Average conditions for permanence in N species nonautonomous competitive reaction – diffusion – advection systems.

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International Conference on Differential Equations and Their Applications.
Brno, 04 – 07 September 2017

Logistic reaction – diffusion – advection model for population growth

By the logistic reaction – diffusion – advection model for population growth we mean the equation

$$\begin{cases} \frac{\partial u}{\partial t} = \nabla\left[\nabla u - \alpha u \nabla m\right] + \lambda u[m(x) - u] & \Omega \times (0, \infty) \\ \frac{\partial u}{\partial n} - \alpha u \frac{\partial m}{\partial n} = 0 & \partial\Omega \times (0, \infty) \end{cases} \tag{logistic}$$

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The effects of the advection term $\alpha u \nabla m$ depends crucially on boundary conditions.

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- In the case of Dirichlet boundary conditions movement up the gradient of $m(x)$ may be either beneficial or harmful to the population.

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For every α there exists an unique non – negative constant $\lambda_* = \lambda_*(\alpha)$ such that the following holds

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The constant λ_* is the principal eigenvalue of an eigenvalue problem related to (logistic). It can be characterized by

$$\lambda_* = \inf_{\varphi \in S} \frac{\int_\Omega e^{\alpha m} |\nabla \varphi|^2}{\int_\Omega e^{\alpha m} m \varphi^2}$$

where $S = \{\varphi \in W^{1,2}(\Omega) : \int_\Omega e^{\alpha m} m \varphi^2 > 0\}$

Two species reaction – diffusion – advection model

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Both species have the same per capita growth rate denoted by $m(x)$.

The authors showed that if only one species has a strong tendency to move upward the environmental gradients the two species can coexist since one species mainly pursues resources at places of locally most favorable environments while the other relies on resources from other parts of the habitat.
If both species have strong biased environments it can lead to overcrowding of the whole population at places of locally most favorable environments which causes the extinction of the species with stronger biased movements.

Definitions and assumptions

By the nonautonomous competitive reaction – diffusion – advection system of Kolmogorov type we mean the system

$$\begin{cases} \dfrac{\partial u_i}{\partial t} = \nabla \left[\mu_i \nabla u_i - \alpha_i u_i \nabla \tilde{f}_i(x) \right] + f_i(t, x, u_1, \ldots, u_N) u_i, \\ \qquad\qquad\qquad\qquad t > 0,\ x \in \Omega,\ i = 1, \ldots, N \\ \mathcal{B}_i u_i = 0, \qquad\qquad t > 0,\ x \in \partial\Omega,\ i = 1, \ldots, N, \end{cases} \tag{R}$$

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- $\tilde{f}_i(x) = \liminf_{t-s\to\infty} \frac{1}{t-s} \int_s^t f_i(\tau, x, 0, \ldots, 0) d\tau$ are nonconstant fuctions for $i = 1, \ldots, N$

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Denote by λ_i the *principal eigenvalue* of the following eigenproblem

$$\begin{cases} \mu_i \nabla^2 \varphi_i(x) + \alpha_i \nabla \tilde{f}_i(x) \nabla \varphi_i(x) = -\lambda_i(\alpha_i) \tilde{f}_i(x) \varphi_i(x) & \text{on } \Omega, \\ \mathcal{B}_i \varphi_i = 0 & \text{on } \partial\Omega. \end{cases} \tag{1}$$

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In the case of Danckwerts boundary conditions we need the following lemma

Lemma 1

The problem (1) subject to Danckwerts boundary conditions has a unique positive principal eigenvalue $\lambda_i(\alpha_i)$ characterized by having a positive eigenfunction if and only if

$$\int_\Omega \tilde{f}_i(x) e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)} < 0$$

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We deal with the positive solutions.

Definition

The solution $u(t,x) = (u_1(t,x), \ldots, u_N(t,x))$ of (R) is positive if $u_i(t,x) > 0$ for all $i = 1, \ldots, N$, $t \in (0, \tau_{\max})$ and $x \in \Omega$.

