



Competitive spatially distributed population dynamics models: Does diversity in diffusion strategies promote coexistence?



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ABSTRACT

We study the interaction between different types of dispersal, intrinsic growth rates and carrying capacities of two competing species in a heterogeneous environment: one of them is subject to a regular diffusion while the other moves in the direction of most per capita available resources. If spatially heterogeneous carrying capacities coincide, and intrinsic growth rates are proportional then competitive exclusion of a regularly diffusing population is inevitable. However, the situation may change if intrinsic growth rates for the two populations have different spatial forms. We also consider the case when carrying capacities are different. If the carrying capacity of a regularly diffusing population is higher than for the other species, the two populations may coexist; as the difference between the two carrying capacities grows, competitive exclusion of the species with a lower carrying capacity occurs.

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1. Introduction

Spatial heterogeneity of the environment and species distribution is an important characteristic in population ecology. The space movements are usually modeled with a diffusion term, and a certain effort was undertaken to explain the role of diffusion coefficients in heterogeneous environments. If the environment is heterogeneous, and the per capita growth functions include a sum of population densities then the population with the slowest diffusion survives in competition with similar species which differ by diffusion coefficient only [12]. However, if we have a Lotka system with only partially shared resources, the situation changes [27]: there is an asymptotically stable coexistence equilibrium once the difference between the diffusion rates is not very significant. An interesting observation in [21] is the evolutionary advantage of space-dependent carrying capacity compared to the homogeneous carrying capacity with the same average value over space.

For diffusing populations, not only the dispersal speed but also the strategy has recently become an object of intensive discussion. This is

aimed to address the following issue: as the diffusion coefficient tends to infinity, regularly diffusing populations tend to be distributed uniformly which is not optimal in a heterogeneous environment in the following sense. The ideal free distribution describes how species can distribute themselves to maximize their total fitness in such a way that any movement in an ideally distributed population will lead to decrease in fitness; in a heterogeneous medium, this corresponds to the case when per capita available resources, not the density, is uniformly distributed. To incorporate movements in the direction of the environmental gradient, an advection term was added to the equation [1,5–10,34] which led to ideally distributed solutions, at least in the case when advection prevails over the random diffusion. The interplay of advection and diffusion coefficients in each of two competing species was explored in the recent paper [10]. The dispersal type which, independently of parameters involved in the equation, has the ideal free distribution as a solution was developed in [3], and according to [23], for a time-independent carrying capacity all positive solutions tend to the ideal free distribution. Let us note that the ideal free distribution was recently suggested as a null model for habitat patch selection in [30], see [25] for some examples of species which tend to disperse according to the inhomogeneous carrying capacity.

There were numerous studies on non-linear diffusion in biological systems, let us note [31], the recent paper [13] and references therein.

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However, the focus of the investigation was on mathematical and/or numerical modeling, in order to more exactly match the laboratory data. If, as in [13], a competition was considered, the same type of diffusion was involved in every equation. To the best of our knowledge, before [12] the influence of diffusion on evolutionary success has not been theoretically analyzed.

The evolutionarily stable strategy is understood in the sense of [11,14]: if an evolutionarily stable strategy is adopted by a resident population, it becomes impossible for a population choosing a different strategy to invade its habitat. In [25] evolutionary stability of carrying capacity driven dispersal over the regular diffusion was justified, if all other parameters of the resident and invasive populations coincide. In the present paper, both intrinsic growth rates and carrying capacities for these two populations may differ.

The idea of superiority of the carrying capacity-driven diffusion strategy compared to the regular (random) diffusion was first outlined in [24] for the logistic growth. The main contributions of the present paper compared to [24] can be summarized as follows:

1. In [24], only populations following the logistic growth law were considered. Here we consider the variety of growth rules (Gompertz, generalized logistic etc.)
2. In [24], the difference between the two populations is diffusion strategy only. While it is important to study the influence of one chosen factor only, in practice a competition involves many different factors. Here an interplay of two couples of parameters is investigated: the first factor is always the diffusion strategy, and the second one includes either carrying capacities or intrinsic growth rates. With the same diffusion strategy, higher carrying capacity would guarantee survival, but with inferior (regular) diffusion this situation may lead to coexistence. We study how optimal diffusion strategy can alleviate the negative influence of less efficient resources exploitation (a lower carrying capacity).
3. The papers [24,25] include only theoretical results in time-independent environments. The combination of theoretical and numerical analysis allows to study the situation when the carrying capacity is time-dependent (for example, due to seasonal changes), to confirm theoretical conclusions and to complement them (for instance, to explore the dependency of the limit solution on the diffusion coefficient for a regularly diffusing population).

The proofs of results of the present paper follow the schemes of the proofs in [23,24] and use some ideas of the monograph [4].

In our present study, we consider different intrinsic growth rates for both populations. If they are spatially similar (for example, proportional), the situation does not differ from the equal growth rates, which means competitive exclusion of a regularly diffusing population. However, if the ratio of intrinsic growth rates is spatially heterogeneous, coexistence is possible. The two equations can also involve different diffusion coefficients; their relation and values influence the transient behavior and convergence rates to the stable equilibrium state.

It is a common belief that a higher carrying capacity of an invader leads to successful invasion and even extinction of the resident. For example, in [33] the carrying capacity was associated with cell mutations, where only the colony (mutating or not) with a higher carrying capacity survived in a competition, see also [2]. The recent paper [18] explored the conjecture whether the main reason for an invader to replace antagonistic indigenous populations can be ascribed to the larger carrying capacity of the former.

