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Permanence in N species nonautonomous competitive reaction–diffusion–advection system of Kolmogorov type in heterogeneous environment.

Joanna Balbus ✉

Faculty of Pure and Applied Mathematics, Wrocław University of Technology,
Wybrzeże Wyspiańskiego 27, Wrocław, Poland

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Abstract. One of the important concept in population dynamics is finding conditions under which the population can coexist. Mathematically formulation of this problem we call permanence or uniform persistence. In this paper we consider N species nonautonomous competitive reaction–diffusion–advection system of Kolmogorov type in heterogeneous environment. Applying Ahmad and Lazer's definitions of lower and upper averages of a function and using the sub- and supersolution methods for PDEs we give sufficient conditions for permanence in such models. We give also a lower estimation on the numbers δ_i which appear in the definition of permanence in form of parameters of system

$$\begin{cases} \frac{\partial u_i}{\partial t} = \nabla[\mu_i \nabla u_i - \alpha_i u_i \nabla \tilde{f}_i(x)] + f_i(t,x,u_1,\dots,u_N)u_i, & t>0,\ x\in\Omega,\ i=1,\dots,N, \\ \mathcal{D}_i u_i = 0, & t>0,\ x\in\partial\Omega,\ i=1,\dots,N. \end{cases}$$

Keywords: advection, subsolution, lower average, permanence.

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1 Introduction

A main problem in population dynamics is the long-term development of population. Uniform persistence (sometimes also called permanence), coexistence and extinction describe important special types of asymptotic behavior of the solutions of associated model equations. In this paper we consider the N species nonautonomous competitive reaction–diffusion–advection system of Kolmogorov type

$$\frac{\partial u_i}{\partial t} = \nabla[\mu_i \nabla u_i - \alpha_i u_i \nabla \tilde{f}_i(x)] + f_i(t,x,u_1,\dots,u_N)u_i, \qquad t>0,\ x\in\Omega,\ i=1,\dots,N, \tag{1.1}$$

✉ Corresponding author. Email: joanna.balbus@pwr.edu.pl. The author was supported as research project (S50082/K3301040110258/15).

which is endowed in appropriate boundary conditions.

In the context of ecology $u_i(t,x)$ denote the densities of the i-th species at time t and a spatial location $x \in \bar{\Omega}$, $\bar{\Omega} \subset \mathbb{R}^n$ is a bounded habitat and

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

accounts for the local growth rate. If the environment is spatially heterogeneous i.e., $\tilde{f}_i(x)$ is not a constant then the population may have tendency to move along the gradient of the $\tilde{f}_i(x)$ $(i = 1, \dots, N)$ in addition to random dispersal. The constants α_i for $1 \le i \le N$ measures the rate at which the population moves up the gradient of $\tilde{f}_i(x)$. Through this paper we only consider the case $\alpha_i \ge 0$, for $1 \le i \le N$ i.e., the populations move up in the direction along which $\tilde{f}_i$ is increasing.

Models of ecology are described by ordinary differential equations (see e.g. [11, 12, 26, 27, 30]) or partial differential equations (see e.g. [3, 4, 6, 10, 18, 19, 21, 24, 29, 31]). In the case of autonomous ODE sufficient conditions for permanence are given in a form of inequalities involving an interaction coefficients of the system (see e.g. [1]).

In [2] S. Ahmad and A. C. Lazer considered an N species nonautonomous competitive Lotka–Volterra system. The authors introduced a notion of upper and lower averages of a function. They found sufficient conditions which guarantee that such system is permanent and globally attractive.

In [25] we extended their results on N species nonautonomous competitive system of Kolmogorov type.

The models of ODEs do not take into account spatial heterogeneity. They give the temporal changes in terms of the global population while partial differential equations give the temporal changes at each point in space in terms of the local densities and the spatial gradients. Dispersal of individuals has important effects from an ecological point of view and in the biological literature we can find that temporally constant tends to reduce dispersal rates (see e.g. [9]) or temporal changes in the environment tends to lead to higher dispersal rates (see e.g. [16]).

One of the popular models which take into account spatial heterogeneity is reaction–diffusion system of PDE

$$\frac{\partial u_i}{\partial t} = \mu_i \Delta u_i + f_i(t, x, u) u_i, \qquad i = 1, \dots, N. \tag{1.2}$$

The system (1.2) is an example of model of the population growth with unconditional dispersal. Unconditional dispersal does not depend on habitat quality. This type of dispersal is investigated by many authors, see for example [3, 10, 14, 15, 17, 22, 23]. In [23] the authors investigated uniform persistence for nonautonomous and randomly parabolic Kolmogorov systems via the skew-product semiflows approach. They obtained sufficient conditions for uniform persistence in such systems in terms of Lyapunov exponents.

In [3] we studied N species nonautonomous reaction–diffusion Kolmogorov system with different boundary conditions, either Dirichlet or Neumann or Robin boundary conditions. We gave sufficient conditions for permanence in such system. Those conditions are given in a form of inequalities involving time averages of intrinsic growth rates, interaction coefficients, migration rates and principal eigenvalues. In nature species do not move completely randomly. Their movements are a combination of both random and biased ones. Such models are called models with conditional dispersal. The most popular model which takes into account some amounts of random motion and a purely directed movement dispersal strategy is reaction–diffusion–advection system. This type strategy is considered widely in literature (see e.g. [7,8,10,18]).

The logistic reaction–diffusion–advection model for the population growth has the following form

$$\begin{cases} \frac{\partial u}{\partial t} = \nabla\left[\nabla u - \alpha u \nabla m\right] + \lambda u[m(x) - u] & \text{in } \Omega \times (0, \infty), \\ \frac{\partial u}{\partial n} - \alpha u \frac{\partial m}{\partial n} = 0 \quad \text{on } \partial\Omega \times (0, \infty). \end{cases} \tag{1.3}$$

The constant α measures the rate at which the population moves up the gradient of $m(x)$. In [8] the authors examined the case $\alpha \geq 0$. The boundary conditions ensures that the boundary acts as a reflecting barrier to the population i.e., no-flux across the boundary. Belgacem and Cosner [4] studied (1.3) with both no-flux and Dirichlet boundary conditions. The authors showed that the effects of the advection term $\alpha u \nabla m$ depend critically on boundary conditions. However, for no-flux boundary condition sufficiently rapid movement in the direction of $m(x)$ is always beneficial. In the case of Dirichlet boundary condition movement up the gradient of $m(x)$ may be either beneficial or harmful to the population. The authors studied the effect of drift on the principal eigenvalues of certain elliptic operators. The eigenvalues determine whether a given model predicts persistence or extinction for the population.

In [8] Cosner and Lou showed that the effects of advection depend crucially on the shape of the habitat of the population. In the case of convex habitat the movement in the direction of the gradient of the growth rate is always beneficial to the population. In the case of nonconvex habitat such advection could be harmful to the population.

In [7] Chen et al. investigated a two species model of reaction–diffusion–advection

$$\begin{cases} \frac{\partial u}{\partial t} = \nabla[\mu \nabla u - \alpha u \nabla m(x)] + (m(x) - u - v)u, \\ \frac{\partial v}{\partial t} = \nabla[\nu \nabla v - \beta v \nabla m(x)] + (m(x) - u - v)v, \end{cases} \tag{1.4}$$

in $\Omega \times (0, \infty)$ with no-flux boundary conditions

$$\mu \partial_n u - \alpha u \partial_n m = \nu \partial_n v - \beta v \partial_n m = 0.$$

They assumed that both species have the same per capita growth rates denoted by $m(x)$. In biological point of view it may mean that the two species are competing for the same resources. They assumed also that $m(x)$ is a nonconstant function. The resource is usually spatially unevenly distributed. Because of that the movement of species is purely random. The model (1.4) consist of two component: random diffusion ($\mu \nabla u$ and $\nu \nabla v$) and directed movement upward along the gradient of $m(x)$ ($\alpha(\nabla m)u$ and $\beta(\nabla m)v$). 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. However, if both species have such strong biased movements 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.

