On Logistic Models with a Carrying Capacity Dependent Diffusion: Stability of Equilibria and Coexistence with a Regularly Diffusing Population

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Abstract

We consider the reaction-diffusion equation describing the population with the logistic type of growth and diffusion stipulated by the carrying capacity K, which leads to the term $D\Delta(u/K)$, where u is the population level. In the logistic model the introduction of the standard diffusion term Δu (incorporated with the zero Neumann boundary conditions) leads to the situation when the population tends to be equally distributed over the space available, even if the carrying capacity $K(x)$ varies significantly with location. The strategy with a K-driven diffusion is compared to the model with standard diffusion, and we demonstrate that for two competing populations with two different strategies, the equilibrium where only the species which follows K-driven diffusion survives, is globally asymptotically stable.

Keywords: logistic equation, diffusion, global attractivity, system of partial differential equations, coexistence, semi-trivial equilibria

AMS subject classification: 92D25, 35K57 (primary), 35K50, 37N25

1 Introduction

Introducing spatial distribution of species in mathematical description of population dynamics aims to explain certain real world phenomena such as stocking and patterns formation. The simplest models of population growth are either ordinary differential or difference equations; however, incorporating diffusion in these models aims to reveal evolutionary mechanisms responsible for population dispersal. Generally, the addition of a regular $D\Delta u$ diffusion term leads to the uniform limit free distribution as $D \to \infty$, which is not feasible for systems where the carrying capacity is space-dependent. Moreover, it brings the conclusion [6] that in the competition of several populations which differ by the dispersion speed only, the slowest population always wins. There were several attempts to model systems with non-uniformly distributed resources, for example, to introduce the advection along an environmental gradient [1, 4]. Usually the zero Neumann boundary conditions were considered (assuming that

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the population is closed and that there is no flux through the isolated boundaries, or that immigration to the domain is compensated by emigration).

In [2, 9] we introduced an alternative type of diffusion when ultimately the population tends to have not a uniform distribution over the domain but the uniform per capita available resources. This means that not u but u/K diffuses. In particular, together with the logistic growth law, this leads to the following initial-boundary value problem:

$$\frac{\partial u(t,x)}{\partial t} = D\Delta\left(\frac{u(t,x)}{K(x)}\right) + r(x)u(t,x)\left(1 - \frac{u(t,x)}{K(x)}\right),\ t>0,\ x\in\Omega, \tag{1.1}$$

with the Neumann boundary condition

$$\frac{\partial\left(\frac{u}{K}\right)}{\partial n} = 0,\ t>0,\ x\in\partial\Omega, \tag{1.2}$$

and the initial condition

$$u(0,x) = u_0(x),\ x\in\Omega. \tag{1.3}$$

The above system models the dynamics of a single population with a diffusion strategy corresponding to the term $D\Delta(u/K)$, where $K(x)$ is the carrying capacity of the environment. In contrast to the "classical" diffusion $D\Delta u$, the term $D\Delta(u/K)$ means that the population moves from the regions with lower to higher per capita available resources.

The purpose of the present paper is to consider two populations competing for the resources — one having the proposed carrying capacity driven diffusion strategy, and the other one dispersing randomly. This approach has been used, for example, in [6, 4, 5]. Dockery *et al* [6] considered n species competing for the resources. The species differ only by their diffusion coefficient and their diffusion strategy is a random dispersal. The main result is that the phenotype with the smallest diffusion coefficient has an evolutionary advantage in the sense that the only stable equilibrium is the one where only this phenotype survives. In [4] the authors consider two competing species, one of which disperses only by random diffusion, and the second one by both random diffusion and advection along an environmental gradient. The diffusion coefficients were assumed to be constant but did not have to be equal for both species. Depending on the relation between the diffusion coefficients and the coefficient of an advection term, results on stability of different equilibrium states were obtained in [4]. In [5] the same authors defined an ideal-free distribution strategy by introducing a diffusion term similar to the one in (1.1). Then they considered two competing species, one assuming the proposed diffusion strategy, and the strategy of the second one differs by a small perturbation function. Furthermore, the authors make a conclusion that if the perturbation is small enough, the phenotype with an ideal-free distribution strategy always survives while the second one extincts. This means that diffusion leads to evolutionary disadvantage which is intuitively hard to interpret.

In the present paper, we demonstrate that the population which disperses in accordance with the resources distribution has an evolutionary advantage over the one with the random dispersal, independently of the values of the diffusion coefficients: they can coincide or be different for the two populations. In contrast to many publications where only local stability is proved while global convergence is justified numerically, we present a rigorous proof of the global asymptotic stability of the equilibrium for which the population with the random dispersal extincts, while the other survives. Moreover, we illustrate by an analytical example that for time-independent carrying capacity, random diffusion leads to a lower average population level. However, this cannot be extended to the case of time-dependent carrying capacity, as another example demonstrates. Really, if available resources are quickly changing, the movement to the place where available resources are highest at the moment may not be the best strategy.

We consider the following system of parabolic equations with the Neumann boundary conditions:

$$\begin{cases} \dfrac{\partial u(t,x)}{\partial t} = D\Delta\left(\dfrac{u(t,x)}{K(x)}\right) + r(x)u(t,x)\left(1-\dfrac{u(t,x)+v(t,x)}{K(x)}\right), \; t>0, \; x\in\Omega, \\ \dfrac{\partial v(t,x)}{\partial t} = \nabla\cdot d(x)\nabla v(t,x) + r(x)v(t,x)\left(1-\dfrac{v(t,x)+u(t,x)}{K(x)}\right), \; t>0, \; x\in\Omega, \\ \dfrac{\partial(u/K)}{\partial n} = d(x)\dfrac{\partial v}{\partial n} = 0, \; x\in\partial\Omega \end{cases} \tag{1.4}$$

with the initial conditions

$$u(0,x) = u_0(x), \quad v(0,x) = v_0(x). \tag{1.5}$$

We assume that $K(x)$ is in the class $C^{1+\alpha}(\overline{\Omega})$, $K(x) > 0$ for any $x \in \overline{\Omega}$, the growth rate $r(x)$ is positive and continuous in $\overline{\Omega}$. For the diffusion coefficient of the second species with a regular diffusion, we assume $d(x) > 0$ in $\overline{\Omega}$ and $d(x) \in C^1(\overline{\Omega})$. Ω is a an open nonempty bounded domain with $\partial\Omega \in C^{2+\alpha}$, $0 < \alpha < 1$. For detailed definitions of Hölder spaces see e.g. [7].

