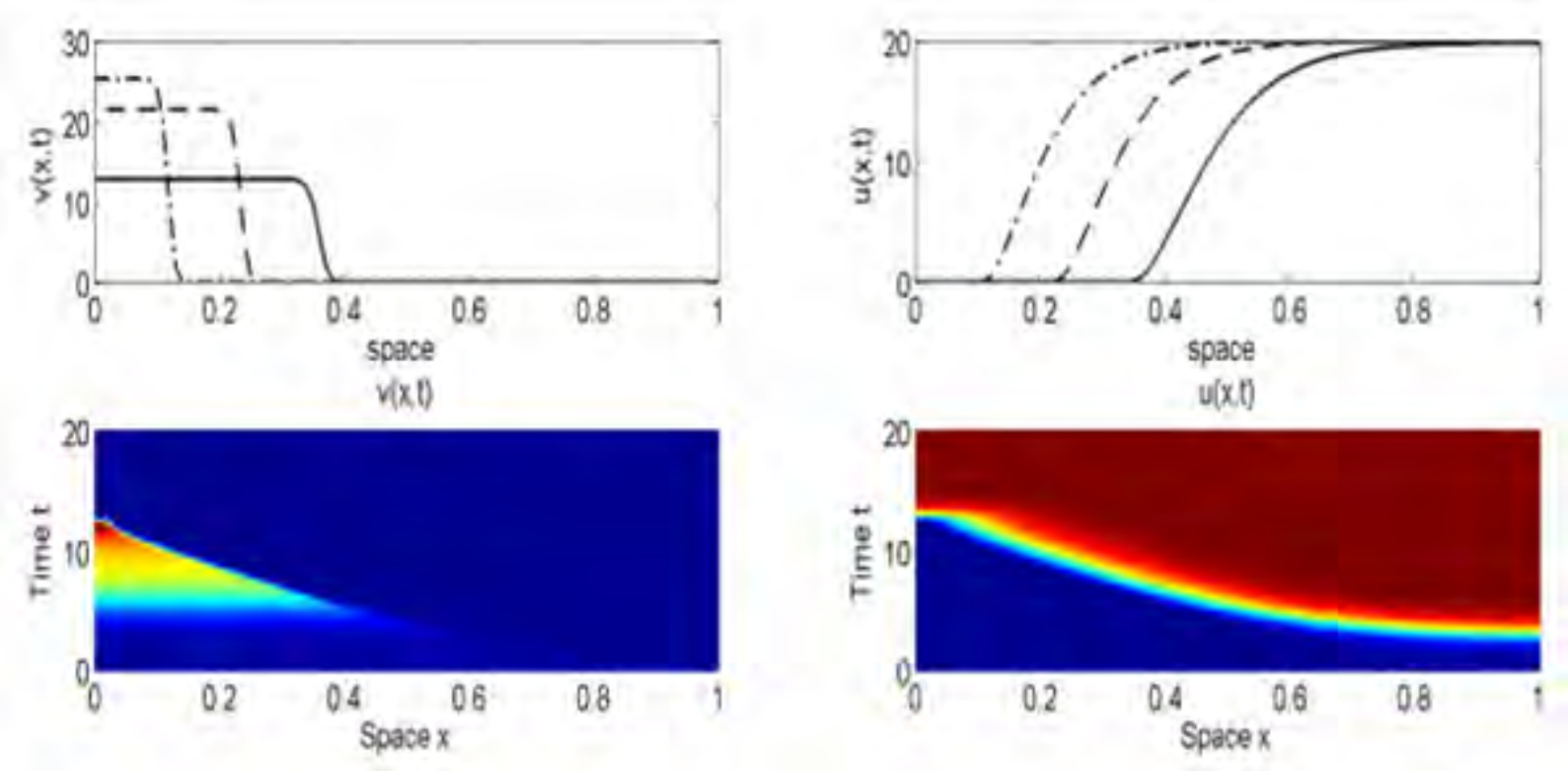

Figure: Spatial-temporal behaviors of the population densities. $D_1 = 10$, $\chi = 100$, $D_2 = 0.1$. The rest parameters are chosen to be the same as in Figure 3. Initial data are small perturbations of $(\bar{u}, \bar{v})$.