In this paper we find sufficient conditions for uniform persistence in the N species nonautonomous competitive system of reaction–diffusion–advection. In contrast to [7,13,20,21] we assume that all species have a different intrinsic per capita growth rates, and we take into account the influence of the jth species of the growth rate of the ith species. The investigation of nonautonomous systems is of great importance biologically since in nature, many systems are subject to certain time dependence which may be neither periodic nor almost periodic. This paper is organized as follows.

In Section 2 we introduce basic assumptions and some results about the principal eigenvalue of the eigenproblem (2.1). We also formulate auxiliary results on the behavior of the positive solutions.

In Section 3 we state and prove the main theorem of this paper. We formulate average conditions which guarantee that system (ARD) is permanent.

In Section 4 we formulate the stronger inequalities which give a lower bound on the population densities in term of interaction coefficients of system (ARD).

2 Preliminaries

Consider a nonautonomous competitive N species model of reaction–diffusion–advection

$$\begin{cases} \frac{\partial u_i}{\partial t} = \nabla[\mu_i \nabla u_i - \alpha_i u_i \nabla \tilde{f}_i(x)] + f_i(t,x,u_1,\dots,u_N)u_i, & t>0,\ x\in\Omega,\ i=1,\dots,N, \\ \mathcal{D}_i u_i = 0, & t>0,\ x\in\partial\Omega,\ i=1,\dots,N, \end{cases} \tag{ARD}$$

where $\tilde{f}_i(x) = \liminf_{t-s\to\infty} \frac{1}{t-s}\int_s^t f_i(\tau,x,0,\dots,0)d\tau$ are nonconstant functions for $i=1,\dots,N$. $\Omega \subset R^n$ is a bounded domain with the sufficiently smooth boundary $\partial\Omega$, $\mu_i > 0$ is a diffusion rate of the i-th species, $\alpha_i \geq 0$ measure the rate at which the population moves up the gradient of the growth rate $\tilde{f}_i(x)$ of the i-th species and $f_i(t,x,u_1,\dots,u_N)$ is the local per capita growth rate of the i-th species.

We define the operator

$$L(\psi_i) = \frac{\partial \psi_i}{\partial t} + \nabla[\mu_i \nabla \psi_i - \alpha_i \psi_i \nabla \tilde{f}_i(x)] + f_i(t,x,u)\psi_i.$$

Further we define the boundary operator $\mathcal{D}_i$ which is either the Dirichlet operator

$$\mathcal{D}_i(u_i) = u_i \quad \text{on } \partial\Omega,$$

or the operator

$$\mathcal{D}_i(u_i) = \mu_i \frac{\partial u_i}{\partial n} - \alpha_i u_i \frac{\partial \tilde{f}_i}{\partial n} \quad \text{on } \partial\Omega,$$

Denote by $\lambda_i(\alpha_i)$ the principal eigenvalue of the eigenproblem

$$\begin{cases} \mu_i \nabla^2 \varphi_i(x) + \alpha_i \nabla \tilde{f}_i(x) \nabla \varphi_i(x) = -\lambda_i(\alpha_i)\tilde{f}_i(x)\varphi_i(x) & \text{on } \Omega, \\ \mathcal{D}_i \varphi_i = 0 \quad \text{on } \partial\Omega. \end{cases} \tag{2.1}$$

In the case of Dirichlet boundary conditions it is known that (2.1) will always have a unique positive principal eigenvalue $\lambda_i^1(\alpha_i)$ which is characterized by having a positive eigenfunction.

In the case of no-flux boundary conditions we need the following lemma.

Lemma 2.1 (see [4]). *The problem (2.1) subject to no-flux boundary conditions has a unique positive principal eigenvalue $\alpha_i(\alpha_i)$ characterized by having a positive eigenfunction if and only if*

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

Definition 2.2. System (ARD) is permanent if there are positive constants $\underline{\delta}_i, \overline{\delta}_i$ such that for each positive solution $u(t,x) = (u_1(t,x), \ldots, u_N(t,x))$ of (ARD)

$$\underline{\delta}_i \le \liminf_{t\to\infty} \frac{u_i(t,x)}{\varphi_i(x)} \le \limsup_{t\to\infty} \frac{u_i(t,x)}{\varphi_i(x)} \le \overline{\delta}_i, \qquad 1 \le i \le N,$$

where the limit is uniform in $x \in \Omega$.

We introduce now a first assumption for a functions f_i which guarantee the existence and the uniqueness of local classical solutions to an initial value problem for (ARD).

(A1) $f_i : [0,\infty) \times \bar{\Omega} \times [0,\infty)^N \to R$ ($1 \le i \le N$), as well as their first derivatives $\frac{\partial f_i}{\partial t}$ $(1 \le i \le N)$, $\frac{\partial f_i}{\partial u_j}$ $(1 \le i,j \le N)$ and $\frac{\partial f_i}{\partial x_k}$ $(1 \le i,k \le N)$ are continuous. Moreover, the derivatives $\frac{\partial f_i}{\partial u_j}$ $(1 \le i,j \le N)$ are bounded and uniformly continuous on sets of the form $[0,\infty) \times \bar{\Omega} \times B$ where B is a bounded subset of $[0,\infty)^N$.

(A1) is a standard assumption guaranteeing that for any sufficiently regular initial function $u_0(x) = (u_{01}(x), \ldots, u_{0N}(x))$, $x \in \Omega$ there exists a unique maximally defined solution $u(t,x) = (u_1(t,x), \ldots, u_N(t,x))$ of (ARD), $(t,x) \in [0,\tau_{\max}) \times \bar{\Omega}$ where $\tau_{\max} > 0$, satisfying the initial condition $u(0,x) = u_0(x)$. The solution $u(t,x)$ is classical: the derivatives occurring in the equations (resp. in the boundary conditions) are defined, and the equations (resp. the boundary conditions) are satisfied pointwise on $(0,\tau_{\max}) \times \Omega$ (resp. on $(0,\tau_{\max}) \times \partial\Omega$). Moreover, the derivatives $\frac{\partial u_i}{\partial t}$ $(i = 1, \ldots, N)$ and $\frac{\partial^2 u_i}{\partial x_k x_l}$ $(1 \le k,l \le N,\ i = 1, \ldots, N)$ are continuous on $(0,\tau_{\max}) \times \bar{\Omega}$.

We deal with the positive solutions of (ARD). By positive solution of (ARD) we mean a solution $u(t,x) = (u_1(t,x), \ldots, u_N(t,x))$ of (ARD) such that $u_i(t,x) > 0$ for $t \in (0,\tau_{\max})$, $x \in \Omega$, $i = 1, \ldots, N$. In other words, positive solutions correspond to initial functions $u_0(x) = (u_{01}(x), \ldots, u_{0N}(x))$ with $u_{0i}(x) \ge 0$, $u_{0i} \not\equiv 0$ for all $i = 1, \ldots, N$.

For each $1 \le i \le N$ there holds

$$0 < \inf_{x\in\Omega} \frac{u_i(0,x)}{\varphi_i(x)} \le \sup_{x\in\Omega} \frac{u_i(0,x)}{\varphi_i(x)} < \infty. \tag{2.2}$$

Lemma 2.3. *For any positive solution $u(t,x) = (u_1(t,x), \ldots, u_N(t,x))$ of (ARD) there exist functions $\underline{\gamma}_i : (0,\tau_{\max}) \to (0,\infty)$ and $\overline{\gamma}_i : (0,\tau_{\max}) \to (0,\infty)$ such that*

$$\underline{\gamma}_i(t)\varphi_i(x) \le u_i(t,x) \le \overline{\gamma}_i(t)\varphi_i(x) \tag{2.3}$$

for all $t \in (0,\tau_{\max})$, $x \in \bar{\Omega}$, $1 \le i \le N$.