Remark 1.1. *The diffusion coefficient $d(x)$ for the second species with the density $v(t,x)$ is in general space-dependent. To match the diffusion coefficients for both species we need to put $d(x) = D/K(x)$.*

Our approach to establishing an evolutionary advantage is to study the stability of so-called semi-trivial equilibria of the system (1.4), which are $(\tilde{u}, 0)$, $(0, \tilde{v})$, when only one species survives [6, 4, 5]. It is easy to see that the functions $\tilde{u}$ and $\tilde{v}$ are solutions of the following elliptic boundary value problems

$$\begin{cases} D\Delta\left(\dfrac{\tilde{u}(x)}{K(x)}\right) + r(x)\tilde{u}(x)\left(1-\dfrac{\tilde{u}(x)}{K(x)}\right) = 0, \; x\in\Omega, & (1.6) \\ \dfrac{\partial(\tilde{u}/K)}{\partial n} = 0, \; x\in\partial\Omega & (1.7) \end{cases}$$

and

$$\begin{cases} \nabla\cdot d(x)\nabla\tilde{v}(x) + r(x)\tilde{v}(x)\left(1-\dfrac{\tilde{v}(x)}{K(x)}\right) = 0, \; x\in\Omega, & (1.8) \\ \dfrac{\partial\tilde{v}}{\partial n} = 0, \; x\in\partial\Omega, & (1.9) \end{cases}$$

respectively.

It is also convenient for future analysis to introduce the substitution $\tilde{w} = \tilde{u}/K$. The steady-state problem (1.6), (1.7) for $\tilde{w}$ becomes

$$\begin{cases} \dfrac{D}{K(x)}\Delta\tilde{w}(x) + r(x)\tilde{w}(x)\left(1-\tilde{w}(x)\right) = 0, \ x \in \Omega, & (1.10) \\ \dfrac{\partial \tilde{w}}{\partial n} = 0, \ x \in \partial\Omega & (1.11) \end{cases}$$

The paper is organized as follows. In Section 2 we present results on existence, uniqueness and positivity of solutions for considered systems. In Section 3 different equilibrium states of system (1.4) are studied and our main result is justified: the semi-trivial equilibrium $(\tilde{u}, 0)$ of system (1.4) is globally asymptotically stable. This means that in the competition for resources the carrying capacity driven diffusion strategy provides survival, while the classical diffusion leads to extinction. However, there is the second approach to estimating fitness, namely by an average limit population level. If the growth rate is constant, then the strategy with a carrying capacity driven diffusion is better than with a regular diffusion in this sense as well. In Section 4 we present two analytical examples exposing the relationship between average population levels for models with the two types of diffusion. If the growth rate is constant and the carrying capacity is time-independent, carrying capacity driven diffusion leads to higher average population levels, which is confirmed by the first example. However, this is not the case, generally, for time-dependent carrying capacities, as the second example demonstrates. Section 5 involves discussion and states some open problems. Finally, Appendix A outlines auxiliary results used earlier in the proofs.

2 Existence and uniqueness theorems

2.1 Scalar equations

In this section we establish some results for scalar equations of the form (1.1)-(1.3) which will be used in our further investigation of systems. The next two theorems have been proven in [9].

Theorem 2.1. *[9] Let $u_0(x) \in C(\Omega)$, $u_0(x) \geq 0$ in Ω and $u_0(x) > 0$ in some open bounded nonempty domain $\Omega_1 \subset \Omega$. Then there exists a unique solution $u(t,x)$ of problem (1.1)-(1.3), and it is positive.*

Theorem 2.2. *[9] The function $u(x) := K(x)$ is an equilibrium solution of (1.1)-(1.3). Moreover, for any $u_0(x) \geq 0$, $u_0(x) \not\equiv 0$ the solution $u(t,x)$ of (1.1)-(1.3) satisfies*

$$\lim_{t\to\infty} u(t,x) = K(x)$$

uniformly in $x \in \overline{\Omega}$.

We will also need existence and convergence results for scalar systems involving a classical diffusion term

$$\begin{aligned} &\frac{\partial v(t,x)}{\partial t} = \nabla \cdot d(x)\nabla v(t,x) + r(x)v(t,x)\left(1 - \frac{v(t,x)}{K(x)}\right), && t > 0, \ x \in \Omega, \\ &\frac{\partial v}{\partial n} = 0, && t > 0, \ x \in \partial\Omega, \\ &v(0,x) = v_0(x), && x \in \Omega. \end{aligned} \tag{2.1}$$

Theorem 2.3. *Let $v_0(x) \in C(\Omega)$, $v_0(x) \geq 0$ in Ω and $v_0(x) > 0$ in some open bounded nonempty domain $\Omega_1 \subset \Omega$. Then there exists a unique solution $v(t,x)$ of the problem (2.1), and it is positive.*

Theorem 2.4. *There exists a unique positive equilibrium $v^*(x)$ of problem (2.1). Moreover, for any $v_0(x) \geq 0$, $v_0(x) \not\equiv 0$ the solution $v(t,x)$ of (2.1) satisfies*

$$\lim_{t\to\infty} v(t,x) = v^*(x)$$

uniformly in $x \in \overline{\Omega}$.

These results are well known and the proofs can be found, for example, in [3, 10].

2.2 Systems

In this section we establish existence and uniqueness results for a positive solution of a time-dependent problem for competing species. We use the method of upper and lower solutions [10]; more precisely, we will apply Theorem 6.1 from Appendix A to system (2.2) obtained after the substitution.