In our study, we considered two cases. In the first case, the mortality term is referred to the crowding effect, the two types of species have similar physical characteristics, including food consumption, but may have different crowding tolerance: a population starts to decrease when the local density exceeds some K which may be different for the two types. If higher (or at least not less) crowding tolerance is incorporated with the directed dispersal while the other

population adopts random diffusion, the regularly diffusing population goes extinct. If random diffusion is combined with a higher crowding tolerance, we prove that this guarantees survival. If the prevalence of this crowding tolerance over the one combined with the directed dispersal is not very significant both populations coexist. Thus diversity in dispersal strategies provides coexistence in this range of parameters. Higher ratios of carrying capacities will bring the population with a lower one to extinction, as numerical examples illustrate. In the second case, the two species have different (space-dependent) consumption rates. However, if these rates are proportional, still competitive exclusion of a regularly diffusing population is observed.

Spatial heterogeneity of the environments plays a crucial role in our study; for the recent investigation of spreading or vanishing of invasive species see, for example, the recent paper [35] and references therein.

The paper is organized as follows. Section 2 describes the model and verifies positivity, existence and uniqueness of a solution for any non-negative (and not identically equal to zero) initial conditions. Section 3 explores the equilibria, in particular, outlines the cases when there is no coexistence. Section 4 includes the main results of the paper: the strategy leading to the ideal free distribution has the advantage of evolutionary stability if intrinsic growth rates are constant and the randomly diffusing population does not have a higher carrying capacity. If it does have, its survival is guaranteed, and numerical examples in Section 5 illustrate that both coexistence and competitive exclusion of the population with the carrying capacity driven dispersal are possible. Section 5 also presents an example of coexistence for different intrinsic growth rates, and Section 6 contains a brief summary of the results of the paper and discussion.

2. Description of the model

In the present paper, we consider the system describing two populations competing for the resources which exist in the isolated domain Ω . This corresponds to the initial-boundary value problem with the Neumann boundary conditions

$$\begin{cases} \frac{\partial u(t, x)}{\partial t} = D_1 \Delta \left(\frac{u(t, x)}{K_1(x)} \right) + r_1(x)u(t, x)g(x, u(t, x), v(t, x), K_1(x)), \\ \frac{\partial v(t, x)}{\partial t} = D_2 \nabla \cdot (d(x)\nabla v(t, x)) \\ \quad + r_2(x)v(t, x)g(x, v(t, x), u(t, x), K_2(x)), \\ t > 0, x \in \Omega, \frac{\partial}{\partial n} \left(\frac{u}{K_1(x)} \right) = d(x) \frac{\partial v}{\partial n} = 0, x \in \partial\Omega \end{cases} \quad (2.1)$$

and the initial conditions

$$u(0, x) = u_0(x), v(0, x) = v_0(x). \quad (2.2)$$

We assume that $K_i(x)$, $r_i(x)$, $i = 1, 2$ are in the class $C^{1+\alpha}(\overline{\Omega})$, and $K_i(x) > 0$, $r_i(x) > 0$ for any $x \in \overline{\Omega}$, and $r_i(x) > 0$ in an open nonempty subdomain of Ω . Here Ω is an open nonempty bounded domain of \mathbb{R}^n with $\partial\Omega \in C^{2+\alpha}$, $0 < \alpha < 1$, and $J_1 \times J_2$ a bounded subset of \mathbb{R}^2 . The set $J_1 \times J_2$ corresponds to the range of the solutions to (2.1) and is determined by the corresponding upper and lower solutions.

For future reference, we denote $Q = (0, \infty) \times \Omega$, $\overline{Q} = [0, \infty) \times \overline{\Omega}$, $\partial Q = (0, \infty) \times \partial\Omega$. To state the assumptions on the functions $f_1(x, u, v, K) = r_1 u g(x, u, v, K)$ and $f_2(x, u, v, K) = r_2 v g(x, v, u, K)$, we will need the following definition [28].

Definition 1. A function $f_i = f_i(x, u_1, u_2, K)$ is said to be quasimonotone nonincreasing if for fixed x, K, u_i , f_i is nonincreasing in u_j for $j \neq i$.

A vector-function $\mathbf{f} = (f_1, f_2)$ is called quasimonotone nonincreasing in $J_1 \times J_2$ if both f_1 and f_2 are quasimonotone nonincreasing in $(u_1, u_2) \in J_1 \times J_2$.

We next list some assumptions on the growth functions $f_1(x, u, v, K) = r_1 u g(x, u, v, K)$ and $f_2(x, u, v, K) = r_2 v g(x, v, u, K)$ which will be used throughout the paper:

- (A1) $\mathbf{f} = (f_1, f_2)$ is quasimonotone nonincreasing in $J_1 \times J_2$;
- (A2) $f_i(\cdot, u, v, K)$ is Hölder continuous in Ω and $f_i(x, \cdot, \cdot, K) \in C^2(J_1 \times J_2)$, $i = 1, 2$;
- (A3) $g(x, u_1, u_2, K) = g(x, u_2, u_1, K) = G(x, u_1 + u_2, K)$;
- (A4) $G(x, K, K) = 0$;
- (A5) $G(x, u, K)$ is strictly monotonically decreasing in u ;
- (A6) $G(x, u, K)$ is strictly monotonically increasing in K .

There are numerous examples of functions $G(x, u, K)$ satisfying the above properties, see, for example, [26] for more details:

- Gilpin–Ayala growth [16] $G(x, u(t, x), K(x)) = r(x)(1 - (\frac{u(t, x)}{K(x)})^\theta)$, $0 < \theta \leq 1$, the logistic growth is a particular case for $\theta = 1$;
- Nicholson’s blowflies type model (see [19,22] for the delayed version of the model) $G(x, u(t, x), K(x)) = r(x)(e^{\alpha(1-u(t, x)/K(x))} - 1)$;
- food-limited growth [32] $G(x, u(t, x), K(x)) = r(x)\frac{1-u(t, x)/K(x)}{1+\beta u(t, x)/K(x)}$, $\beta > 0$;
- Gompertz growth [17] $G(x, u(t, x), K(x)) = r(x)\ln(\frac{K(x)}{u(t, x)})$.