Proof. Fix a positive solution $u(t,x) = (u_1(t,x), \ldots, u_N(t,x))$ of (ARD). Denote by $v_i(t,x)$, $1 \le i \le N$, $t \ge 0$, $x \in \bar{\Omega}$, the solution of the following boundary value problem

$$\begin{cases} \frac{\partial v_i}{\partial t} = \mu_i \nabla^2 v_i + \alpha_i \nabla \tilde{f}_i \nabla v_i, & t > 0,\ x \in \Omega, \\ \mathcal{D}_i v_i = 0 \quad t > 0,\ x \in \partial\Omega, \end{cases}$$

satisfying the initial condition $v_i(0,x) = u_i(0,x)$, $x \in \Omega$. $\mathcal{D}_i$ denote Dirichlet boundary conditions or Neumann boundary conditions. $\mathcal{D}_i v_i = \frac{\partial v_i}{\partial n}$ where n is the outward pointing normal vector and $\frac{\partial}{\partial n}$ is the normal derivative. It follows from standard maximum principles for parabolic PDEs that there are functions $\tilde{\tilde{\gamma}}_i : (0,\infty) \to (0,\infty)$ and $\underline{\tilde{\gamma}}_i : (0,\infty) \to (0,\infty)$ such that

$$\underline{\tilde{\gamma}}_i(t)\varphi_i(x) \leq v_i(t,x) \leq \tilde{\tilde{\gamma}}_i(t)\varphi_i(x) \tag{2.4}$$

for all $t > 0$, $x \in \bar{\Omega}$.

For $T \in (0, \tau_{\max})$ and $1 \leq i \leq N$ put

$$M_i = \sup\{|f_i(\tau, x, u_1(\tau, x, u_1(\tau, x), \ldots, u_N(\tau, x))| : \tau \in [0,T], x \in \bar{\Omega})\}.$$

We prove that

$$e^{\frac{\alpha_i}{\mu_i}\tilde{f}(x)-Mt} v_i(t,x) \leq u_i(t,x)$$

for $t \in [0,T]$ and $x \in \bar{\Omega}$.

We have

$$\begin{aligned}
L\left(v_i e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)-M_i t}\right) &= \frac{\partial}{\partial t}\left(v_i e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)-M_i t}\right) - \nabla\left[\mu_i \nabla\left[v_i e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)-M_i t}\right] - \alpha_i v_i e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)-M_i t}\nabla[\tilde{f}_i(x)]\right] \\
&\quad - f_i(t,x,u) v_i e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)-M_i t} \\
&= \frac{\partial}{\partial t}\left(v_i e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)-M_i t}\right) - M_i v_i e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)-M_i t} \\
&\quad - e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)-M_i t} v_i(\mu_i \nabla^2 v_i + \alpha_i \nabla \tilde{f}_i(x)\nabla v_i) - f_i(t,x,u) v_i e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)-M_i t} \\
&= v_i e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)-M_i t}(\mu_i \nabla^2 v_i + \alpha_i \nabla \tilde{f}_i(x)\nabla v_i) - M_i v_i e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)-M_i t} \\
&\quad - v_i e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)-M_i t}(\mu_i \nabla^2 v_i + \alpha_i \nabla \tilde{f}_i(x)\nabla v_i) - f_i(t,x,u_1,\ldots,u_N) v_i e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)-M_i t} \\
&= -v_i e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)-M_i t}(M_i + f_i(t,x,u_1,\ldots,u_N)) \\
&\leq 0
\end{aligned}$$

for $t \in (0,T]$ and $x \in \bar{\Omega}$.

In the case of Dirichlet boundary conditions we have

$$u_i(t,x) \geq v_i(t,x) e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)-M_i t} \tag{2.5}$$

for $t > 0$, $x \in \bar{\Omega}$ and $i = 1, \ldots, N$. In the case of no-flux boundary conditions we have

$$\begin{aligned}
\mathcal{D}\left(v_i e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)-Mt}\right) &= \mu_i \frac{\partial v_i}{\partial n}\left(v_i e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)-Mt}\right) - \alpha_i\left(v_i e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)-Mt}\right)\frac{\partial \tilde{f}_i}{\partial n} \\
&= \mu_i e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)-Mt}\frac{\partial v_i}{\partial n} = 0.
\end{aligned}$$

Again we have (2.5). In a similar way we show that

$$u_i(t,x) \leq v_i e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)+M_i t} \tag{2.6}$$

for $t \in (0,T]$, $x \in \Omega$, $i = 1, \ldots, N$.

By (2.4), (2.5) and (2.6) we have the desired inequality. □

For $i = 1, \dots, N$, the function $f_i(t, x, 0, \dots, 0)$ is called the intrinsic growth rate of the i-th species. In [7] the authors assume that the two species have the same per capita growth rate. We assume that all species have a different per capita growth rates.For this reason, our model is more realistic. To reflect the heterogeneity of environment, we assume that $\tilde{f}_i(x)$, $i = 1, \dots, N$ are non constant functions. The functions $\tilde{f}_i(x)$ can reflect the quality and quantity of resources available at the location x, where the favorable region $\{x \in \Omega : \tilde{f}_i(x) > 0\}$ acts as a resource and the unfavorable part $\{x \in \Omega : \tilde{f}_i(x) < 0\}$ is a sink region.

The assumption below is a standard boundedness assumption.

(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.

We write

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

For a bounded continuous function $c : [0, \infty) \to R$ we define its lower average by

$$m[c] := \liminf_{t-s\to\infty} \frac{1}{t-s} \int_s^t c(\tau) d\tau,$$

and its upper average by

$$M[c] := \limsup_{t-s\to\infty} \frac{1}{t-s} \int_s^t c(\tau) d\tau.$$

Further we write

$$m[f_i] := \liminf_{t-s\to\infty} \frac{1}{t-s} \int_s^t \min_{x\in\bar{\Omega}} f_i(\tau, x, 0 \dots, 0) d\tau,$$
$$M[f_i] := \limsup_{t-s\to\infty} \frac{1}{t-s} \int_s^t \min_{x\in\bar{\Omega}} f_i(\tau, x, 0 \dots, 0) d\tau.$$

We have the following inequalities:

$$\underline{a}_i \le m[f_i] \le M[f_i] \le \bar{a}_i.$$

(A3) $m[f_i] > 0$, $1 \le i \le N$,

(A4) $\frac{\partial f_i}{\partial u_j}(t, x, u) \le 0$ for all $t \ge 0$, $x \in \bar{\Omega}$, $u \in [0, \infty)^N$, $1 \le i, j \le N$, $i \ne j$,

(A5) there exist $\underline{b}_{ii} > 0$ such that $\frac{\partial f_i}{\partial u_i}(t, x, u) \le -\underline{b}_{ii}$ for all $t \ge 0$, $x \in \bar{\Omega}$, $u \in [0, \infty)^N$, $1 \le i \le N$.

We introduce now a family of ODEs which will be useful in investigating positive solutions of (ARD).