Theorem 2.5. *For any $u_0(x), v_0(x) \in C(\Omega)$, problem (1.4) has a unique solution (u,v). Moreover, if the initial condition $(u_0(x), v_0(x))$ is nonnegative and nontrivial, then $u(t,x) > 0$, $v(t,x) > 0$ for any $t > 0$.*

Proof. After the substitution $w(t,x) = u(t,x)/K(x)$, system (1.4) becomes

$$\begin{cases} \dfrac{\partial w(t,x)}{\partial t} = \dfrac{D}{K(x)} \Delta w(t,x) + r(x) w(t,x) \left(1 - w(t,x) - \dfrac{v(t,x)}{K(x)}\right), \ t>0, \ x \in \Omega, \\ \dfrac{\partial v(t,x)}{\partial t} = \nabla \cdot d(x) \nabla v(t,x) + r(x) v(t,x) \left(1 - w(t,x) - \dfrac{v(t,x)}{K(x)}\right), \ t>0, \ x \in \Omega, \\ \dfrac{\partial w}{\partial n} = d(x) \dfrac{\partial v}{\partial n} = 0, \ x \in \partial\Omega. \end{cases} \tag{2.2}$$

It is easy to check that this system is of the form (6.1). Denote

$$(\rho_w, \rho_v) = \left(\max\left\{ \sup_{x\in\Omega} \frac{u_0(x)}{K(x)}, 1 \right\}, \max\left\{ \sup_{x\in\Omega} v_0(x), \sup_{x\in\Omega} K(x) \right\} \right)$$

and define $\mathbf{S}_\rho \equiv \left\{ (w,v) \in C([0,\infty)\times\overline{\Omega}); (0,0) \leq (w,v) \leq (\rho_w, \rho_v) \right\}$.

For any functions $a_1(t,x)$, $a_2(t,x) \in C([0,\infty)\times\overline{\Omega})$ such that $a_1(t,x) \leq a_2(t,x)$, $(t,x) \in [0,\infty)\times\overline{\Omega}$, we denote by $\langle a_1, a_2 \rangle$ the set of continuous functions

$$\langle a_1, a_2 \rangle = \left\{ a(t,x) \in C([0,\infty)\times\overline{\Omega}) \,\middle|\, a_1(t,x) \leq a(t,x) \leq a_2(t,x), \ (t,x) \in [0,\infty)\times\overline{\Omega} \right\}. \tag{2.3}$$

The functions $f_1(w,v) = rw(1-w-v/K)$, $f_2(w,v) = rv(1-w-v/K)$ are C^1 and therefore Lipschitz continuous in $\mathbf{S}_\rho$. Next, the function $f_1(\cdot, v)$ is nonincreasing in $v \in \langle 0, \rho_v \rangle$, and $f_2(w,\cdot)$ is nonincreasing in $w \in \langle 0, \rho_w \rangle$, and therefore the vector function (f_1, f_2) is quasi-monotone nonincreasing in $\mathbf{S}_\rho$. Moreover, $(K(x)u_0(x), v_0(x)) \in \mathbf{S}_\rho$, and conditions (6.4) are satisfied for ρ_w, ρ_v defined above. Therefore all the conditions of Theorem 6.1 in Appendix A are satisfied, thus there exists a unique solution (w,v) of (2.2), and it is positive. Obviously, $(u,v) = (Kw, v)$ is the unique positive solution of (1.4) in $\mathbf{S}_\rho$. $\square$

3 Stability of semi-trivial equilibria

In this section we will state the results on stability of the semi-trivial equilibria for system (1.4). Some preliminary results on the existence of equilibria are presented in Section 3.1.

3.1 Existence and uniqueness of equilibria

Lemma 3.1. *The function $\tilde{u}(x) = K(x)$ is the only positive solution of (1.6)-(1.7).*

Proof. According to equations (1.6)-(1.7), the function $\tilde{u}$ is an equilibrium solution of scalar system (1.1)-(1.2). Therefore by Theorem 2.2 the unique positive solution of (1.6)-(1.7) is $\tilde{u}(x) = K(x)$. □

Lemma 3.2. *There exists a unique positive solution $\tilde{v}(x) = v^*(x)$ of (1.8)-(1.9). Moreover, if $K(x) \not\equiv const$ then*

$$\int\limits_{\Omega} r(x)K(x)dx > \int\limits_{\Omega} r(x)v^*(x)dx \tag{3.1}$$

Proof. Noting that the solution $\tilde{v}(x)$ of (1.8)-(1.9) is also an equilibrium solution of (2.1) and using Theorem 2.4, we obtain the first statement of the lemma. Next, denoting $\delta = K(x) - v^*(x)$ and substituting δ into equation (1.8), we obtain

$$\nabla \cdot d(x)\nabla v^* + \frac{r}{K}(K-\delta)\delta = 0.$$

Integrating over Ω and using (1.9) which implies $\int\limits_{\Omega} \nabla \cdot d(x)\nabla v^* \, dx = 0$, we get

$$\int\limits_{\Omega} r\delta \, dx - \int\limits_{\Omega} r\frac{\delta^2}{K} \, dx = 0, \quad \text{so} \quad \int\limits_{\Omega} r\delta \, dx = \int\limits_{\Omega} r\frac{\delta^2}{K} > 0, \text{ if } v^* \not\equiv K.$$

Thus, $\int\limits_{\Omega} r(x)K(x) \, dx > \int\limits_{\Omega} r(x)v^*(x) \, dx$, unless $v^*(x) \equiv K(x)$. One can check that $K(x)$ is not a solution of (1.8)-(1.9) unless $K = const$ which concludes the proof. □

Remark 3.1. *If the growth rate r is constant, it follows from Lemma 3.2 that the average population level in the equilibrium state is always greater in the case of carrying capacity driven diffusion than in the case of classical diffusion, see Example 1.*

The next result is concerned with a coexistence state for system (1.4) of competing species.