Model (2.1) can be viewed as competition of two species with similar physical characteristics but possibly different growth rates and crowding tolerance (u starts to decrease as soon as the sum of densities of u and v exceeds K_1 , while v as it becomes greater than K_2). In contrast with (2.1), we will also consider the system where the resource consumptions (carrying capacities) of the two types of competing species are different:

$$\begin{cases} \frac{\partial u(t, x)}{\partial t} = D_1 \Delta \left(\frac{u(t, x)}{K_1(x)} \right) \\ \quad + r_1(x)u(t, x)g \left(x, u(t, x), \frac{K_1(x)v(t, x)}{K_2(x)}, K_1(x) \right), \\ \frac{\partial v(t, x)}{\partial t} = D_2 \nabla \cdot (d(x)\nabla v(t, x)) \\ \quad + r_2(x)v(t, x)g \left(x, u(t, x), \frac{K_1(x)v(t, x)}{K_2(x)}, K_1(x) \right), \\ t > 0, x \in \Omega, \frac{\partial}{\partial n} \left(\frac{u}{K_1(x)} \right) = d(x)\frac{\partial v}{\partial n} = 0, x \in \partial\Omega, \end{cases} \quad (2.3)$$

where g satisfies (A2)–(A6). For example, in the case of the logistic growth the first two equations of (2.3) have the form

$$\begin{cases} \frac{\partial u(t, x)}{\partial t} = D_1 \Delta \left(\frac{u(t, x)}{K_1(x)} \right) + r_1(x)u(t, x) \left(1 - \frac{u(t, x)}{K_1(x)} - \frac{v(t, x)}{K_2(x)} \right), \\ \frac{\partial v(t, x)}{\partial t} = D_2 \nabla \cdot (d(x)\nabla v(t, x)) \\ \quad + r_2(x)v(t, x) \left(1 - \frac{u(t, x)}{K_1(x)} - \frac{v(t, x)}{K_2(x)} \right), t > 0, x \in \Omega. \end{cases}$$

The property (A5) of the maximal per capita growth rates for small population levels is not satisfied for growth functions with the Allee effect, see [26] for appropriate examples.

Consider the initial-boundary value problem with the Neumann boundary condition and the carrying capacity driven diffusion

$$\frac{\partial u(t, x)}{\partial t} = D \Delta \left(\frac{u(t, x)}{K(t, x)} \right) + u(t, x)G(x, u(t, x), K(x)), \quad (t, x) \in Q, \quad (2.4)$$

$$\frac{\partial}{\partial n} \left(\frac{u}{K} \right) = 0, \quad (t, x) \in \partial Q, u(0, x) = u_0(x), x \in \Omega. \quad (2.5)$$

Existence, uniqueness and stability results for scalar equations of the form (2.4)–(2.5) were obtained in [23].

Lemma 1. [23, 25, Theorems 1,6] *Let $f(x, u, K) = uG(x, u, K)$ satisfy (A2), (A4), (A5), $u_0(x) \in C(\Omega)$, $u_0(x) \geq 0$ 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 the problem (2.4)–(2.5), it is positive and satisfies $\lim_{t \rightarrow \infty} u(t, x) = K(x)$ uniformly in $x \in \Omega$.

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

$$\begin{cases} \frac{\partial v(t, x)}{\partial t} = \nabla \cdot D(x)\nabla v(t, x) + v(t, x)G(x, v(t, x), K(x)), t > 0, x \in \Omega, \\ \frac{\partial v}{\partial n} = 0, t > 0, x \in \partial\Omega, v(0, x) = v_0(x), x \in \Omega. \end{cases} \quad (2.6)$$

Lemma 2. [25, Theorem 4] *Let $f(x, v, K) = vG(x, v, K)$ satisfy (A2), (A4), (A5). Then there exists a unique positive equilibrium $v^*(x)$ of the problem (2.6). Moreover, for any $v_0(x) \geq 0$, $v_0(x) \not\equiv 0$ the solution $v(t, x)$ of (2.6) satisfies $\lim_{t \rightarrow \infty} v(t, x) = v^*(x)$ uniformly in $x \in \Omega$.*

The next theorem provides existence and uniqueness of solutions for coupled systems of equations.

Theorem 1. *Let $f_1(x, u, v, K) = r_1 u g(x, u, v, K)$ and $f_2(x, u, v, K) = r_2 v g(x, v, u, K)$ satisfy (A1)–(A5). Then for any $u_0(x), v_0(x) \in C(\Omega)$, problem (2.1) 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. We will apply Theorem 8 from Appendix A to the system obtained after the substitution $w(t, x) = u(t, x)/K_1(x)$; system (2.1) becomes

$$\begin{cases} \frac{\partial w(t, x)}{\partial t} = \frac{D_1}{K_1(x)} \Delta w(t, x) \\ \quad + r_1(x)w(t, x)\tilde{g}(x, w(t, x), v(t, x), K_1(x)), \\ \frac{\partial v(t, x)}{\partial t} = D_2 \nabla \cdot (d(x)\nabla v(t, x)) \\ \quad + r_2(x)v(t, x)\tilde{g}(x, v(t, x), w(t, x), K_2(x)), \\ t > 0, x \in \Omega, \frac{\partial w}{\partial n} = d(x)\frac{\partial v}{\partial n} = 0, x \in \partial\Omega, \end{cases} \quad (2.7)$$

where $\tilde{g}(x, w(t, x), v(t, x), K(x)) = g(x, K(x)w(t, x), v(t, x), K(x))$. Next, choose a constant ρ_w such that $\rho_w \geq \sup_{(t, x) \in Q_T} \frac{u_0(t, x)}{K_1(x)}$ and $\tilde{g}(t, x, \rho_w, 0, K_1) < 0$, which can be done according to (A5). Note that since u_0 is bounded in $\bar{\Omega}$ and K_1, K_2 are bounded from below, $\sup_{x \in \Omega} (u_0(x)/K_1(x)) < \infty$. Similarly, choose $\rho_v > \sup_{x \in \Omega} v_0(x)$ such that $\tilde{g}(x, 0, \rho_v, K_2) < 0$. It is easy to check that conditions (A.4) are satisfied for ρ_w, ρ_v defined above and

$$\begin{aligned} (u_0(x)/K_1(x), v_0(x)) &\in \mathbf{S}_\rho \\ &:= \{(w, v) \in C(\{0, \infty\} \times \bar{\Omega}) : (0, 0) \leq (w, v) \leq (\rho_w, \rho_v)\}. \end{aligned}$$

