



# 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  $\Delta u$  (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.

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## 1. Introduction

Introducing spatial distribution of species in mathematical description of population dynamics aims to explain certain real world phenomena such as stocking and pattern 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  $D \rightarrow \infty$ , which is not feasible for systems where the carrying capacity is space-dependent. Moreover, it brings the conclusion [1] 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 [2,3]. Usually the zero Neumann boundary conditions were considered (assuming that 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 [4,5] we introduced an alternative type of diffusion when ultimately the population does not tend to have 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:

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

with the Neumann boundary condition

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

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and the initial condition

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

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 [1,3,6]. Dockery et al. [1] 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 [3] 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 [3]. In [6] 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:

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

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  $d(x) \in C^1(\overline{\Omega})$ .  $\Omega$  is 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 [1,3,6]. It is easy to see that the functions  $\tilde{u}$  and  $\tilde{v}$  are solutions of the following elliptic boundary value problems

$$\begin{cases} D\Delta\left(\frac{\tilde{u}(x)}{K(x)}\right) + r(x)\tilde{u}(x)\left(1 - \frac{\tilde{u}(x)}{K(x)}\right) = 0, & x \in \Omega, & \text{(a)} \\ \frac{\partial(\tilde{u}/K)}{\partial n} = 0, & x \in \partial\Omega & \text{(b)} \end{cases} \tag{1.6}$$

and

$$\begin{cases} \nabla \cdot d(x)\nabla \tilde{v}(x) + r(x)\tilde{v}(x)\left(1 - \frac{\tilde{v}(x)}{K(x)}\right) = 0, & x \in \Omega, & \text{(a)} \\ \frac{\partial \tilde{v}}{\partial n} = 0, & x \in \partial\Omega, & \text{(b)} \end{cases} \tag{1.7}$$

respectively.

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