Theorem 3.1. *If $K(x) \not\equiv const$ then there is no coexistence state (u_s, v_s) for system (1.4).*

Proof. Let us assume the contrary that there exists a strictly positive equilibrium solution (u_s, v_s) of (1.4). Then (u_s, v_s) satisfies

$$\begin{cases} D\Delta\left(\dfrac{u_s(x)}{K(x)}\right) + r(x)u_s(x)\left(1 - \dfrac{u_s(x)+v_s(x)}{K(x)}\right) = 0, \; x \in \Omega, \\ \nabla \cdot d(x)\nabla v_s(x) + r(x)v_s(x)\left(1 - \dfrac{v_s(x)+u_s(x)}{K(x)}\right) = 0, \; x \in \Omega, \\ \dfrac{\partial(u_s/K)}{\partial n} = d(x)\dfrac{\partial v_s}{\partial n} = 0, \; x \in \partial\Omega \end{cases} \tag{3.2}$$

By adding the first two equations in (3.2) and proceeding as in the proof of Lemma 3.2 we can show that the strict inequality

$$\int_\Omega r(x)K(x)dx > \int_\Omega r(x)(u_s(x)+v_s(x))dx \tag{3.3}$$

is valid unless $u_s(x)+v_s(x) \equiv K(x)$. Therefore, we need to consider two cases

1. If $\mathbf{u_s(x)}+\mathbf{v_s(x)} \equiv \mathbf{K(x)}$, then $w_s = u_s/K$ and v_s satisfy

$$\begin{aligned} &\Delta w_s = 0, \quad x \in \Omega & &\nabla \cdot d(x)\nabla v_s = 0, \quad x \in \Omega \\ &\frac{\partial w_s}{\partial n} = 0, \quad x \in \partial\Omega & &\frac{\partial v_s}{\partial n} = 0, \quad x \in \partial\Omega \end{aligned}$$

   and therefore $w_s = const$, $v_s = const$ (see e.g. [7]). Since $w_sK + v_s = K$ and K is not constant, it follows that $v_s = 0$, $w_s = 1$, which contradicts $v_s > 0$.

2. Let $\mathbf{u_s(x)}+\mathbf{v_s(x)} \not\equiv \mathbf{K(x)}$. Consider the eigenvalue problem

$$\begin{aligned} &\frac{D}{K(x)}\Delta\psi(x) + r(x)\psi(x)\left(1 - \frac{v_s(x)}{K(x)} - w_s(x)\right) = \sigma\psi(x), \quad & x \in \Omega \\ &\frac{\partial \psi}{\partial n} = 0, & x \in \partial\Omega \end{aligned} \tag{3.4}$$

   According to the variational characterization of eigenvalues [3], its principal eigenvalue is given by

$$\sigma_1 = \sup_{\psi \neq 0, \psi \in W^{1,2}} \frac{-\int_\Omega D|\nabla\psi|^2 dx + \int_\Omega K\psi^2 r(1 - v_s/K - w_s)dx}{\int_\Omega K\psi^2 dx}$$

   Upon substituting $\psi = 1$ and using (3.3), we obtain

$$\sigma_1 \geq \frac{\int_\Omega r(K - v_s - w_sK)dx}{\int_\Omega K dx} > 0 \tag{3.5}$$

   However, since (w_s, v_s) is an equilibrium solution of (2.2), w_s satisfies

$$\begin{aligned} &\frac{D}{K(x)}\Delta w_s(x) + r(x)w_s(x)\left(1 - \frac{v_s(x)}{K(x)} - w_s(x)\right) = 0, \quad & x \in \Omega \\ &\frac{\partial w_s}{\partial n} = 0, & x \in \partial\Omega \end{aligned}$$

   and is therefore a positive principal eigenfunction of (3.4) with the principal eigenvalue 0. This is a contradiction with (3.5).

□

3.2 Stability analysis

In this section we describe all possible equilibrium states of system (1.4) and discuss their stability.

Definition. The equilibrium (c,d) of (1.4) is **globally asymptotically stable** if for any nonnegative nontrivial $u_0, v_0 \in C(\overline{\Omega})$ the solution $(u(t,x), v(t,x))$ of (1.4), (1.5) satisfies

$$(u,v) \to (c,d) \quad \text{as} \quad t \to \infty.$$

uniformly in $x \in \overline{\Omega}$.

We first state the main result of the present paper.

Theorem 3.2. *The semi-trivial equilibrium $(K,0)$ of (1.4) is globally asymptotically stable.*

The proof is postponed until the end of the section. The next theorem deals with the stability of the second semi-trivial equilibrium of (1.4).

Theorem 3.3. *The semi-trivial equilibrium $(0, v^*(x))$ of (1.4) is unstable.*

Proof. Once again, we consider problem (2.2) obtained after the substitution $w = u/K$. The semi-trivial equilibrium of (2.2) corresponding to the semi-trivial equilibrium $(0, v^*(x))$ of (1.4) is again $(0, v^*(x))$. Since $K(x)$ is strictly positive and bounded from above in $\overline{\Omega}$, stability of the equilibrium $(0, v^*(x))$ of system (1.4) is equivalent to stability of the equilibrium $(0, v^*(x))$ of (2.2) and therefore we will investigate the latter system. To this end, let us consider the linearization of (2.2) around $(0, v^*(x))$

$$\begin{cases} \dfrac{\partial w(t,x)}{\partial t} = \dfrac{D}{K(x)}\Delta w(t,x) + r(x)w(t,x)\left(1 - \dfrac{v^*(x)}{K(x)}\right), \ t>0, \ x \in \Omega, \\ \dfrac{\partial v(t,x)}{\partial t} = \nabla \cdot d(x)\nabla v(t,x) + r(x)v(t,x)\left(1 - \dfrac{2v^*(x)}{K(x)}\right) - r(x)v^*(x)w(t,x), \ t>0, \ x \in \Omega, \\ \dfrac{\partial w}{\partial n} = d(x)\dfrac{\partial v}{\partial n} = 0, \ x \in \partial\Omega \end{cases}$$

and study the associated eigenvalue problem

$$\begin{aligned} & \frac{D}{K(x)}\Delta\psi(x) + r(x)\psi(x)\left(1 - \frac{v^*(x)}{K(x)}\right) = \sigma\psi(x), \ x \in \Omega \\ & \frac{\partial \psi}{\partial n} = 0, \ x \in \partial\Omega \end{aligned} \tag{3.6}$$

$$\begin{aligned} & \nabla \cdot d(x)\nabla\phi(x) + r(x)\phi(x)\left(1 - \frac{2v^*(x)}{K(x)}\right) - r(x)v^*(x)\psi(x) = \sigma\phi(x), \ x \in \Omega \\ & d(x)\frac{\partial \phi}{\partial n} = 0, \ x \in \partial\Omega \end{aligned} \tag{3.7}$$