Therefore all the conditions of Theorem 8 from Appendix A are satisfied, thus there exists a unique solution (w, v) of (2.7) in \mathbf{S}_ρ , and it is positive. Obviously, $(u, v) = (K_1 w, v)$ is the unique positive solution of (2.1). \square

The same result is valid for (2.3).

3. Equilibrium solutions

We study an evolutionary advantage by investigating the stability of so-called semi-trivial equilibria of systems (2.1) and (2.3), which are $(\bar{u}, 0)$, $(0, \bar{v})$, when only one species survives and, when it exists, a coexistence equilibrium. It is easy to see that the functions \bar{u} and \bar{v} are the solutions of the following two elliptic boundary value problems,

respectively:

$$\left\{ \begin{aligned} D_1 \Delta \left(\frac{\tilde{u}(x)}{K_1(x)} \right) + r_1(x) \tilde{u}(x) g(x, \tilde{u}(x), 0, K_1) = 0, \quad x \in \Omega, \end{aligned} \right. \quad (3.1)$$

$$\left\{ \begin{aligned} \frac{\partial(\tilde{u}/K_1)}{\partial n} = 0, \quad x \in \partial\Omega, \end{aligned} \right. \quad (3.2)$$

$$\left\{ \begin{aligned} D_2 \nabla \cdot (d(x) \nabla \tilde{v}(x)) + r_2(x) \tilde{v}(x) g(x, \tilde{v}(x), 0, K_2) = 0, \quad x \in \Omega, \end{aligned} \right. \quad (3.3)$$

$$\left\{ \begin{aligned} \frac{\partial \tilde{v}}{\partial n} = 0, \quad x \in \partial\Omega. \end{aligned} \right. \quad (3.4)$$

It is also convenient for future analysis to introduce the substitution $\tilde{w} = \tilde{u}/K_1$. The steady-state problem (3.1)–(3.2) for \tilde{w} becomes

$$\left\{ \begin{aligned} \frac{D_1}{K_1(x)} \Delta \tilde{w}(x) + r_1(x) \tilde{w}(x) \tilde{g}(x, \tilde{w}(x), 0, K_1) = 0, \quad x \in \Omega, \end{aligned} \right. \quad (3.5)$$

$$\left\{ \begin{aligned} \frac{\partial \tilde{w}}{\partial n} = 0, \quad x \in \partial\Omega, \end{aligned} \right. \quad (3.6)$$

where we denote $\tilde{g}(x, w, v, K) = g(x, Kw, v, K)$.

Lemma 3. [25, Lemma 3] *Let the growth function g satisfy the assumptions (A2)–(A5). The function $\tilde{u}(x) = K_1(x)$ is the only positive solution of (3.1)–(3.2).*

The next result is concerned with a coexistence state for system (2.1) of competing species.

Theorem 2. *Let the growth function g satisfy (A1)–(A6), $r_1(x) \equiv r_1$, $r_2(x) \equiv r_2$ be constant, $K_1(x) \geq K_2(x)$ for $x \in \Omega$ and either $K_1(x) = K_2(x) = K(x) \neq \text{const}$ or $K_1(x) > K_2(x)$ in an open nonempty subdomain of Ω , then there is no coexistence state (u_s, v_s) for system (2.1).*

Proof. Let us assume the contrary that there exists a strictly positive equilibrium solution (u_s, v_s) of (2.1). Then (u_s, v_s) satisfies

$$\left\{ \begin{aligned} D_1 \Delta \left(\frac{u_s(x)}{K_1(x)} \right) + r_1 u_s(x) g(x, u_s(x), v_s(x), K_1(x)) = 0, \quad x \in \Omega, \\ D_2 \nabla \cdot (d(x) \nabla v_s(x)) + r_2 v_s(x) g(x, v_s(x), u_s(x), K_2(x)) = 0, \quad x \in \Omega, \\ \frac{\partial(u_s/K_1)}{\partial n} = d(x) \frac{\partial v_s}{\partial n} = 0, \quad x \in \partial\Omega \end{aligned} \right. \quad (3.7)$$

After dividing each of the first two equations in (3.7) by r_i , $i = 1, 2$, adding them and using property (A3) for g we obtain

$$\frac{D_1}{r_1} \Delta \left(\frac{u_s(x)}{K_1(x)} \right) + \frac{D_2}{r_2} \nabla \cdot (d(x) \nabla v_s(x)) + u_s(x) G(x, u_s(x) + v_s(x), K_1(x)) + v_s(x) G(x, u_s(x) + v_s(x), K_2(x)) = 0$$