Let $u(t, x) = (u_1(t, x), \dots, u_N(t, x))$, $t \in [0, \tau_{\max})$, be a positive solution of (ARD), where f_i satisfies (A1), (A2), (A4) and (A5). For each $1 \le i \le N$ we define $\xi_i(t)$, $t \in [0, \infty)$ to be the positive positive solution of the following initial value problem

$$\begin{cases} \xi_i'(t) = (\max_{x\in\bar{\Omega}} f_i(t, x, 0, \dots, 0) - \lambda_i(\alpha_i) \min\limits_{x\in\bar{\Omega}} \tilde{f}_i(x) - \underline{b}_{ii}\xi_i)\xi_i, \\ \xi_i(0) = \sup_{x\in\bar{\Omega}} \left\{ \frac{u_i(0,x)}{\varphi_i(x)} e^{-\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)} \right\}. \end{cases} \tag{2.7}$$

Note that, by (2.1), $\xi_i(0)$ is finite for $i = 1, \dots, N$.

Lemma 2.4. *Assume that (A1), (A2), (A4) and (A5) hold. Then for any positive solution $u(t,x) = (u_1(t,x),\dots,u_N(t,x))$ of (ARD), and any $1 \le i \le N$, there holds*

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

for $t \in [0,\tau_{\max})$, $x \in \bar{\Omega}$ where $\xi_i(t)$ is the positive solution of (2.7).

Proof. Fix $1 \le i \le N$. We prove that $\xi_i(t) e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)} \varphi(x)$ is a supersolution for $u_i(t,x)$.

By assumptions (A4) and (A5),

$$\hat{f}_i(t,x,u) \le \max_{x\in\bar{\Omega}} f_i(t,x,0,\dots,0) - \underline{b}_{ii}\xi_i(t) \quad t \in (0,\tau_{\max}), x \in \Omega, \tag{2.8}$$

where

$$\hat{f}_i(t,x,u) := f_i(t,x,u_1(t,x),\dots,u_{i-1}(t,x),\xi_i(t),u_{i+1}(t,x),\dots,u_N(t,x)).$$

Hence by (2.1), (2.7), (2.8)

$$\begin{aligned}
&L(\xi_i(t) e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)} \varphi_i(x)) \\
&= \frac{\partial}{\partial t}(\xi_i(t) e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)} \varphi_i(x)) - \nabla\left[\mu_i \nabla[\xi_i(t) e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)} \varphi_i(x)] - \alpha_i \xi_i(t) e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)} \varphi_i(x) \nabla \tilde{f}_i(x)\right] \\
&\quad - f_i(t,x,u)\xi_i(t) e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)} \varphi_i(x) \\
&= \xi_i(t) e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)} \varphi_i(x) \frac{\partial \xi_i}{\partial t} - \xi_i(t) e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)} \left(\alpha_i \nabla \tilde{f}_i(x) \nabla \varphi_i(x) + \nabla^2 \varphi_i(x)\right) \\
&\quad - f_i(t,x,u)\xi_i(t) e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)} \varphi_i(x) \\
&\underset{(2.1),(2.7)}{=} \xi_i(t) e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)} \varphi_i(x) \left(-\lambda_i(\alpha_i) \max_{x\in\bar{\Omega}} \tilde{f}_i(x) + \max_{x\in\bar{\Omega}} f_i(t,x,0,\dots,0) - \underline{b}_{ii}\xi_i(t)\right) \\
&\quad + \xi_i(t) e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)} \lambda_i(\alpha_i)\tilde{f}_i(x)\varphi_i(x) - f_i(t,x,u)\xi_i(t) e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)} \varphi_i(x) \\
&\underset{(2.8)}{\ge} \xi_i(t) e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)} \varphi_i(x) \Big(-\alpha_i(\lambda_i(\alpha_i)) \min_{x\in\bar{\Omega}} \tilde{f}(x) + \max_{x\in\bar{\Omega}} f_i(t,x,0,\dots,0) - \underline{b}_{ii}\xi_i \\
&\qquad + \lambda_i(\alpha_i)\tilde{f}_i(x) - (\max_{x\in\bar{\Omega}} f_i(t,x,0,\dots,0) - \underline{b}_{ii}\xi_i)\Big) \\
&\ge 0
\end{aligned}$$

for $t \in (0,\tau_{\max})$ and $x \in \bar{\Omega}$.

In the case of Dirichlet boundary conditions we have

$$\mathcal{D}(\xi_i(t) e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)} \varphi_i(x)) > 0, \qquad x \in \partial\Omega,\ t \in (0,\tau_{\max}).$$

In the case of no-flux boundary conditions we have

$$\begin{aligned}
\mathcal{D}(\xi_i(t) e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)} \varphi_i(x)) &= \mu_i \frac{\partial}{\partial n}(\xi_i(t) e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)} \varphi_i(x)) - \alpha_i \xi_i(t) e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)} \varphi_i(x) \frac{\partial \tilde{f}_i(x)}{\partial n} \\
&= \mu_i \xi_i(t) e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)} \frac{\varphi_i(x)}{\partial n} = 0, \qquad x \in \partial\Omega,\ t \in (0,\tau_{\max})
\end{aligned}$$

for $t \in (0,\tau_{\max})$ and $x \in \partial\Omega$. Moreover,

$$\xi_i(0) e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)} \varphi_i(x) = \sup_{x\in\bar{\Omega}} \left\{ \frac{u_i(0,x)}{\varphi_i(x)} e^{-\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)} \right\} e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)} \varphi_i(x) \ge u_i(0,x)$$

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

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

for all $t \in (0, \tau_{\max})$ and $x \in \bar{\Omega}$. $\square$

Lemma 2.5. *Assume (A1)–(A5) and $\bar{a}_i - \lambda_i(\alpha_i)\min_{x\in\bar{\Omega}} \tilde{f}_i(x) \ge 0$. Then for any maximally defined positive solution $u(t,x) = (u_1(t,x), \dots, u_N(t,x))$ of (ARD) we have*

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

(ii) $\limsup_{t\to\infty} u_i(t,x) \le \frac{z_i}{\underline{b}_{ii}}$, *where $z_i = \bar{a}_i - \lambda_i(\alpha_i)\min_{x\in\bar{\Omega}} \tilde{f}_i(x)$ where the limit is uniformly in $x \in \Omega$.*

Proof. By the standard comparison results for ODEs

$$\limsup_{t\to\infty} \xi_i(t) \le \frac{z_i}{\underline{b}_{ii}} < \infty, \tag{2.9}$$

where $z_i = \bar{a}_i - \lambda_i(\alpha_i)\min_{x\in\bar{\Omega}} \tilde{f}_i(x) \ge 0$. Lemma 2.4 and (2.9) imply that there exists $t_1 \ge 0$ such that $C(\bar{\Omega})$ norm of $u_i(t,x)$ is bounded on $[t_1, \tau_{\max})$ by $(\frac{z_i}{\underline{b}_{ii}}) + 1$. From this it follows that the solutions of system (ARD) is defined for $t \in [0, \infty)$. This proves (i). The proof of (ii) is now straightforward. $\square$

Now we present the Vance and Coddinton result [28] which we use in the proof of the main theorem of this paper.

First we define $c : [t_0, \infty) \to \mathbb{R}$, where $t_0 > 0$ to be a bounded continuous function where $\underline{c}, \bar{c} > 0$ are such that $-\underline{c} \le c(t) \le \bar{c}$ for all $t \ge t_0$.. Assume moreover that there are $L > 0$ and $\beta > 0$ such that

$$\frac{1}{L}\int_t^{t+L} c(\tau)d\tau \ge \beta$$

for all $t \ge t_0$.

Proposition 2.6. *For any positive solution $\zeta(t)$ of the initial value problem*

$$\begin{cases} \zeta' = (c(t) - d\zeta)\zeta, \\ \zeta(t_0) = \zeta_0 > 0, \end{cases}$$

where the function c is as above and d is a positive constant there holds

$$\frac{\beta}{d} e^{-L(\underline{c}+\beta)} \le \liminf_{t\to\infty} \zeta(t) \le \limsup_{t\to\infty} \zeta(t) \le \frac{\bar{c}}{d}.$$

Assumptions (A3) and (A5) imply that there exist $L > 0$ and $\beta > 0$ such that

$$\frac{1}{L}\int_t^{t+L} \max_{x\in\bar{\Omega}} f_i(\tau, x, 0, \dots, 0)d\tau \ge \beta$$

for all $t \ge 0$ and $1 \le i \le N$.