If the principal eigenvalue is positive then the semi-trivial equilibrium $(0, v^*)$ is unstable. Consider the first equation in (3.6), according to the variational characterization of the eigenvalues [3] the principal eigenvalue is given by

$$\sigma_1 = \sup_{\psi \neq 0, \psi \in W^{1,2}} \frac{-\int\limits_\Omega D|\nabla\psi|^2 dx + \int\limits_\Omega K\psi^2 r(1 - v^*/K)dx}{\int\limits_\Omega K\psi^2 dx}.$$

Upon substituting $\psi = 1$ and using (3.1), we have $\sigma_1 \geq \dfrac{\int\limits_\Omega r(K - v^*)dx}{\int\limits_\Omega K dx} > 0$, which concludes the proof. $\square$

The following theorem deals with the trivial equilibrium.

Theorem 3.4. *The trivial equilibrium* $(0,0)$ *of system (1.4) is unstable. Moreover, it is a repelling equilibrium.*

Proof. Similar to the proof of Theorem 3.3, we linearize system (2.2) around the origin to obtain the following eigenvalue problem:

$$\begin{aligned}
&\frac{D}{K(x)}\Delta\psi(x) + r(x)\psi(x) = \sigma\psi(x),\ x \in \Omega \\
&\frac{\partial\psi}{\partial n} = 0,\ x \in \partial\Omega \\
&\nabla \cdot d(x)\nabla\phi(x) + r(x)\phi(x) = \sigma\phi(x),\ x \in \Omega \\
&d(x)\frac{\partial\phi}{\partial n} = 0,\ x \in \partial\Omega
\end{aligned} \tag{3.8}$$

Integrating (3.8) we obtain

$$\sigma_1 = \frac{\int\limits_\Omega r\phi_1\, dx}{\int\limits_\Omega \phi_1\, dx}$$

where ϕ_1 is the principal eigenfunction of (3.8), and ϕ_1 can be chosen positive. Therefore, $\sigma_1 > 0$ and the trivial equilibrium of (1.4) is unstable.

Next, we want to show that the trivial equilibrium $(0,0)$ is a repeller according to the definition (2) of Theorem 6.2. Let $\delta = \inf_{x\in\Omega} K(x)/4 > 0$ and let $u_0(x) \geq 0, v_0(x) \geq 0$ be such that $u_0(x) + v_0(x) < \delta$ and $(u_0(x), v_0(x)) \neq (0,0)$. Let us add the first two equations of the system (1.4) and then integrate over the domain Ω using the Neumann boundary conditions. We obtain

$$\frac{d}{dt}\int\limits_\Omega (u(t,x) + v(t,x))dx = \int\limits_\Omega r(x)(u(t,x) + v(t,x))\left(1 - \frac{u(t,x) + v(t,x)}{K(x)}\right)dx$$

Next, we note that $\rho = \inf_{x\in\Omega} r(x) > 0$ and as long as $u(t,x) + v(t,x) \leq 2\delta$ there holds

$$\frac{d}{dt}\int\limits_\Omega (u(t,x) + v(t,x))dx \geq \rho\int\limits_\Omega (u(t,x) + v(t,x))\left(1 - \frac{2\delta}{K(x)}\right)dx$$

or, substituting $\delta = \inf_{x\in\Omega} K(x)/4$,

$$\frac{d}{dt}\int\limits_\Omega (u(t,x) + v(t,x))dx \geq \frac{\rho}{2}\int\limits_\Omega (u(t,x) + v(t,x))dx.$$

Thus using Gronwall's lemma we obtain

$$\int\limits_\Omega (u(t,x) + v(t,x))dx \geq e^{\frac{\rho}{2}t}\int\limits_\Omega (u_0(x) + v_0(x))dx$$

And since $\int\limits_{\Omega}(u_0(x)+v_0(x))dx > 0$, we obtain that the integral $\int\limits_{\Omega}(u(t,x)+v(t,x))dx$ grows exponentially with time as long as $u(t,x)+v(t,x) \le 2\delta$. We therefore conclude that there exists $t_0 > 0$ such that $u(t_0,x)+v(t_0,x) > \delta$ for some $x \in \Omega$ and hence the trivial equilibrium is a repeller. $\square$

We are now ready to prove the main result.

Proof of Theorem 3.2.
Define the operator T_t by $T_t(\mathbf{u}_0) = \mathbf{u}$, where $\mathbf{u}_0 \equiv (u_0, v_0)$ and $\mathbf{u} \equiv (u, v)$ is a solution of (1.4)-(1.5). According to Lemma 6.1 from Appendix A, the first condition on T_t from Theorem 6.2 is satisfied. Next, condition (2) is guaranteed by Theorem 3.4, and condition (3) follows from Theorems 2.1-2.4. Finally, condition (4) can be deduced from Theorem 2.5 and Lemma 6.1 and therefore system (1.4) is a strongly monotone dynamical system and we can apply Theorem 6.2 from Appendix A. Since the semi-trivial equilibrium $(0, v^*)$ is unstable and therefore is not asymptotically stable, it excludes the possibility of (c) in Theorem 6.2. Finally, there is no coexistence state therefore the equilibrium $(K, 0)$ is globally asymptotically stable. $\square$

