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

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Logistic reaction – diffusion – advection model for population growth

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

\[
\begin{align*}
\frac{\partial u}{\partial t} &= \nabla [\nabla u - \alpha u \nabla m] + \lambda u [m(x) - u] \quad \Omega \times (0, \infty) \\
\frac{\partial u}{\partial n} - \alpha u \frac{\partial m}{\partial n} &= 0 \quad \partial \Omega \times (0, \infty)
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The effects of the advection term $\alpha u \nabla m$ depends crucially on boundary conditions.
For Danckwerts boundary conditions sufficiently rapid movements in the direction of $m(x)$ is always beneficial.
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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.

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

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The constant $\lambda_*$ 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 $S = \{ \varphi \in W^{1,2}(\Omega) : \int_{\Omega} e^{\alpha m} m\varphi^2 > 0 \}$. 

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By the two species reaction – diffusion – advection model we mean the system

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\begin{align*}
\frac{\partial u}{\partial t} &= \nabla [\mu \nabla u - \alpha u \nabla m] + [m(x) - u - v]u \quad \Omega \times (0, \infty) \\
\frac{\partial v}{\partial t} &= \nabla [\nu \nabla v - \beta v \nabla m] + [m(x) - u - v]v \quad \Omega \times (0, \infty) \\
\mu \frac{\partial u}{\partial n} - \alpha u \frac{\partial m}{\partial n} &= 0 \quad \partial \Omega \times (0, \infty) \\
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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

\[
\begin{align*}
\frac{\partial u_i}{\partial t} &= \nabla \left[ \mu_i \nabla u_i - \alpha_i u_i \nabla \tilde{f}_i(x) \right] + f_i(t, x, u_1, \ldots, u_N) u_i, \\
B_i u_i &= 0,
\end{align*}
\]

\( t > 0, \ x \in \Omega, \ i = 1, \ldots, N \)

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\]

where

- \( u_i(t, x) \) – population density of the \( i \)-th species at time \( t \) and spatial location \( x \in \bar{\Omega} \),
- \( \mu_i > 0 \) – migration rate of the \( i \)-th species,
- \( \tilde{f}_i(x) = \liminf_{t-s \to \infty} \frac{1}{t-s} \int_s^t f_i(\tau, x, 0, \ldots, 0) d\tau \) are nonconstant functions for \( i = 1, \ldots, N \).
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Denote by \( \lambda_i \) the principal eigenvalue of the following eigenproblem

\[
\begin{align*}
\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) \quad \text{on } \Omega, \\
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In the case of Dirichlet boundary conditions it follows that (1) will always have a unique positive eigenvalue \( \lambda_i^1(\alpha_i) \) which is characterized by having a positive eigenfunction.
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In the case of Danckwerts boundary conditions we need the following lemma
Lemma 1

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

$$\int_{\Omega} \tilde{f}_i(x) e^{\frac{\alpha_i}{\mu_i} \tilde{f}_i(x)} < 0$$
Lemma 1

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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 $i = 1, \ldots, N$, $t \in (0, \tau_{\text{max}})$ and $x \in \Omega$. 
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\[(A1)\quad f_i: [0, \infty) \times \bar{\Omega} \times [0, \infty)^N \rightarrow \mathbb{R} \quad (1 \leq i \leq N),\]
as well as their first derivatives $\partial f_i/\partial t \quad (1 \leq i \leq N)$, $\partial f_i/\partial u_j \quad (1 \leq i, j \leq N)$,
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(A2) The functions $[ [0, \infty) \times \bar{\Omega} \ni (t, x) \mapsto f_i(t, x, 0, \ldots, 0) \in \mathbb{R} ]$, $1 \leq i \leq N$, are bounded.
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Define

$$a_i := \inf \{ f_i(t, x, 0, \ldots, 0) : t \geq 0, \ x \in \bar{\Omega} \},$$

$$\bar{a}_i := \sup \{ f_i(t, x, 0, \ldots, 0) : t \geq 0, \ x \in \bar{\Omega} \}.$$
(A3) \( \frac{\partial f_i}{\partial u_j}(t, x, u) \leq 0 \) for all \( t \geq 0, x \in \bar{\Omega}, u \in [0, \infty)^N, 1 \leq i, j \leq N, i \neq j \).
(A3) \((\partial f_i/\partial u_j)(t, x, u) \leq 0\) for all \(t \geq 0, \ x \in \overline{\Omega}, \ u \in [0, \infty)^N, \ 1 \leq i, j \leq N, \ i \neq j.\)