After integrating over Ω using the boundary conditions we have

$$\int_{\Omega} [u_s(x) G(x, u_s(x) + v_s(x), K_1(x)) + v_s(x) G(x, u_s(x) + v_s(x), K_2(x))] dx = 0, \quad (3.8)$$

and by property (A6) and $K_1 \geq K_2$

$$\int_{\Omega} G(x, u_s(x) + v_s(x), K_2(x)) dx \leq \int_{\Omega} G(x, u_s(x) + v_s(x), K_1(x)) dx, \quad (3.9)$$

where the equality is attained for $K_1 \equiv K_2$ only. Thus

$$\int_{\Omega} (u_s + v_s) G(x, u_s + v_s, K_1) dx \geq 0. \quad (3.10)$$

Integrating the equality $G(x, u_s + v_s, K_1)(u_s + v_s) = G(x, u_s + v_s, K_1)(u_s + v_s - K_1) + G(x, u_s + v_s, K_1)K_1$ over Ω and using (3.10) we obtain

$$0 \leq \int_{\Omega} G(x, u_s + v_s, K_1)(u_s + v_s - K_1) dx + \int_{\Omega} G(x, u_s + v_s, K_1)K_1(x) dx. \quad (3.11)$$

The Mean Value Theorem and $G(x, K_1, K_1) = 0$ in (A4) imply

$$\begin{aligned} G(x, u_s(x) + v_s(x), K_1(x)) &= G(x, u_s(x) + v_s(x), K_1(x)) - G(x, K_1, K_1) \\ &= G_v(x, \xi, K_1(x))(u_s(x) + v_s(x) - K_1(x)), \end{aligned} \quad (3.12)$$

where G_v is the derivative of G in the second variable, $\xi(x)$ is between $u_s(x) + v_s(x)$ and $K_1(x)$ for each $(t, x) \in (0, \infty) \times \Omega$. Using (3.12), equality (3.11) can be rewritten as

$$\begin{aligned} &\int_{\Omega} G(x, u_s + v_s, K_1) K_1(x) dx \\ &\geq - \int_{\Omega} G_v(x, \xi, K_1)(u_s + v_s - K_1)^2 dx > 0, \end{aligned} \quad (3.13)$$

unless $u_s(x) + v_s(x) \equiv K_1(x)$, where for the last inequality we used the fact that $G_v < 0$ due to (A5). Thus we have to consider the following two cases.

1. If $u_s(x) + v_s(x) \equiv K_1(x) \equiv K_2(x)$, then $w_s = u_s/K_1$ and v_s satisfy $\Delta w_s = 0$, $x \in \Omega$, $\frac{\partial w_s}{\partial n} = 0$, $x \in \partial\Omega$ and $\nabla \cdot d(x) \nabla v_s = 0$, $x \in \Omega$, $\frac{\partial v_s}{\partial n} = 0$, $x \in \partial\Omega$, respectively, and therefore by the maximum principle $w_s = \text{const}$, $v_s = \text{const}$ (see e.g. [15, Theorem 3.6]). Since $w_s K_1 + v_s = K_1$ and K_1 is not constant, it follows that $v_s = 0$, $w_s = 1$, which contradicts $v_s > 0$.
2. Let $u_s(x) + v_s(x) \neq K_1(x)$ or $K_1(x) > K_2(x)$ in some nonempty open domain. Consider the eigenvalue problem

$$\begin{aligned} \frac{D_1}{K_1(x)} \Delta \psi(x) + r_1 \psi(x) \tilde{g}(x, w_s(x), v_s(x), K_1(x)) &= \sigma \psi(x), \quad x \in \Omega, \\ \frac{\partial \psi}{\partial n} &= 0, \quad x \in \partial\Omega. \end{aligned} \quad (3.14)$$

According to the variational characterization of eigenvalues [4, Theorem 2.1], its principal eigenvalue is given by

$$\sigma_1 = \sup_{\psi \neq 0, \psi \in W^{1,2}} \frac{- \int_{\Omega} D_1 |\nabla \psi|^2 dx + \int_{\Omega} K_1 r_1 \psi^2 \tilde{g}(x, w_s, v_s, K_1) dx}{\int_{\Omega} K_1 \psi^2 dx}$$

Upon substituting $\psi = 1$ and using (3.13) together with $r_1(x) \equiv r_1$, we obtain

$$\sigma_1 \geq \frac{r_1 \int_{\Omega} K_1 \tilde{g}(x, w_s, v_s, K_1) dx}{\int_{\Omega} K_1 dx} > 0 \quad (3.15)$$

However, since (w_s, v_s) is an equilibrium solution of (2.7), w_s satisfies

$$\begin{aligned} \frac{D_1}{K_1(x)} \Delta w_s(x) + r_1 w_s \tilde{g}(x, w_s, v_s, K_1) &= 0, \quad x \in \Omega, \\ \frac{\partial w_s}{\partial n} &= 0, \quad x \in \partial\Omega, \end{aligned}$$

and is therefore a positive principal eigenfunction of (3.14) with the principal eigenvalue 0. This is a contradiction with (3.15). \square

Remark 1. The case of proportional growth rates $r_1(x) = \alpha r_2(x)$, $\alpha > 0$ is also considered in Theorem 2, since $r_2(x)$ can be involved as a part of function g .

Theorem 3. *If the growth function g satisfies (A1)–(A6), $r_1(x) \equiv r_1$, $r_2(x) \equiv r_2$ are constant, and for some positive $\beta > 0$, $K_1(x) = \beta K_2(x) \neq \text{const}$, then there is no coexistence state (u_s, v_s) for system (2.3).*