4 Examples

First, let us illustrate the fact that for the same $K(x)$ and constant r, the carrying capacity driven diffusion leads to a higher average population level than the regular diffusion.
Example 1. The function

$$u(x) = \cos x + A, \quad x \in [0, \pi] \tag{4.1}$$

is a stationary solution of the equation with a regular diffusion

$$\frac{\partial u(t,x)}{\partial t} = D\Delta u(t,x) + ru(t,x)\left(1 - \frac{u(t,x)}{K(x)}\right),\ t > 0,\ x \in [0,\pi], \tag{4.2}$$

where

$$K(x) = \frac{r(\cos x + A)^2}{r(\cos x + A) - D\cos x}. \tag{4.3}$$

Here $A > 1$ and $A > \left|\dfrac{r-D}{r}\right|$, thus $K(x)$ is everywhere positive. One can also check that the solution satisfies the Neumann boundary conditions $\dfrac{\partial u}{\partial x} = 0$, $x = 0, \pi$.

The stationary solution of the relevant equation with the carrying capacity driven diffusion

$$\frac{\partial u(t,x)}{\partial t} = D_1\Delta\left(\frac{u(t,x)}{K(x)}\right) + r(x)u(t,x)\left(1 - \frac{u(t,x)}{K(x)}\right),\ t > 0,\ x \in [0,\pi], \tag{4.4}$$

equals $K(x)$ defined in (4.3), here D_1 is an arbitrary positive number.

Let us demonstrate that the average population level of the stationary solution in the case of (4.4) is higher than for (4.2), i.e.

$$A\pi = \int_0^\pi (\cos x + A)\, dx = \int_0^\pi u(x)\, dx < \int_0^\pi K(x)\, dx$$

$$= \int_0^\pi \frac{r(\cos x + A)^2}{r(\cos x + A) - D\cos x}\,dx = A\pi + \int_0^\pi \frac{D\cos x(\cos x + A)}{r(\cos x + A) - D\cos x}\,dx. \tag{4.5}$$

We will prove that the second (integral) term in the last inequality is positive, which is enough to justify the inequality. To this end let us show that "the positive part" of the function under the integral (for $x \in [0, \pi/2]$) is greater than its "negative part" (for $x \in [\pi/2, \pi]$):

$$\frac{D\cos x(\cos x + A)}{r(\cos x + A) - D\cos x} > \frac{D(\cos(\pi - x)(\cos(\pi - x) + A)}{r(\cos(\pi - x) + A) - D\cos(\pi - x)}, \quad x \in \left[0, \frac{\pi}{2}\right).$$

This is equivalent to positivity of the following expression for $x \in [0, \pi/2)$:

$$\frac{D\cos x(\cos x + A)}{r(\cos x + A) - D\cos x} + \frac{D\cos x(A - \cos x)}{r(A - \cos x) + D\cos x}$$

$$= D\cos x\, \frac{(\cos x + A)(r(A - \cos x) + D\cos x) + (A - \cos x)(r(\cos x + A) - D\cos x)}{(r(\cos x + A) - D\cos x)(r(A - \cos x) + D\cos x)} > 0$$

The denominator is positive since $A > |r - D|/D$, $D > 0$, $\cos x > 0$. The numerator is positive since it equals

$$D\cos x[2r(A^2 - \cos^2 x) + 2D\cos^2 x] > 0, \quad A > 1.$$

This confirms the conclusion that the carrying capacity driven diffusion is advantageous for the total population size, and the difference between the two solutions increases with the increase of D (if $D = 0$, the two stationary solutions coincide).

The next example illustrates that for time-dependent carrying capacities, a regular diffusion can lead to higher average population levels.

Example 2. Consider the problem with the carrying capacity driven diffusion in a variable environment

$$\frac{\partial u(t,x)}{\partial t} = D_1 \Delta\left(\frac{u(t,x)}{K(t,x)}\right) + r(x)u(t,x)\left(1 - \frac{u(t,x)}{K(t,x)}\right),\ t > 0,\ x \in \Omega, \tag{4.6}$$

$$\frac{\partial\left(\frac{u}{K}\right)}{\partial n} = 0,\ t > 0,\ x \in \partial\Omega, \tag{4.7}$$

where $\Omega = [0, \pi]$, with

$$K(t,x) = e^{-Dt}\cos(x) + A, \quad A > 2.$$

Also consider the problem with the classical diffusion

$$\frac{\partial v(t,x)}{\partial t} = D\Delta v(t,x) + r(x)v(t,x)\left(1 - \frac{v(t,x)}{K(t,x)}\right),\ t > 0,\ x \in \Omega, \tag{4.8}$$

$$\frac{\partial v}{\partial n} = 0,\ t > 0,\ x \in \partial\Omega, \tag{4.9}$$

with the same carrying capacity $K(t,x)$ and the constant growth rate $r(x) \equiv r > 0$. Define an average of any function $f(t,x)$ as

$$\langle f \rangle = \lim_{T\to\infty} \frac{1}{T} \int\limits_0^T \int\limits_\Omega f(t,x)\,dx\,dt$$

when such a limit exists. We will show that there are solutions $u(t,x)$ and $v(t,x)$ of (4.6)-(4.7) and (4.8)-(4.9), respectively, such that $v(0,x) = u(0,x)$ and the following inequality holds

$$\langle u \rangle < \langle v \rangle \tag{4.10}$$

First note that $v(t,x) = K(t,x)$ is a solution of (4.8)-(4.9) with the initial condition $v(0,x) = \cos(x) + A$, and $K(t,x)$ is not a solution of (4.6)-(4.7). Then, integrating equation (4.6) from 0 to T in t and from 0 to π in x and using (4.7), we have

$$\int_0^\pi (u(T,x) - u(0,x))dx = \int_0^T \int_0^\pi ru(1 - \frac{u}{K})dxdt \tag{4.11}$$