If we let $c(t) = \max_{x\in\bar{\Omega}} f_i(t,x,0,\dots,0)$, $d_i = b_{ii}$ and $\bar{a}_i > \lambda_i(\alpha_i)\min_{x\in\bar{\Omega}} f_i(x)$ then Proposition 2.6 implies that there exists $\hat{\delta}_i > 0$ which does not depend of the solution $\xi_i(t)$ such that

$$\hat{\delta}_i \le \liminf_{t\to\infty} \xi_i(t) \le \limsup_{t\to\infty} \xi_i(t) \le \frac{\bar{a}_i - \lambda_i(\alpha_i)\min\limits_{x\in\bar{\Omega}} \tilde{f}_i(x)}{\underline{b}_{ii}}. \tag{2.10}$$

For $1 \leq i, j \leq N$ and $\varepsilon \geq 0$ we define $\overline{b}_{ij}(\varepsilon)$ as the supremum

$$\left\{ -\frac{\partial f_i}{\partial u_j}(t,x,u) : t \geq 0,\ x \in \bar{\Omega},\ u \in \left[0, \frac{\bar{a}_1 - \lambda_1(\alpha_1)\min\limits_{x\in\bar{\Omega}} f_1(x)}{\underline{b}_{11}} + \varepsilon\right] \right.$$
$$\left. \times \cdots \times \left[0, \frac{\bar{a}_N - \lambda_N(\alpha_N)\min\limits_{x\in\bar{\Omega}} f_N(x)}{\underline{b}_{NN}} + \varepsilon\right] \right\}.$$

Instead of $\overline{b}_{ij}(0)$ we write $\overline{b}_{ij}$. Assumptions (A4) and (A5) imply that $\overline{b}_{ij} \geq 0$, $1 \leq i, j, \leq N$. By (A1) it follows that $\overline{b}_{ij}(\varepsilon) < \infty$ and $\lim_{\varepsilon\to 0^+} \overline{b}_{ij}(\varepsilon) = \overline{b}_{ij}$ for $1 \leq i, j \leq N$.

3 Average conditions for permanence

In this section we formulate the main theorem of this paper. We establish conditions which guarantee that the system (ARD) is permanent. Through this section we assume that φ_i is normalized so that $\max_{x\in\bar{\Omega}} \varphi_i(x) = 1$ for $i = 1, \ldots, N$.

Theorem 3.1. *Assume (A1) through (A5) and $\bar{a}_i > \lambda_i(\alpha_i)\min\limits_{x\in\bar{\Omega}} \tilde{f}_i(x)$ for $i = 1, \ldots, N$. If*

$$m[f_i] > \lambda_i(\alpha_i)\max_{x\in\bar{\Omega}} \tilde{f}_i(x) + \sum_{\substack{j=1\\ j\neq i}}^{N} e^{\frac{\alpha_j}{\mu_j}\max\limits_{x\in\bar{\Omega}} \tilde{f}_j(x)} \frac{\overline{b}_{ij}(M[f_j] - \lambda_j(\alpha_j)\min\limits_{x\in\bar{\Omega}} \tilde{f}_j(x))}{\underline{b}_{jj}} \tag{3.1}$$

for all $1 \leq i \leq N$ then system (ARD) is permanent.

Proof. Let $\epsilon_0 > 0$ be such that

$$m[f_i] > \lambda_i(\alpha_i)\max_{x\in\bar{\Omega}} \tilde{f}_i(x) + \sum_{\substack{j=1\\ j\neq i}}^{N} e^{\frac{\alpha_j}{\mu_j}\max\limits_{x\in\bar{\Omega}} \tilde{f}_j(x)} \frac{\overline{b}_{ij}(\epsilon_0)(M[f_j] - \lambda_j(\alpha_j)\min\limits_{x\in\bar{\Omega}} \tilde{f}_j(x))}{\underline{b}_{jj}}$$

for all $1 \leq i \leq N$.

Fix a positive solution $u(t,x) = (u_1(t,x), \ldots, u_N(t,x))$ of (ARD).

Let $\xi_i(t)$, $t \geq 0$, $1 \leq i \leq N$ be the solution of (2.5) corresponding to $u(t,x)$. Let $t_0 \geq 0$ be such that $\xi_i(t) \leq \frac{\bar{a}_i - \lambda_i(\alpha_i)\min_{x\in\bar{\Omega}} \tilde{f}_i(x)}{\underline{b}_{ii}} + \frac{\epsilon}{2}$ for all $t \geq t_0$, $1 \leq i \leq N$.

Denote by $\eta_i(t)$, $1 \leq i \leq N$, $t \geq t_0$ the positive solution of the initial value problem

$$\begin{cases} \eta_i'(t) = \left(\min\limits_{x\in\bar{\Omega}} f_i(t,x,0,\ldots,0) - \lambda_i(\alpha_i)\max\limits_{x\in\bar{\Omega}} f_i(x) - \overline{b}_{ii}(\epsilon_0)\eta_i(t) \right. \\ \qquad\qquad \left. - \sum\limits_{\substack{j=1\\ j\neq i}}^{N} \overline{b}_{ij}(\epsilon_0)\xi_j(t) e^{\frac{\alpha_j}{\mu_j}\max\limits_{x\in\bar{\Omega}} f_j(x)} \right)\eta_i, \\ \eta_i(t_0) = \inf\limits_{x\in\bar{\Omega}} \left\{ \dfrac{u_i(t_0,x)}{\varphi_i(x)} e^{-\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)} \right\}. \end{cases} \tag{3.2}$$

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

By Lemma 2.4 it follows that

$$u_i(t,x) \leq \xi_i(t) e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)} \varphi_i(x) \leq \xi_i(t) e^{\frac{\alpha_i}{\mu_i}\max_{x\in\bar{\Omega}}\tilde{f}_i(x)}$$

for $t \geq t_0$ and $x \in \bar{\Omega}$.

Assumption (A1) and Lemma 2.1 imply that

$$\begin{aligned} f_i(t,x,\tilde{u}) &\geq \min_{x\in\bar{\Omega}} f_i(,x,0,\ldots,0) - \overline{b}_{ii}(\varepsilon_0)\eta_i(t)\varphi_i(x) - \sum_{\substack{j=1\\ j\neq i}}^{N} u_j(t,x) \\ &\geq \min_{x\in\bar{\Omega}} f_i(,x,0,\ldots,0) - \overline{b}_{ii}(\varepsilon_0)\eta_i(t)\varphi_i(x) - \sum_{\substack{j=1\\ j\neq i}}^{N} \xi_j(t) e^{\frac{\alpha_i}{\mu_i}\max_{x\in\bar{\Omega}}\tilde{f}_i(x)}, \end{aligned} \tag{3.3}$$

where

$$f_i(t,x,\tilde{u}) := f_i(t,x,u_i(t,x),\ldots,u_{i-1}(t,x),\eta_i(t)\varphi_i(x),u_{i+1}(t,x),\ldots,u_N(t,x)).$$