Proof. The proof is similar to the proof of Theorem 2. Assuming there is a stationary solution (u_s, v_s) , dividing each of the first two equations by r_i , $i = 1, 2$, multiplying the second equation by β , adding them and using property (A3) for g and integrating over Ω we get $\int_{\Omega} (u_s(x) + \beta v_s(x)) G(x, u_s(x) + \beta v_s(x), K_1(x)) dx = 0$. Thus

$$\begin{aligned} &\int_{\Omega} G(x, u_s + \beta v_s(x), K_1) K_1(x) dx \\ &\geq - \int_{\Omega} G_v(x, \xi, K_1)(u_s + \beta v_s - K_1)^2 dx > 0, \end{aligned} \quad (3.16)$$

unless $u_s(x) + \beta v_s(x) \equiv K_1(x)$. If $u_s(x) + \beta v_s(x) \equiv K_1(x)$, then $\Delta(u_s/K_1) = 0$, due to the boundary conditions $u_s(x) = cK_1(x)$, while $v_s(x) = K_1(x)(1 - c)/\beta$ is constant, which is possible for $c = 1$ only, as $K_1(x)$ is variable. If $u_s(x) + \beta v_s(x) \neq K_1(x)$, using the variational characterization of eigenvalues and substituting either $\psi = K_1$ in the original form or $\psi = 1$ in the form obtained after the substitution $u/K_1 = w$, we obtain $\sigma_1 \geq \frac{r_1 \int_{\Omega} K_1 \tilde{g}(x, w_s, \beta v_s, K_1) dx}{\int_{\Omega} K_1 dx} > 0$, which leads to the conclusion that there is no coexistence equilibrium. \square

4. Stability analysis

In the case when there is no coexistence equilibrium, we proceed to the analysis of the trivial and the semi-trivial equilibria. We first consider the case when the carrying capacities satisfy $K_1 \geq K_2$, the growth rates may be different but both r_1 and r_2 are constant.

Theorem 4 deals with the stability of the second semi-trivial equilibrium of (2.1). After the substitution $w(t, x) = u(t, x)/K_1(x)$, system (2.1) becomes (2.7), where $\tilde{g}(x, w(t, x), v(t, x), K(x)) = g(x, K(x)w(t, x), v(t, x), K(x))$.

The following result is a generalization of [25, Lemma 4].

Lemma 4. *Let the growth function g satisfy the assumptions (A1)–(A6), $r_1(x) \equiv r_1$, $r_2(x) \equiv r_2$ be constant, $K_1(x) \geq K_2(x)$ and either $K_1(x) \neq \text{const}$ or $K_1(x) > K_2(x)$ on a nonempty open domain. Then there exists a unique positive solution $\tilde{v}(x) = v^*(x)$ of (3.3)–(3.4) satisfying*

$$\int_{\Omega} r_1 g(x, 0, v^*, K_1) K_1(x) dx > 0. \tag{4.1}$$

Proof. Similarly to (3.8) in the proof of Theorem 2, we obtain

$$\int_{\Omega} v^*(x) G(x, v^*, K_2) dx = 0. \tag{4.2}$$

Next, $G(x, v^*, K_2) \leq G(x, v^*, K_1)$ by (A6), by the assumption $K_1(x) \geq K_2(x)$ of the theorem and $v^* > 0$, hence

$$\int_{\Omega} v^*(x) G(x, v^*, K_1) dx \geq 0. \tag{4.3}$$

As in the proof of Theorem 2, $v^*(x)G(x, v^*, K_1) = (v^* - K_1)(G(x, v^*, K_1) - G(x, K_1, K_1)) + K_1 G(x, v^*, K_1) = (v^* - K_1)^2 G_v(x, \xi, K_1) + K_1 G(x, v^*, K_1)$, thus

$$\begin{aligned} & \int_{\Omega} K_1(x) G(x, v^*(x), K_1(x)) dx \\ & \geq - \int_{\Omega} G_v(x, \xi, K_1(x)) (v^*(x) - K_1(x))^2 dx, \end{aligned} \tag{4.4}$$

where the right-hand side is positive unless $K_1(x) \equiv \text{const}$, since $G_v < 0$ due to (A5). Thus we have a strict inequality in (4.3) if $K_1(x) > K_2(x)$ on a nonempty open domain, which concludes the proof. \square

Remark 2. Note that properties (A4) and (A5) yield that $g(x, 0, v, K_1) \geq 0$ for any $v \leq K_1$. Thus inequality (4.1) can be treated as the condition $v^* < K_1$ in an integral sense.

Remark 3. A similar inequality $\int_{\Omega} r_1 g(x, 0, \beta v^*, K_1) K_1(x) dx > 0$ is valid for (2.3) in the case $K_1 = \beta K_2 \neq \text{const}$, where $\beta \in (0, 1]$, which leads to the result similar to the following theorem.

Theorem 4. *If $K_1 \geq K_2$ and either $K_1(x) \equiv K_2(x) \neq \text{const}$ or $K_1(x) > K_2(x)$ in a nonempty open domain, and $r_1(x) \equiv r_1$, $r_2(x) \equiv r_2$ are constant then the semi-trivial equilibrium $(0, v^*(x))$ of (2.1) is unstable.*

Proof. Consider problem (2.7) obtained after the substitution $w = u/K_1$. The semi-trivial equilibrium of (2.7) corresponding to the semi-trivial equilibrium $(0, v^*(x))$ of (2.1) is also $(0, v^*(x))$. Since $K_1(x)$ is strictly positive and bounded from above in Ω , stability of the equilibrium $(0, v^*(x))$ of system (2.1) is equivalent to stability of the equilibrium $(0, v^*(x))$ of (2.7), thus we will investigate the latter system.

First consider the linearization of (2.7) around $(0, v^*(x))$

$$\begin{cases} \frac{\partial w(t, x)}{\partial t} = \frac{D_1}{K_1(x)} \Delta w(t, x) + r_1 \tilde{g}(x, 0, v^*, K_1) w(t, x), & t > 0, x \in \Omega, \\ \frac{\partial v(t, x)}{\partial t} = \nabla \cdot (D_2 d(x) \nabla v(t, x)) + r_2 \tilde{g}(x, v^*, 0, K_2) v(t, x) \\ \quad + r_2 v^*(x) \tilde{g}_v(x, v^*, 0, K_2) v(t, x) \\ \quad + r_2 v^*(x) \tilde{g}_w(x, v^*, 0, K_2) w(t, x), & t > 0, x \in \Omega, \\ \frac{\partial w}{\partial n} = d(x) \frac{\partial v}{\partial n} = 0, & x \in \partial \Omega \end{cases}$$