Next, it has been shown in [9, Theorem 1] that there exists an upper solution of (4.6)-(4.7) and therefore $u(T,x)$ is uniformly bounded for any $T > 0$. Once again, denoting $\delta = K - u$, dividing equation (4.11) by T and taking the limit as $T \to \infty$, we obtain

$$0 = \lim_{T\to\infty} \frac{1}{T} \int_0^T \int_0^\pi r\delta \left(1 - \frac{\delta}{K}\right) dx\, dt,$$

or

$$\lim_{T\to\infty} \frac{1}{T} \int_0^T \int_0^\pi r\delta dxdt = \lim_{T\to\infty} \frac{1}{T} \int_0^T \int_0^\pi r\frac{\delta^2}{K} dxdt > 0,$$

since as we mentioned earlier $\delta \not\equiv 0$. Therefore,

$$\lim_{T\to\infty} \frac{1}{T} \int_0^T \int_0^\pi K(t,x)dxdt > \lim_{T\to\infty} \frac{1}{T} \int_0^T \int_0^\pi u(t,x)dxdt$$

where $u(t,x)$ is a solution of (4.6)-(4.7) with any nontrivial initial condition. In particular, with $u(0,x) = \cos(x) + A = v(0,x)$. Hence, $\langle v \rangle = \langle K \rangle > \langle u \rangle$.

5 Discussion and Open Problems

In [5] Cantrell and Cosner considered the system of two competing species which use different diffusion strategies and, generally, can be written as follows:

$$\begin{cases} \dfrac{\partial u}{\partial t} = \mu \nabla \cdot (\nabla u - u \nabla P) + u\,(m - u - v)\,,\ t > 0,\ x \in \Omega, \\ \dfrac{\partial v}{\partial t} = \nu \nabla \cdot (\nabla v - v \nabla Q) + v\,(m - u - v)\,,\ t > 0,\ x \in \Omega, \\ (\nabla u - u\nabla P) \cdot n = (\nabla v - v\nabla Q) \cdot n = 0,\ x \in \partial\Omega \end{cases} \tag{5.1}$$

Here, m is the carrying capacity of the environment and functions P and Q represent the diffusion strategies of two species. Note that if $P = \ln m$ then the first species uses the so-called 'ideal-free dispersal' strategy. Namely, in the absence of the second species $u = m$ is an equilibrium solution. The authors considered the case of *equal diffusion coefficients* $\mu = \nu$. Their main result is that $P = \ln m$ is a locally evolutionary stable strategy (ESS) meaning that if $Q = \ln m + \varepsilon R$, $R \neq const$ then $(u^*, 0)$ is a globally asymptotically stable equilibrium for $\varepsilon > 0$ small enough. The second result is that in the setting of (5.1) no other strategy can be locally ESS.

System (1.4) considered in our paper is also a system of two competing species with different diffusion strategies. First species also uses an ideal-free dispersal strategy however different from one considered by Cantrell and Cosner. More precisely, our diffusive term can be written as

$$D\Delta(u/K) = D\nabla \cdot \left(\frac{1}{K} \nabla u - \frac{u}{K} \nabla \ln K \right)$$

so we have an extra $1/K$ term in the parenthesis compared to (5.1). Next, the second species uses a random diffusion strategy $\nabla \cdot d(x) \nabla v$ with *any positive diffusion coefficient*. Our main result is that the equilibrium $(K, 0)$ is *globally asymptotically stable*. In other words, the ideal-free dispersal strategy $D\Delta(u/K)$ is always beneficial in comparison with the classical diffusion $\nabla \cdot d(x) \nabla u$ independently of diffusion coefficients.

Finally, let us outline some open problems.

1. Consider two competing species using different ideal-free dispersal strategies, for example, (5.1) and the model considered in the present paper. Does the co-existence equilibrium exist? Is the strategy of the present paper locally or even globally stable, or unstable?

2. For the equation with the carrying-capacity driven diffusion, consider the dependency on the diffusion coefficient D. If the system includes two equations which differ by the diffusion coefficient only, which population would survive (or is co-existence possible)?

3. Generalize the results of this paper to other than logistic growth laws.

4. In this paper and some other publications, the global stability of the population following a certain strategy was a criterion for evolutionary success. Compare, like in [5], equation (1.1) with its small perturbation.

5. In Section 4 we have illustrated the fact that for a carrying capacity driven diffusion with a time-independent carrying capacity and a constant growth rate, the average population level is higher than for the regular diffusion model, which is not the case if the carrying capacity can vary with time. Give the general description of the models which lead to higher limit average population for a carrying capacity driven diffusion.

6. Consider models with periodic time-dependent carrying capacity and growth rates. For simplicity, investigate stability of possible equilibria (couples of periodic functions) in the case when the dispersion rate D is very high. Investigate the same problem for variable growth rates and also for intermediate dispersion rates.

6 Appendix A

In this section we present auxiliary results used in the proofs of Sections 2 and 3. The next theorem from [10] deals with the time-dependent solution of the system of the form

$$\frac{\partial u_i}{\partial t} - L_i u_i = f_i(x, u_1, u_2), \quad t > 0, \ x \in \Omega$$

$$\frac{\partial u_i}{\partial n} = 0, \ x \in \partial\Omega \tag{6.1}$$
$$u_i(0,x) = u_{i,0}(x), \ x \in \Omega, \quad i = 1,2,$$

where for $i = 1,2$ the operators L_i defined as

$$L_i u := \sum_{i,j=1}^{n} a_{ij}(t,x)\frac{\partial^2 u}{\partial x_i \partial x_j} + \sum_{i=1}^{n} b_i(t,x)\frac{\partial u}{\partial x_i} \tag{6.2}$$

are uniformly elliptic, namely, there exist positive numbers λ and Λ such that for every vector $\xi = (\xi_1, ..., \xi_n) \in \mathbb{R}^n$

$$\lambda|\xi|^2 \le \sum_{i,j=1}^{n} a_{ij}(t,x)\xi_i\xi_j \le \Lambda|\xi|^2, \ \ (t,x) \in [0,T] \times \overline{\Omega}. \tag{6.3}$$

We assume that the coefficients of L are Hölder continuous in $[0,T) \times \Omega, \ \forall T > 0$ and the vector-function (f_1, f_2) is continuously differentiable and monotone nonincreasing in $\mathbb{R}^+ \times \mathbb{R}^+$.