Spiky solutions

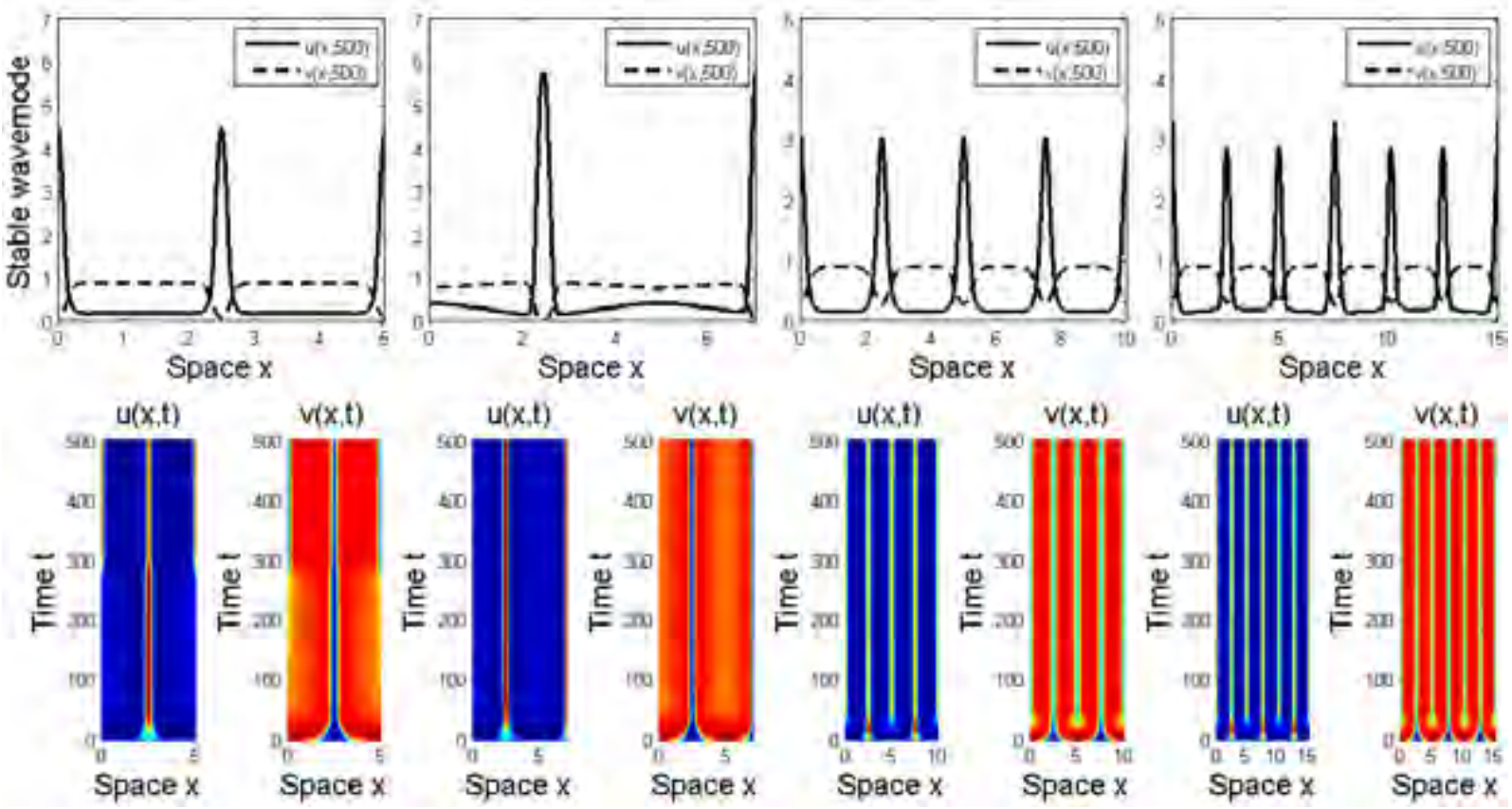

Figure: Formation of stable and multi-spikes over $\Omega = (0, L)$. Numerical simulations suggest that large domains support more stable spikes than small domains.

Summmary

1. Lotka-Volterra competition model with advection
2. Global existence in $1D$ ($2D$ and ND with some conditions)
3. Existence and stability of nonconstant positive steady states
4. Wavemode selection mechanism
5. Transition layer solutions

Open problems

1. Global existence and boundedness in ND; blow-ups?
2. Stability of the interior or boundary layers
3. Large-time behavior? Lyapunov functional
4. Travelling wave? Pattern formation


Thank you...


Happy New Year
2015