and study the associated eigenvalue problem

$$\begin{aligned} & \frac{D_1}{K_1(x)} \Delta \psi(x) + r_1 \tilde{g}(x, 0, v^*, K_1) \psi(x) = \sigma \psi(x), \quad x \in \Omega, \\ & \frac{\partial \psi}{\partial n} = 0, \quad x \in \partial \Omega, \end{aligned} \tag{4.5}$$

$$\begin{aligned} & \nabla \cdot D_2 d(x) \nabla \phi(x) + r_2 \tilde{g}(x, v^*, 0, K_2) \phi(x) \\ & + r_2 v^*(x) \tilde{g}_v(x, v^*, 0, K_2) \phi(x) + r_2 v^*(x) \tilde{g}_w(x, v^*, 0, K_2) \psi(x) = \sigma \phi(x), \\ & x \in \Omega, d(x) \frac{\partial \phi}{\partial n} = 0, \quad x \in \partial \Omega. \end{aligned} \tag{4.6}$$

If the principal eigenvalue is positive then the semi-trivial equilibrium $(0, v^*)$ is unstable. Consider the first equation in (4.5), according to the variational characterization of the eigenvalues [4] the principal eigenvalue is given by

$$\sigma_1 = \sup_{\psi \neq 0, \psi \in W^{1,2}} \frac{- \int_{\Omega} D_1 |\nabla \psi|^2 dx + \int_{\Omega} K_1 r_1 \psi^2 \tilde{g}(x, 0, v^*, K_1) dx}{\int_{\Omega} K_1 \psi^2 dx}.$$

After substituting $\psi = 1$, applying (4.1) in Lemma 4 and using $r_1(x) \equiv r_1$, we have $\sigma_1 \geq \frac{r_1 \int_{\Omega} \tilde{g}(x, 0, v^*, K_1) K_1 dx}{\int_{\Omega} K_1 dx} > 0$, which concludes the proof. \square

Theorem 5. *The trivial equilibrium $(0, 0)$ of system (2.1) is unstable; moreover, it is a repelling equilibrium.*

Proof. Similar to the proof of Theorem 4, we linearize system (2.7) around the origin to obtain the following eigenvalue problem:

$$\begin{cases} \frac{D_1}{K_1(x)} \Delta \psi(x) + r_1 \tilde{g}(x, 0, 0, K_1) \psi(x) = \sigma \psi(x), \quad x \in \Omega, \\ \frac{\partial \psi}{\partial n} = 0, \quad x \in \partial \Omega, \\ \nabla \cdot \left(\frac{D_2}{K_2(x)} \nabla \phi(x) \right) + r_2 \tilde{g}(x, 0, 0, K_2) \phi(x) = \sigma \phi(x), \quad x \in \Omega, \\ d(x) \frac{\partial \phi}{\partial n} = 0, \quad x \in \partial \Omega \end{cases} \tag{4.7}$$

Integrating the equation in (4.7) over Ω , we obtain $\sigma_1 = \frac{\int_{\Omega} r_2(x) \tilde{g}(x, 0, 0, K_2) \phi_1 dx}{\int_{\Omega} \phi_1 dx}$, where ϕ_1 is the principal eigenfunction of (4.7), $\tilde{g}(x, 0, 0, K_2) > 0$ by (A4) and (A5), and ϕ_1 can be chosen positive.

Therefore, $\sigma_1 > 0$ and the trivial equilibrium of (2.1) is unstable. Let us show that the trivial equilibrium $(0, 0)$ is a repeller according to the definition (2) of Theorem 9.

Denote $K(x) = \min\{K_1(x), K_2(x)\} > 0$, $r(x) = \min\{r_1(x), r_2(x)\} > 0$, then the right-hand sides in (2.1) can only become smaller after changing K_1 and K_2 by K , according to (A6); also, as long as $u(t, x) + v(t, x) \leq K(x)$, the following inequalities are satisfied

$$\begin{cases} \frac{\partial u(t, x)}{\partial t} \geq D_1 \Delta \left(\frac{u(t, x)}{K_1(x)} \right) + r(x) u(t, x) g(x, u(t, x), v(t, x), K(x)), \\ \frac{\partial v(t, x)}{\partial t} \geq D_2 \nabla \cdot (d(x) \nabla v(t, x)) \\ \quad + r(x) v(t, x) g(x, v(t, x), u(t, x), K(x)) \end{cases} \tag{4.8}$$

for any $t > 0$ and $x \in \Omega$. To show that the trivial equilibrium is a repeller we add the inequalities in (4.8) and integrate over Ω using the boundary conditions

$$\frac{d}{dt} \int_{\Omega} (u + v) dx \geq \int_{\Omega} r(u + v)g(x, u, v, K) dx \tag{4.9}$$

which is valid for any u, v such that $u + v \leq K$. Let us take $0 < \delta \leq \inf_{x \in \Omega} K(x)/4$ and $\rho > 0$ such that $r(x)G(x, 2\delta, K) \geq \rho > 0$ which we can find according to (A5). Then (4.9) holds as long as $u(t, x) + v(t, x) \leq 2\delta$.

By Theorem 1, the solution is positive for any $t > 0$ and $(u_0(x), v_0(x)) \neq (0, 0)$, so we can choose $u_0(x) + v_0(x) < \delta$ and $t_0 > 0$ small enough such that $0 < \delta_1 < u_1(x) + v_1(x) < \delta$, where $u_1(x) = u(t_1, x)$, $v_1(x) = v(t_1, x)$. As long as $u(t, x) + v(t, x) \leq 2\delta$, inequality (4.9) is satisfied. Thus using Gronwall’s lemma we obtain

$$\int_{\Omega} (u(t, x) + v(t, x)) dx \geq e^{\rho(t-t_1)} \int_{\Omega} (u_1(x) + v_1(x)) dx,$$

and since $\int_{\Omega} (u_1(x) + v_1(x)) dx > 0$, we obtain that the integral $\int_{\Omega} (u(t, x) + v(t, x)) dx$ grows exponentially with time as long as $u(t, x) + v(t, x) \leq 2\delta$. We therefore conclude that there exists $t_2 > 0$ such that $u(t_2, x) + v(t_2, x) > \delta$ for some $x \in \Omega$ and hence the trivial equilibrium is a repeller. □

Finally, we can state the main stability results.