For any two positive constants $\rho_1, \ \rho_2$ define

$$\mathbf{S}_\rho \equiv \left\{(u_1,u_2) \in C([0,\infty) \times \overline{\Omega}); (0,0) \le (u_1,u_2) \le (\rho_1,\rho_2)\right\}$$

Theorem 6.1. *[10, Theorem 8.7.2] Let (f_1, f_2) be a quasimonotone nonincreasing Lipschitz function in $\boldsymbol{S}_\rho$ and let (f_1, f_2) satisfy*

$$\begin{aligned} &f_1(t,x,\rho_1,0) \le 0 \le f_1(t,x,0,\rho_2) \\ &f_2(t,x,0,\rho_2) \le 0 \le f_2(t,x,\rho_1,0) \end{aligned} \tag{6.4}$$

for any $x \in \Omega, \ t > 0$. Then for any $(u_{1,0}, u_{2,0}) \in \boldsymbol{S}_\rho$ there exists a unique solution of (6.1) $\boldsymbol{u} \equiv (u_1,u_2)$ in $\boldsymbol{S}_\rho$, and $u_i(t,x) > 0$ for $x \in \Omega, \ t > 0$ when $u_{i,0} \ne 0$, $i = 1,2$.

The next lemma [3] implies the monotonicity property for solutions of (6.1).

Lemma 6.1. *Let $(u_i(t,x), v_i(t,x)), \ i = 1,2$, be two solutions of system (6.1) such that $u_1(0,x) \ge u_2(0,x)$ and $v_1(0,x) \le v_2(0,x)$ for any $x \in \Omega$. Then $u_1(t,x) \ge u_2(t,x)$ and $v_1(t,x) \le v_2(t,x)$ for any $x \in \Omega$ and any $t > 0$. Moreover, if*

$$(u_1(0,x), v_1(0,x)) \ne (u_2(0,x), v_2(0,x)),$$

then $u_1(t,x) > u_2(t,x)$ and $v_1(t,x) < v_2(t,x)$ for any $x \in \Omega$ and any $t > 0$

For the proof see [3] Theorem 1.20 and remarks thereafter. The final statement of the lemma follows from the strong maximum principle for parabolic equations [11] applied to the differences $u_1 - u_2$ and $v_2 - v_1$.

The next result [8] classifies all possible equilibria for a monotone dynamical system. We will present a particular case of Theorem B [8]. Denote $X^+ = C_+(\overline{\Omega}) \times C_+(\overline{\Omega})$, where $C_+(\overline{\Omega})$ is the class of all nonnegative functions from $C(\overline{\Omega})$; $I = \langle 0, \tilde{u}_1 \rangle \times \langle 0, \tilde{u}_2 \rangle$, where $(\tilde{u}_1, 0)$ and $(0, \tilde{u}_2)$ are the semi-trivial equilibria of (6.1), where $\langle \cdot, \cdot \rangle$ was defined in (2.3).

Theorem 6.2. *Let operator T_t be defined as $T_t(\boldsymbol{u}_0) = \boldsymbol{u}$, where $\boldsymbol{u}_0 \equiv (u_{1,0}, u_{2,0})$ and $\boldsymbol{u} \equiv (u_1,u_2) = (T_t(u_{1,0}), T_t(u_{2,0}))$ is a solution of (6.1). Let the following conditions hold:*

(1) T is strictly order preserving, which means that $u_1(x) \geq v_1(x)$ and $u_2(x) \leq v_2(x)$ imply $T_t(u_1(x)) \geq T_t(v_1(x))$ and $T_t(u_2(x)) \leq T_t(v_2(x))$.

(2) $T_t(\mathbf{0}) = \mathbf{0}$ for all $t \geq 0$ and $\mathbf{0}$ is a repelling equilibrium. That is there exists a neighbourhood U of $\mathbf{0}$ in X^+ such that for each $(u_1, u_2) \in U$, $(u_1, u_2) \neq \mathbf{0}$, there is $t_0 > 0$ such that $T_{t_0}(u_1, u_2) \notin U$.

(3) $T_t((u_1, 0)) = (T_t(u_1), 0)$ and $T_t(u_1) \geq 0$ if $u_1 \geq 0$. There exists $\tilde{u}_1 > 0$ such that $T_t((\tilde{u}_1, 0)) = (\tilde{u}_1, 0)$ for any $t \geq 0$. The symmetric conditions hold for $T_t((0, u_2))$.

(4) If $u_{i,0} \geq 0$, $u_{i,0} \neq 0$, $i = 1, 2$ then $T_t(u_{i,0}) > 0$, $i = 1, 2$. If $u_1(x) \geq v_1(x)$, $u_2(x) \leq v_2(x)$ and $u_1(x) \neq v_1(x)$, $u_2(x) \neq v_2(x)$ then $T_t(u_1(x)) > T_t(v_1(x))$ and $T_t(u_2(x)) < T_t(v_2(x))$.

Then exactly one of the following holds:

(a) There exists a positive coexistence equilibrium $(u_{1,s}, u_{2,s})$ of (6.1).

(b) $(u_1, u_2) \to (\tilde{u}_1, 0)$ as $t \to \infty$ for every $(u_{1,0}, u_{2,0}) \in I$.

(c) $(u_1, u_2) \to (0, \tilde{u}_2)$ as $t \to \infty$ for every $(u_{1,0}, u_{2,0}) \in I$.

Moreover, if (b) or (c) holds then for every $(u_{1,0}, u_{2,0}) \in X^+ \backslash I$ and $u_{i,0} \neq 0$, $i = 1, 2$ either $(u_1, u_2) \to (\tilde{u}_1, 0)$ or $(u_1, u_2) \to (0, \tilde{u}_2)$ as $t \to \infty$.

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