\((\partial f_i/\partial u_j)(t, x, u_1, \ldots, u_N)\) 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 \( b_{ii} > 0 \) such that \( \frac{\partial f_i}{\partial u_i}(t, x, u) \leq -b_{ii} \) for all \( t \geq 0, \ x \in \bar{\Omega}, \ u \in [0, \infty)^N, \ 1 \leq i \leq N \).
Fix a positive solution $u(t, x) = (u_1(t, x), \ldots, u_N(t, x))$ of system (R). For each $1 \leq i \leq N$ let $\xi_i(t), t \in [0, \infty)$, be the positive solution of the following problem

$$
\begin{cases}
\xi'_i = \left( \max_{x \in \bar{\Omega}} f_i(t, x, 0, \ldots, 0) - \lambda_i(\alpha_i) \min_{x \in \bar{\Omega}} \tilde{f}_i(x) - b_{ii} \xi_i \right) \xi_i, \\
\xi_i(0) = \sup_{x \in \bar{\Omega}} u_i(0, x).
\end{cases}
$$

(2)
Fix a positive solution $u(t, x) = (u_1(t, x), \ldots, u_N(t, x))$ of system (R). For each $1 \leq i \leq N$ let $\xi_i(t)$, $t \in [0, \infty)$, be the positive solution of the following problem

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\begin{aligned}
\xi_i' &= \left( \max_{x \in \bar{\Omega}} f_i(t, x, 0, \ldots, 0) - \lambda_i(\alpha_i) \min_{x \in \bar{\Omega}} \tilde{f}_i(x) - b_{ii} \xi_i \right) \xi_i, \\
\xi_i(0) &= \sup_{x \in \bar{\Omega}} u_i(0, x).
\end{aligned}
$$

(2)

**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

$$
\limsup_{t \to \infty} \xi_i(t) \leq \frac{\bar{a}_i + \lambda_i(\alpha_i) \max_{x \in \bar{\Omega}} \tilde{f}_i(x)}{b_{ii}}, \quad 1 \leq i \leq N.
$$
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 $t \in [0, \tau_{\text{max}})$, $x \in \bar{\Omega}$ 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) $\tau_{\text{max}} = \infty$, and

(ii) $\limsup_{t \to \infty} u_i(t, x) \leq \frac{\bar{a}_i + \lambda_i(\alpha_i) \min_{x \in \bar{\Omega}} \tilde{f}_i(x)}{b_{ii}}$, \quad 1 \leq i \leq N,

(3)

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

Definition

For $1 \leq i, j \leq N$ and $\varepsilon_0 \geq 0$ we define $b_{ij}(\varepsilon_0) := \sup \{ -\partial f_i / \partial u_j(t, x, u) : t \geq 0, x \in \bar{\Omega}, u \in [0, a_1 b_{11} + \varepsilon_0] \times \cdots \times [0, a_N b_{NN} + \varepsilon_0] \}$.

$\lim_{\varepsilon_0 \to 0^+} b_{ij}(\varepsilon_0) = b_{ij}, \quad 1 \leq i, j \leq N$. 

Assumptions (A3) and (A4) imply that $b_{ij}(\varepsilon_0) \geq 0, 1 \leq i, j \leq N$, and $b_{ii}(\varepsilon_0) > 0, 1 \leq i \leq N$, whereas it follows from (A5) that $b_{ij}(\varepsilon_0) < \infty$, and $\lim_{\varepsilon_0 \to 0^+} b_{ij}(\varepsilon_0) = b_{ij}, \quad 1 \leq i, j \leq N$. 