By (2.1), (3.2), (3.3) we have

$$\begin{aligned} & L(\eta_i(t)e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)}\varphi_i(x)) \\ = \quad & \frac{\partial}{\partial t}(\eta_i(t)e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)}\varphi_i(x)) - \nabla\left[\mu_i\nabla[\eta_i(t)e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)}\varphi_i(x)] - \alpha_i\eta_i(t)e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)}\varphi_i(x)\nabla\tilde{f}_i(x)\right] \\ & - f_i(t,x,u)\eta_i(t)e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)}\varphi_i(x) \\ = \quad & \eta_i(t)e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)}\varphi_i(x)\frac{\partial\eta_i}{\partial t} - \eta_i(t)e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)}\left(\alpha_i\nabla\tilde{f}_i(x)\nabla\varphi_i(x) + \nabla^2\varphi_i(x)\right) \\ & - f_i(t,x,u)\eta_i(t)e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)}\varphi_i(x) \\ \underset{(2.1),(3.2)}{=} \quad & \eta_i(t)e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)}\varphi_i(x)\Bigg(-\lambda_i(\alpha_i)\min_{x\in\bar{\Omega}} f_i(x) + \min_{x\in\bar{\Omega}} f_i(t,x,0,\ldots,0) - \overline{b}_{ii}(\varepsilon)\eta_i(t) \\ & \qquad - \sum_{\substack{j=1\\ j\neq i}}^{N} \overline{b}_{ij}(\varepsilon)\xi_j(t)e^{\frac{\alpha_j}{\mu_j}\max_{x\in\bar{\Omega}}\tilde{f}_j(x)}\Bigg) + \eta_i(t)e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)}\lambda_i(\alpha_i)\tilde{f}_i(x)\varphi_i(x) \\ & - f_i(t,x,u)\xi_i(t)e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)}\varphi_i(x) \\ \underset{(3.3)}{\leq} \quad & \eta_i(t)e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)}\varphi_i(x)\Bigg(-\lambda_i(\alpha_i)\max_{x\in\bar{\Omega}}\tilde{f}_i(x) + \min_{x\max_{\in\bar{\Omega}}} f_i(t,x,0,\ldots,0) - \overline{b}_{ii}\eta_i \\ & \qquad - \sum_{\substack{j=1\\ j\neq i}}^{N} \overline{b}_{ij}(\varepsilon)\xi_j(t)e^{\frac{\alpha_j}{\mu_j}\max_{x\in\bar{\Omega}}\tilde{f}_j(x)} + \lambda_i(\alpha_i)\tilde{f}_i(x) \\ & \qquad - \left(\min_{x\in\bar{\Omega}} f_i(t,x,0,\ldots,0) - \overline{b}_{ii}(\varepsilon)\eta_i - \sum_{\substack{j=1\\ j\neq i}}^{N} \overline{b}_{ij}(\varepsilon)\xi_j(t)e^{\frac{\alpha_j}{\mu_j}\max_{x\in\bar{\Omega}}\tilde{f}_j(x)}\right)\Bigg) \\ \leq \quad & 0 \end{aligned}$$

for $t \geq t_0$ and $x \in \Omega$. In the case of the Dirichlet boundary conditions we have

$$\mathcal{D}(\eta_i(t)e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i}\varphi_i(x)) > 0, \qquad x \in \partial\Omega,\ t \in (0, \tau_{max}).$$

In the case of the no-flux boundary conditions we have

$$\begin{aligned}\mathcal{D}(\eta_i(t)e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)}\varphi_i(x)) &= \mu_i\frac{\partial}{\partial n}(\eta_i(t)e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)}\varphi_i(x)) - \alpha_i\eta_i(t)e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)}\varphi_i(x)\frac{\partial\tilde{f}_i(x)}{\partial n}\\ &= \mu_i\eta_i(t)e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)}\frac{\partial\varphi_i(x)}{\partial n} = 0\end{aligned}$$

for $t \geq t_0$ and $x \in \partial\Omega$.

Moreover

$$\eta_i(t_0)e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)}\varphi_i(x) = \inf_{x\in\bar{\Omega}}\left\{\frac{u_i(t_0,x)}{\varphi_i(x)}e^{-\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)}\right\}e^{\frac{\alpha_i}{\mu_i}\tilde{f}_i(x)}\varphi_i(x) \leq u_i(t_0,x)$$

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

Fix $1 \leq i \leq N$. Now it suffices to apply Proposition 2.6 to equation (3.2) where

$$c(t) = \min_{x\in\bar{\Omega}} f_i(t,x,0,\dots,0) - \lambda_i(\alpha_i)\max_{x\in\bar{\Omega}}\tilde{f}_i(x) - \sum_{\substack{j=1\\j\neq i}}^{N}\bar{b}_{ij}(\epsilon_0)\xi_j(t)e^{\frac{\alpha_j}{\mu_j}\max_{x\in\bar{\Omega}}\tilde{f}_j(x)}$$

and $d = \bar{b}_{ii}(\epsilon_0)$.

Now we show that the quantities appearing in Proposition 2.6 can be chosen independently of the solution $u(t,x)$ at least for sufficiently large t.

It is easy to see that c is bounded from above with the bound independent of $u(t,x)$.

Take β and β' such that

$$0 < \beta < \beta' < m[f_i] - \lambda_i(\alpha_i)\max_{x\in\bar{\Omega}}\tilde{f}_i(x) - \sum_{\substack{j=1\\j\neq i}}^{N}e^{\frac{\alpha_j}{\mu_j}\max_{x\in\bar{\Omega}}\tilde{f}_j(x)}\frac{\bar{b}_{ij}(\epsilon_0)(M[f_j] - \lambda_j(\alpha_j)\min_{x\in\bar{\Omega}} f_j(x))}{\underline{b}_{jj}}. \tag{3.4}$$

Integrating inequality (2.7) from t to $t+L$ we have that

$$\frac{\underline{b}_{jj}}{L}\int_t^{t+L}\xi_j(t)dt = \frac{1}{L}\int_t^{t+L}\max_{x\in\bar{\Omega}} f_j(t,x,0,\dots,0)dt - \lambda_j(\alpha_j)\min_{x\in\bar{\Omega}}\tilde{f}_j(x) - \frac{|\ln\xi_j(t+L) - \ln\xi_j(t)|}{L}.$$

Hence

$$\underline{b}_{jj}M[\xi_j] = M[f_j] - \lambda_j(\alpha_j)\min_{x\in\bar{\Omega}}\tilde{f}_j(x) - \frac{|\ln\xi_j(t+L) - \ln\xi_j(t)|}{L}$$

for $1 \leq j \leq N$ and $t \geq t_1$ and $L \geq L_0$.

Inequality (2.10) implies that there exists $L_0 > 0$ such that for any positive solution of $u(t,x)$ we can find $t_0 \geq 0$ such that

$$\frac{|\ln\xi_j(t+L) - \ln\xi_j(t)|}{L} < \frac{(\beta' - \beta)\underline{b}_{jj}}{N\max_{k\neq j}\bar{b}_{kl}(\epsilon_0)}. \tag{3.5}$$

Therefore

$$M[\xi_j] = \frac{M[f_j]}{\underline{b}_{jj}} - \frac{\lambda_j(\alpha_j)\min_{x\in\bar{\Omega}}\tilde{f}_j(x)}{\underline{b}_{jj}} - \frac{1}{\underline{b}_{jj}}\frac{|\ln\xi_j(t+L) - \ln\xi_j(t)|}{L}.$$