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(A1) $f_i \colon [0, \infty) \times \bar{\Omega} \times [0, \infty)^N \to \mathbb{R}$ $(1 \le i \le N)$, *as well as their first derivatives* $\partial f_i / \partial t$ $(1 \le i \le N)$, $\partial f_i / \partial u_j$ $(1 \le i, j \le N)$, *and* $\partial f_i / \partial x_k$ $(1 \le i \le N,\ 1 \le k \le n)$, *are continuous.*

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(A2) *The functions* $[\,[0,\infty) \times \bar{\Omega} \ni (t,x) \mapsto f_i(t,x,0,\dots,0) \in \mathbb{R}\,]$, $1 \le i \le N$, *are bounded.*

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Define

$$\underline{a}_i := \inf\{\, f_i(t,x,0,\dots,0) : t \ge 0,\ x \in \bar{\Omega}\,\},$$
$$\overline{a}_i := \sup\{\, f_i(t,x,0,\dots,0) : t \ge 0,\ x \in \bar{\Omega}\,\}.$$

(A3) $(\partial f_i/\partial u_j)(t,x,u) \leq 0$ *for all* $t \geq 0$, $x \in \bar{\Omega}$, $u \in [0,\infty)^N$, $1 \leq i,j \leq N$, $i \neq j$.

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$(\partial f_i/\partial u_j)(t, x, u_1, \ldots, u_N)$ measures the influence of the j-th species on the growth rate of the i-th species. Systems of type (R) for which (A3) holds we call *competitive*.

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(A4) *There exist $\underline{b}_{ii} > 0$ such that $(\partial f_i/\partial u_i)(t,x,u) \le -\underline{b}_{ii}$ for all $t \ge 0$, $x \in \bar{\Omega}$, $u \in [0,\infty)^N$, $1 \le i \le N$.*

Fix a positive solution $u(t,x) = (u_1(t,x), \ldots, u_N(t,x))$ of system (R). For each $1 \le i \le N$ let $\xi_i(t)$, $t \in [0,\infty)$, be the positive solution of the following problem

$$\begin{cases} \xi_i' = \big(\max\limits_{x\in\bar{\Omega}} f_i(t,x,0,\ldots,0) - \lambda_i(\alpha_i)\min_{x\in\bar{\Omega}} \tilde{f}_i(x) - \underline{b}_{ii}\xi_i\big)\xi_i, \\ \xi_i(0) = \sup\limits_{x\in\bar{\Omega}} u_i(0,x). \end{cases} \tag{2}$$

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Lemma 2

Assume **(A1)** through **(A4)** and let $\bar a_i > 0$. Then for each solution $\xi_i(t)$ of the problem (2) there holds

$$\limsup_{t\to\infty} \xi_i(t) \le \frac{\bar a_i + \lambda_i(\alpha_i)\max_{x\in\bar\Omega}\tilde f_i(x)}{\underline{b}_{ii}}, \quad 1 \le i \le N.$$

Lemma 3

Assume **(A1)** through **(A4)**. Then for any positive solution $u(t,x) = u_1(t,x), \ldots, u_N(t,x)$ of (R) and any $1 \leq i \leq N$ there holds

$$u_i(t,x) \leq \xi_i(t) e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i} \varphi(x)$$

for $t \in [0, \tau_{\max})$, $x \in \bar{\Omega}$ where $\xi_i(t)$ is the positive solution of (2).

Lemma 4 [dissipativity]

Assume **(A1)** through **(A4)** and **(A5)** and $\bar{a}_i > 0$. Then for any maximally defined positive solution $u(t,x) = (u_1(t,x), \ldots, u_N(t,x))$ of system (R) there holds

(i) $\tau_{\max} = \infty$, and

(ii)

$$\limsup_{t\to\infty} u_i(t,x) \le \frac{\bar{a}_i + \lambda_i(\alpha_i) \min_{x\in\bar{\Omega}} \tilde{f}_i(x)}{\underline{b}_{ii}}, \qquad 1 \le i \le N, \tag{3}$$

uniformly for $x \in \bar{\Omega}$.