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**Definition**

For $1 \leq i, j \leq N$ and $\varepsilon_0 \geq 0$ we define

$$b_{ij}(\varepsilon_0) := \sup \left\{ -\frac{\partial f_i}{\partial u_j}(t, x, u) : t \geq 0, \ x \in \bar{\Omega}, \ u \in \left[0, \frac{\bar{a}_1}{b_{11}} + \varepsilon_0\right] \times \ldots \times \left[0, \frac{\bar{a}_N}{b_{NN}} + \varepsilon_0\right] \right\},$$

$$b_{ij}(0) := b_{ij}.$$
The derivatives $\frac{\partial f_i}{\partial u_j}, 1 \leq i, j \leq N$, are bounded and Lipschitz continuous on sets of the form $[0, \infty) \times \bar{\Omega} \times B$, where $B$ is a bounded subset of $[0, \infty)^N$.

**Definition**

For $1 \leq i, j \leq N$ and $\varepsilon_0 \geq 0$ we define

$$
\bar{b}_{ij}(\varepsilon_0) := \sup \left\{ -\frac{\partial f_i}{\partial u_j}(t, x, u) : t \geq 0, \ x \in \bar{\Omega}, \ u \in \left[ 0, \frac{\bar{a}_1}{b_{11}} + \varepsilon_0 \right] \times \ldots \times \left[ 0, \frac{\bar{a}_N}{b_{NN}} + \varepsilon_0 \right] \right\},
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Assumptions (A3) and (A4) imply that $\bar{b}_{ij}(\varepsilon_0) \geq 0$, $1 \leq i, j \leq N$, and $\bar{b}_{ii}(\varepsilon_0) > 0$, $1 \leq i \leq N$, whereas it follows from (A5) that $\bar{b}_{ij}(\varepsilon_0) < \infty$, and $\lim_{\varepsilon_0 \to 0^+} \bar{b}_{ij}(\varepsilon_0) = \bar{b}_{ij}$, for $1 \leq i, j \leq N$. 
Averaging

Definition

We define the *lower average* of a function \( f_i \) as

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

Definition

We define the *upper average* of a function \( f_i \) as

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M[f_i] := \limsup_{t-s \to \infty} \frac{1}{t-s} \int_{s}^{t} \max_{x \in \bar{\Omega}} f_i(\tau, x, 0, \ldots, 0) \, d\tau.
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(A6) $m[f_i] > 0, \quad 1 \leq i \leq N.$
Permanence in reaction – diffusion – advection system of Kolmogorov type

**Definition**

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

$$\delta_i \varphi_i(x) \leq u_i(t, x) \leq R_i \quad \text{(permanence)}$$

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

Joanna Balbus

Average conditions for permanence in $N$ species nonautonomous competitive reaction–diffusion–advection systems.
Average conditions for permanence in reaction–diffusion–advection system of Kolmogorov type

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

\[ 1 \leq i \leq N, \quad (AC) \]
Theorem 1 [Main Theorem]

Assume (A1) through (A6). If (AC) holds then system (R) is permanent.
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The following result will be useful to prove Theorem 1.
Proposition 2 [Vance - Coddington Estimates]

Let $c : [t_0, \infty) \rightarrow \mathbb{R}$, 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

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

for all $t \geq t_0$. 

Joanna Balbus
Average conditions for permanence in N species nonautonomous systems.
Proposition 2 [Vance - Coddington Estimates] continued

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

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

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}.
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(permance-logistic)
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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

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

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 $1 \leq i \leq N$. 

Joanna Balbus

Average conditions for permanence in $N$ species nonautonomous competitive reaction–diffusion–advection systems.
Let $t_0 > 0$ be such a moment that

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

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

$$\begin{aligned}
\eta_i' &= \left(\min_{x \in \bar{\Omega}} f_i(t, x, 0, \ldots, 0) - \lambda_i(\alpha_i) \max_{x \in \bar{\Omega}} \tilde{f}_i(x) - b_{ii}(\varepsilon_0)\eta_i - \sum_{j=1, j \neq i}^N b_{ij}(\varepsilon_0)\xi_j(t) e^{\frac{\alpha_i}{\mu_j}} \max_{x \in \bar{\Omega}} f_j(x)\right) \eta_i \\
\eta_i(t_0) &= \inf_{x \in \Omega} \frac{u_i(t_0, x)}{\varphi_i(x)}.
\end{aligned}$$

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

(4)
Now we apply Proposition 1 to (4) where

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