Then we have that

$$
\begin{aligned}
m & \left[\min_{x\in\bar\Omega} f_i(t,x,0,\dots,0) - \lambda_i(\alpha_i)\max_{x\in\bar\Omega}\tilde f_i(x) - \sum_{\substack{j=1\\ j\neq i}}^{N} \overline{b}_{ij}(\epsilon_0)\xi_j(t))e^{\frac{\alpha_j}{\mu_j}\max_{x\in\bar\Omega}\tilde f_j(x)} \right] \\
& \geq m\left[\min_{x\in\bar\Omega} f_i(t,x,0,\dots,0)\right] - \lambda_i(\alpha_i)\max_{x\in\bar\Omega}\tilde f_i(x) - \sum_{\substack{j=1\\ j\neq i}}^{N} \overline{b}_{ij}(\epsilon_0) m[\xi_j(t)] e^{\frac{\alpha_j}{\mu_j}\max_{x\in\bar\Omega}\tilde f_j(x)} \\
& = m\left[\min_{x\in\bar\Omega} f_i(t,x,0,\dots,0)\right] - \lambda_i(\alpha_i)\max_{x\in\bar\Omega}\tilde f_i(x) \\
& \quad - \sum_{\substack{j=1\\ j\neq i}}^{N} \overline{b}_{ij}(\epsilon_0))e^{\frac{\alpha_j}{\mu_j}\max_{x\in\bar\Omega}\tilde f_j(x)} \left(\frac{M[f_i]}{\underline{b}_{ii}} - \frac{\lambda_i(\alpha_i)\min_{x\in\bar\Omega}\tilde f_i(x)}{\underline{b}_{ii}} - \frac{1}{\underline{b}_{ii}} \frac{|\ln\xi_j(t+L) - \ln\xi_j(t)|}{L} \right) \\
& = m[f_i] - \lambda_i(\alpha_i)\max_{x\in\bar\Omega}\tilde f_i(x) - \sum_{\substack{j=1\\ j\neq i}}^{N} e^{\frac{\alpha_j}{\mu_j}\max_{x\in\bar\Omega}\tilde f_j(x)} \left(\frac{\overline{b}_{ij}(\epsilon_0)}{\underline{b}_{jj}} (M[f_i] - \lambda_i(\alpha_i)\min_{x\in\bar\Omega}\tilde f_i(x) \right) \\
& \quad + \sum_{\substack{j=1\\ j\neq i}}^{N} e^{\frac{\alpha_j}{\mu_j}\max_{x\in\bar\Omega}\tilde f_j(x)} \frac{\overline{b}_{ij}(\epsilon_0)}{\underline{b}_{jj}} \frac{|\ln\xi_j(t+L) - \ln\xi_j(t)|}{L} > \beta
\end{aligned}
$$

for sufficiently large t. Now it suffices to apply Proposition 2.6 and the proof is completed. □

4 Lower estimation of δ_i

In this section we give a lower estimation on the numbers δ_i which appear in the definition of permanence in terms of the parameters of system (ARD). The assumptions in this section are slightly stronger than (2.9). Through this section we assume that φ_i is normalized so that $\max_{x\in\bar\Omega}\varphi_i(x) = 1$ for $i = 1,\dots,N$.

Theorem 4.1. *Assume (A1) through (A5) and (AC). Assume, moreover, that for some $1 \le i \le N$ a stronger inequality*

$$
m[f_i] > \lambda_i(\alpha_i)\max_{x\in\bar\Omega}\tilde f_i(x) + \sum_{\substack{j=1\\ j\neq i}}^{N} e^{\frac{\alpha_j}{\mu_j}\max_{x\in\bar\Omega}\tilde f_j(x)} \frac{\overline{b}_{ij}(\overline{a}_j - \lambda_j(\alpha_j)\min_{x\in\bar\Omega}\tilde f_j(x))}{\underline{b}_{jj}} \tag{4.1}
$$

holds.

(i) If

$$
\underline{a}_i > \lambda_i(\alpha_i)\max_{x\in\bar\Omega}\tilde f_i(x) + \sum_{\substack{j=1\\ j\neq i}}^{N} e^{\frac{\alpha_j}{\mu_j}\max_{x\in\bar\Omega}\tilde f_j(x)} \frac{\overline{b}_{ij}(\overline{a}_j - \lambda_j(\alpha_j)\min_{x\in\bar\Omega}\tilde f_j(x))}{\underline{b}_{jj}}, \tag{4.2}
$$

then

$$
\delta_i \geq \frac{1}{\underline{b}_{ii}} \left(\underline{a}_i - \lambda_i(\alpha_i)\max_{x\in\bar\Omega}\tilde f_i(x) - \sum_{\substack{j=1\\ j\neq i}}^{N} e^{\frac{\alpha_j}{\mu_j}\max_{x\in\bar\Omega}\tilde f_j(x)} \frac{\overline{b}_{ij}(\overline{a}_j - \lambda_j(\alpha_j)\min_{x\in\bar\Omega}\tilde f_j(x))}{\underline{b}_{jj}} \right).
$$

(ii) If

$$\underline{a}_i \le \lambda_i(\alpha_i)\max_{x\in\bar\Omega}\tilde f_i(x) + \sum_{\substack{j=1\\ j\ne i}}^{N} e^{\frac{\alpha_j}{\mu_j}\max_{x\in\bar\Omega}\tilde f_j(x)} \frac{\bar b_{ij}(\bar a_j - \lambda_j(\alpha_j)\min_{x\in\bar\Omega}\tilde f_j(x))}{\underline{b}_{jj}}, \tag{4.3}$$

then

$$\delta_i \ge \frac{\beta}{\bar b_{ii}}\exp(-L(m[f_i]-\underline{a}_i)),$$

where β is positive constant satisfying

$$\beta < m[f_i] - \lambda_i(\alpha_i)\max_{x\in\bar\Omega}\tilde f_i(x) - \sum_{\substack{j=1\\ j\ne i}}^{N} e^{\frac{\alpha_j}{\mu_j}\max_{x\in\bar\Omega}\tilde f_j(x)} \frac{\bar b_{ij}(\bar a_j - \lambda_j(\alpha_j)\min_{x\in\bar\Omega}\tilde f_j(x))}{\underline{b}_{jj}} \tag{4.4}$$

and $L > 0$ is such that

$$\frac{1}{L}\int_t^{t+L}\min_{x\in\bar\Omega} f_i(\tau,x,0,\dots,0)d\tau > \beta + \lambda_i(\alpha_i)\tilde f_(x) + \sum_{\substack{j=1\\ j\ne i}}^{N} e^{\frac{\alpha_j}{\mu_j}\max_{x\in\bar\Omega}\tilde f_j(x)} \frac{\bar b_{ij}(\bar a_j - \lambda_j(\alpha_j)\min_{x\in\bar\Omega}\tilde f_j(x))}{\underline{b}_{jj}}$$

for all $t \ge 0$.

Proof. Fix a positive solution $u(t,x) = (u_1(t,x),\dots,u_N(t,x))$ of (ARD). Lemma 2.5 implies that for each ϵ there is $t_0 \ge 0$ such that

$$u_i(t,x) \le \frac{\bar a_i - \lambda_i(\alpha_i)\min_{x\in\bar\Omega}\tilde f_i(x)}{\underline{b}_{ii}} + \frac{\epsilon}{2}$$

for $t \ge t_0$ $x \in \bar\Omega$, $1 \le i \le N$. For each $\epsilon > 0$ we define the positive solution $\hat\eta_i$, $t \ge t_0$ of the IVP

$$\begin{cases} \hat\eta_i'(t) = \Bigg(\min_{x\in\bar\Omega} f_i(t,x,0,\dots,0) - \lambda_i(\alpha_i)\max_{x\in\bar\Omega} f_i(x) - \bar b_{ii}(\epsilon)\hat\eta_i(t) \\ \qquad - \sum_{\substack{j=1\\ j\ne i}}^{N} e^{\frac{\alpha_j}{\mu_j}\max_{x\in\bar\Omega}\tilde f_j(x)}\bar b_{ij}(\epsilon)\left(\frac{\bar a_j - \lambda_j(\alpha_j)\min_{x\in\bar\Omega}\tilde f_j}{\underline{b}_{jj}} + \epsilon\right)\Bigg)\hat\eta_i \\ \hat\eta_i(t_0) = \inf_{x\in\bar\Omega}\left\{\frac{u_i(t_0,x)}{\varphi_i(x)}e^{-\frac{\alpha_i}{\mu_i}\tilde f_i(x)}\right\}. \end{cases}$$

Similarly as in the main theorem we prove that $u_i(t,x) \ge \hat\eta_i(t)\varphi_i(x)$ for all $t \ge t_0$, $x \in \bar\Omega$. Assume (4.2).