(A5) *The derivatives* $\partial f_i/\partial u_j$, $1 \le i, j \le N$, *are bounded and Lipschitz continuous on sets of the form* $[0,\infty) \times \bar{\Omega} \times B$, *where* B *is a bounded subset of* $[0,\infty)^N$.

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Definition

For $1 \le i, j \le N$ and $\varepsilon_0 \ge 0$ we define

$$\overline{b}_{ij}(\varepsilon_0) := \sup\left\{ -\frac{\partial f_i}{\partial u_j}(t, x, u) : t \ge 0,\ x \in \bar{\Omega},\ u \in \left[0, \frac{\overline{a}_1}{\underline{b}_{11}} + \varepsilon_0\right] \times \dots \times \left[0, \frac{\overline{a}_N}{\underline{b}_{NN}} + \varepsilon_0\right] \right\},$$

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Assumptions (A3) and (A4) imply that $\overline{b}_{ij}(\varepsilon_0) \ge 0$, $1 \le i, j \le N$, and $\overline{b}_{ii}(\varepsilon_0) > 0$, $1 \le i \le N$, whereas it follows from (A5) that $\overline{b}_{ij}(\varepsilon_0) < \infty$, and $\lim_{\varepsilon_0 \to 0^+} \overline{b}_{ij}(\varepsilon_0) = \overline{b}_{ij}$, for $1 \le i, j \le N$.

Averaging

Definition

We define the *lower average* of a function f_i as

$$m[f_i] := \liminf_{t-s\to\infty} \frac{1}{t-s} \int\limits_s^t \min_{x\in\bar{\Omega}} f_i(\tau, x, 0, \ldots, 0)\, d\tau,$$

Definition

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(A6) $m[f_i] > 0$, $1 \le i \le N$.

Permanence in reaction – diffusion – advection system of Kolmogorov type

Definition

System (R) is *permanent*, if there exist positive constants δ_i and R_i such that for each positive solution $u(t,x) = (u_1(t,x), \dots, u_N(t,x))$ of system (R) there exists $T = T(u) > 0$ with the property

$$\delta_i \varphi_i(x) \le u_i(t,x) \le R_i \qquad \text{(permanence)}$$

for all $1 \le i \le N$, $t \ge T$, $x \in \bar{\Omega}$.

Average conditions for permanence in reaction – diffusion – advection system of Kolmogorov type

$$m[f_i] > \lambda_i \mu_i + \sum_{\substack{j=1 \\ j \neq i}}^{N} e^{\frac{\alpha_j}{\mu_j} \max_{x \in \bar{\Omega}} \tilde{f}_j(x)} \frac{\overline{b}_{ij}(M[f_j] - \lambda_j(\alpha_j) \min_{x \in \bar{\Omega}} \tilde{f}_j(x))}{\underline{b}_{jj}},$$

$$1 \leq i \leq N, \quad \text{(AC)}$$

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- J. Balbus *Permanence in N species nonautonomous competitive reaction – diffusion – advection system of Kolmogorov type in heterogeneous environment*, submitted for publication.

Theorem 1 [Main Theorem]

Assume **(A1)** through **(A6)**. If **(AC)** holds then system (R) is permanent.

- J. Balbus *Permanence in N species nonautonomous competitive reaction – diffusion – advection system of Kolmogorov type in heterogeneous environment*, submitted for publication.

The following result will be useful to prove Theorem 1.

Permanence in logistic equation of ODEs

Proposition 2 [Vance - Coddington Estimates]

Let $c\colon [t_0, \infty) \to \mathbb{R}$, where $t_0 \geq 0$, be a bounded continuous function, where $c_* > 0$ and $c^* > 0$ are such that $-c_* \leq c(t) \leq c^*$ for all $t \geq t_0$, and let $d > 0$. Assume moreover that there are $L > 0$ and $\beta > 0$ such that

$$\frac{1}{L} \int\limits_{t}^{t+L} c(\tau)\, d\tau \geq \beta$$

for all $t \geq t_0$.