Let $\epsilon_0 > 0$ be so small that

$$\underline{a}_i > \lambda_i(\alpha_i)\max_{x\in\bar\Omega}\tilde f_i(x) + \sum_{\substack{j=1\\ j\ne i}}^{N} e^{\frac{\alpha_j}{\mu_j}\max_{x\in\bar\Omega}\tilde f_j(x)}\bar b_{ij}(\epsilon_0)\left(\frac{\bar a_j - \lambda_j(\alpha_j)\min_{x\in\bar\Omega}\tilde f_j(x)}{\underline{b}_{jj}} + \epsilon_0\right).$$

For each $\epsilon \in (0,\epsilon_0]$, by standard comparison principle for ODEs there holds

$$\liminf_{t\to\infty}\hat\eta_i(t) \ge \frac{1}{\bar b_{ii}(\epsilon)}\left(\underline{a}_i - \lambda_i(\alpha_i)\max_{x\in\bar\Omega}\tilde f_i(x) - \sum_{\substack{j=1\\ j\ne i}}^{N} e^{\frac{\alpha_j}{\mu_j}\max_{x\in\bar\Omega}\tilde f_j(x)}\bar b_{ij}(\epsilon)\left(\frac{\bar a_j - \lambda_j(\alpha_j)\min_{x\in\bar\Omega}\tilde f_j(x)}{\underline{b}_{jj}} + \epsilon\right)\right).$$

If $\epsilon \to 0$, then

$$\liminf_{t\to\infty} \hat{\eta}_i(t) \geq \frac{1}{\overline{b}_{ii}} \left(\underline{a}_i - \lambda_i(\alpha_i) \max_{x\in\bar{\Omega}} \tilde{f}_i(x) - \sum_{\substack{j=1\\ j\neq i}}^{N} e^{\frac{\alpha_j}{\mu_j} \max_{x\in\bar{\Omega}} \tilde{f}_j(x)} \overline{b}_{ij} \left(\frac{\overline{a}_j - \lambda_j(\alpha_j) \min_{x\in\bar{\Omega}} \tilde{f}_j(x)}{\underline{b}_{jj}} \right) \right).$$

Now we assume (4.3). Let $\beta > 0$ be such that

$$\beta < m[f_i] - \lambda_i(\alpha_i) \max_{x\in\bar{\Omega}} \tilde{f}_i(x) - \sum_{\substack{j=1\\ j\neq i}}^{N} e^{\frac{\alpha_j}{\mu_j} \max_{x\in\bar{\Omega}} \tilde{f}_j(x)} \frac{\overline{b}_{ij}(\epsilon_0)(\overline{a}_j - \lambda_j(\alpha_j) \min_{x\in\bar{\Omega}} \tilde{f}_j(x))}{\underline{b}_{jj}}$$

and take $L > 0$ such that

$$\frac{1}{L} \int_t^{t+L} \min_{x\in\bar{\Omega}} f_i(t,x,0,\dots,0) > \beta + \lambda_i(\alpha_i) \max_{x\in\bar{\Omega}} \tilde{f}_i(x) - \sum_{\substack{j=1\\ j\neq i}}^{N} \frac{\overline{b}_{ij}(\epsilon_0)(\overline{a}_j - \lambda_j(\alpha_j) \min_{x\in\bar{\Omega}} \tilde{f}_j(x))}{\underline{b}_{jj}}$$

for all $t \geq 0$. Let $\epsilon_0 > 0$ be so small that

$$\beta < m[f_i] - \lambda_i(\alpha_i) \max_{x\in\bar{\Omega}} \tilde{f}_i(x) - \sum_{\substack{j=1\\ j\neq i}}^{N} e^{\frac{\alpha_j}{\mu_j} \max_{x\in\bar{\Omega}} \tilde{f}_j(x)} \overline{b}_{ij}(\epsilon_0) \left(\frac{\overline{a}_j - \lambda_j(\alpha_j) \min_{x\in\bar{\Omega}} \tilde{f}_j(x)}{\underline{b}_{jj}} + \epsilon \right).$$

For $\epsilon \in (0, \epsilon_0]$ put

$$\begin{aligned} \hat{c}(t) := {} & \min_{x\in\bar{\Omega}} f_i(t,x,0,\dots,0) - \lambda_i(\alpha_i) \max_{x\in\bar{\Omega}} \tilde{f}_i(x) \\ & - \sum_{\substack{j=1\\ j\neq i}}^{N} e^{\frac{\alpha_j}{\mu_j} \max_{x\in\bar{\Omega}} \tilde{f}_j(x)} \overline{b}_{ij}(\epsilon_0) \left(\frac{\overline{a}_j - \lambda_j(\alpha_j) \min_{x\in\bar{\Omega}} \tilde{f}_j(x)}{\underline{b}_{jj}} + \epsilon \right). \end{aligned}$$

It is easy to see that

$$\hat{c}(t) \geq -\underline{\hat{c}}$$

for all $t \geq t_0$, where

$$\underline{\hat{c}} = -\underline{a}_i + \lambda_i(\alpha_i) \max_{x\in\bar{\Omega}} \tilde{f}_i(x) + \sum_{\substack{j=1\\ j\neq i}}^{N} e^{\frac{\alpha_j}{\mu_j} \max_{x\in\bar{\Omega}} \tilde{f}_j(x)} \overline{b}_{ij} \left(\frac{\overline{a}_j - \lambda_j(\alpha_j) \min_{x\in\bar{\Omega}} \tilde{f}_j(x)}{\underline{b}_{jj}} + \epsilon \right).$$

Now it suffices to apply Proposition 2.6 which gives the following inequality

$$\begin{aligned} \liminf_{t\to\infty} \hat{\eta}_i(t) \geq \frac{\beta}{\overline{b}_{ii}}(\epsilon_0) \exp \Bigg\{ -L \Bigg(& \beta - \overline{a}_i + \lambda_i(\alpha_i) \max \tilde{f}_i(x) \\ & + \sum_{\substack{j=1\\ j\neq i}}^{N} e^{\frac{\alpha_j}{\mu_j} \max_{x\in\bar{\Omega}} \tilde{f}_j(x)} \overline{b}_{ij}(\epsilon_0) \left(\frac{\overline{a}_j - \lambda_j(\alpha_j) \min \tilde{f}_j(x)}{\underline{b}_{jj}} + \epsilon \right) \Bigg) \Bigg\}. \end{aligned}$$

If $\epsilon \to 0$ then

$$\begin{aligned}\liminf_{t\to\infty} \frac{u_i(t,x)}{\varphi(x)} & \\ \geq \frac{\beta}{\overline{b}_{ii}} \exp & \left\{ -L \left(\beta - \overline{a}_i + \lambda_i(\alpha_i) \max \tilde{f}_i(x) + \sum_{\substack{j=1 \\ j\neq i}}^{N} e^{\frac{\alpha_j}{\mu_j} \max\limits_{x\in\bar{\Omega}} \tilde{f}_j(x)} \overline{b}_{ij} \left(\frac{\overline{a}_j - \lambda_j(\alpha_j) \min \tilde{f}_j(x)}{\underline{b}_{jj}} \right) \right) \right\}.\end{aligned}$$

Therefore from (4.4)

$$\liminf_{t\to\infty} \frac{u_i(t,x)}{\varphi(x)} \geq \frac{\beta}{\underline{b}_{ii}} \exp(-L(m[f_i] - \overline{a}_i)). \qquad \square$$

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