Proposition 2 [Vance - Coddington Estimates] continued

Then for any solution $\zeta(t)$ of the initial value problem

$$\begin{cases} \zeta' = (c(t) - d\zeta)\zeta \\ \zeta(t_0) = \zeta_0, \end{cases}$$

where $\zeta_0 > 0$, there holds

$$\frac{\beta}{d} e^{-L(c_* + \beta)} \leq \liminf_{t\to\infty} \zeta(t) \leq \limsup_{t\to\infty} \zeta(t) \leq \frac{c^*}{d}. \quad \text{(permanence-logistic)}$$

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(permanence-logistic)

- R. R. Vance and E. A. Coddington, *A nonautonomous model of population growth*, J. Math. Biol. **27** (1989), no. 5, 491–506.

proof of Theorem 1

The right-hand side of the inequality (permanence) is satisfied by Lemma 3 (ii). By assumption (A5) we can choose $\varepsilon_0 > 0$ such that

$$m[f_i] > \lambda_i \mu_i + \sum_{\substack{j=1\\ j\neq i}}^{N} e^{\frac{\alpha_j}{\mu_j}\max_{x\in\bar{\Omega}} \tilde{f}_j(x)} \frac{\overline{b}_{ij}(\varepsilon_0) M[f_j] - \lambda_j(\alpha_j)\min_{x\in\bar{\Omega}} \tilde{f}_j(x)}{\underline{b}_{jj}}, \qquad 1 \leq i \leq N,$$

for all $1 \leq i \leq N$.
Fix a positive solution $u(t,x) = (u_1(t,x), \ldots, u_N(t,x))$ of system (R). Let $\xi_i(t)$, $1 \leq i \leq N$, $t \geq 0$, be the solutions of (2). Fix $1 \leq i \leq N$.

sketch of the proof of Theorem 1 [continued]

Let $t_0 > 0$ be such a moment that

$$u(t,x) \in \left[0, \frac{\overline{a}_1}{\underline{b}_{11}} + \varepsilon_0\right] \times \cdots \times \left[0, \frac{\overline{a}_N}{\underline{b}_{NN}} + \varepsilon_0\right] \quad \text{for} \quad t > t_0 \quad x \in \bar{\Omega}.$$

Let $\eta_i(t)$, $t \geq t_0$, be the positive solution of the following problem

$$\begin{cases} \eta_i' = \big(\min_{x\in\bar{\Omega}} f_i(t,x,0,\ldots,0) - \lambda_i(\alpha_i)\max_{x\in\bar{\Omega}} \tilde{f}_i(x) - \overline{b}_{ii}(\varepsilon_0)\eta_i - \\ \qquad \sum_{\substack{j=1 \\ j\neq i}}^{N} \overline{b}_{ij}(\varepsilon_0)\xi_j(t)e^{\frac{\alpha_j}{\mu_j}\max_{x\in\bar{\Omega}} f_j(x)}\big)\eta_i \\ \eta_i(t_0) = \inf_{x\in\Omega} \frac{u_i(t_0,x)}{\varphi_i(x)}. \end{cases} \tag{4}$$

It is easy to see that $u_i(t,x) \geq \eta_i(t)e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)}\varphi_i(x)$ for all $t \geq t_0$ and $x \in \bar{\Omega}$.

sketch of the proof of Theorem 1 [continued]

Now we apply Proposition 1 to (4) where

$$c(t) = \min_{x \in \bar{\Omega}} f_i(t, x, 0, \ldots, 0) - \lambda_i \mu_i - \sum_{\substack{j=1 \\ j \neq i}}^{N} \overline{b}_{ij}(\varepsilon_0) \xi_j(t) \quad \text{i} \quad d = \overline{b}_{ii}(\varepsilon_0).$$

sketch of the proof Theorem 1 [continued]

To prove the permanence of system (R) we show that the parameters in Theorem 1 do not depend on the solution $u(t, x)$, for sufficiently large t. □