Theorem 6. *Let r_1 and r_2 be constant, $K_1(x) \geq K_2(x)$ for any $x \in \Omega$, either $K_1(x) \neq \text{const}$ or $K_1(x) > K_2(x)$ in some nonempty bounded domain, and (A2)–(A6) be satisfied for the functions $f_1(x, u, v, K) = r_1 u g(x, u, v, K)$ and $f_2(x, u, v, K) = r_2 v g(x, v, u, K)$. Then the semi-trivial equilibrium $(K_1, 0)$ of (2.1) is globally asymptotically stable, i.e. for any nonnegative nontrivial $u_0, v_0 \in C(\bar{\Omega})$ the solution $(u(t, x), v(t, x))$ of (2.1), (2.2) satisfies $(u, v) \rightarrow (K_1, 0)$ as $t \rightarrow \infty$ uniformly in $x \in \bar{\Omega}$.*

Proof. 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 (2.1)–(2.2). According to Lemma 5 from Appendix A, the first condition on T_t from Theorem 9 is satisfied. Next, condition (2) is guaranteed by Theorem 5, and condition (3) follows from Lemma 1. Finally, condition (4) can be deduced from Theorem 1 and Lemma 5 and therefore system (2.1) is a strongly monotone dynamical system and we can apply Theorem 9 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 9. Finally, there is no coexistence state therefore the equilibrium $(K_1, 0)$ is globally asymptotically stable. □

Remark 4. We would like to remark here that although the solutions of (2.1) still converge to $(K_1(x), 0)$ with time for any $D_1, d(x)$ and constant r_1, r_2 , the speed of convergence depends on the diffusion coefficient and the ratio r_1/r_2 , see examples in Section 5 for numerical illustration.

Next, let us discuss the case $K_1(x) \leq K_2(x)$ for any $x \in \Omega$.

Theorem 5 is still valid, the zero equilibrium is unstable, and it is a repeller. However, other results cannot be extended to this case. In particular, the advantage of carrying-capacity driven diffusion is not sufficient to provide competitive exclusion in the case when the other species has a higher carrying capacity.

Theorem 7. *If $K_1(x) \leq K_2(x)$ for all $x \in \Omega$ and both $r_2(x) > 0$ and $K_1(x) < K_2(x)$ in a nonempty open domain, then the semi-trivial equilibrium $(K_1(x), 0)$ of (2.1) is unstable.*

Proof. First, let us note that since $K_1(x) \leq K_2(x)$ for all $x \in \Omega$ and $r_2(x) > 0$, $K_1(x) < K_2(x)$ in a nonempty open domain, $g(x, K_1(x), 0, K_2(x)) \geq 0$ by (A4) and (A6), and

$$\int_{\Omega} r_2(x)g(x, K_1, 0, K_2) dx > 0. \tag{4.10}$$

The proof follows the steps of the proof of Theorem 4. Further, consider the linearization of (2.1) around $(K_1(x), 0)$ and study the second part of the associated eigenvalue problem

$$\begin{aligned} \nabla \cdot (d(x)\nabla \phi(x)) + \phi(x)r_2(x)g(x, K_1, 0, K_2) &= \sigma \phi(x), x \in \Omega, \\ \frac{\partial \phi}{\partial n} &= 0, x \in \partial \Omega. \end{aligned} \tag{4.11}$$

If the principal eigenvalue is positive then the equilibrium $(K_1(x), 0)$ is unstable. Again, following the variational characterization of the eigenvalues [4], we obtain that the principal eigenvalue of (4.11) is given by

$$\sigma_1 = \sup_{\phi \neq 0, \phi \in W^{1,2}} \frac{-\int_{\Omega} d(x)|\nabla \phi|^2 dx + \int_{\Omega} \phi^2 r_2(x)g(x, K_1, 0, K_2) dx}{\int_{\Omega} \phi^2 dx}. \tag{4.12}$$

Choosing the eigenfunction $\phi = 1$, we have $\sigma_1 \geq \frac{\int_{\Omega} r_2(x)g(x, K_1, 0, K_2) dx}{\int_{\Omega} dx} > 0$ by (4.10), thus $(K_1(x), 0)$ is unstable, which concludes the proof. □

In Section 5 we will see that both coexistence and competitive exclusion of u and v in (2.1) are possible.

5. Numerical examples

If the carrying capacities are the same and the growth rates are proportional then there is no coexistence equilibrium, and the choice of the carrying capacity driven diffusion leads to the competitive exclusion of a randomly diffusing population. In all the examples, we considered either the logistic

$$\begin{cases} \frac{\partial u(t, x)}{\partial t} = D_1 \Delta \left(\frac{u}{K_1} \right) + r_1 u \left(1 - \frac{u+v}{K_1} \right), & t > 0, x \in \Omega, \\ \frac{\partial v(t, x)}{\partial t} = \nabla \cdot \left(\frac{D_2}{K_2} \nabla v \right) + r_2 v \left(1 - \frac{u+v}{K_2} \right), & t > 0, x \in \Omega, \\ \frac{\partial (u/K_1)}{\partial n} = \frac{1}{K_2(x)} \frac{\partial v}{\partial n} = 0, & x \in \partial \Omega \end{cases} \tag{5.1}$$

or the Gilpin–Ayala type of growth

$$\begin{cases} \frac{\partial u(t, x)}{\partial t} = D_1 \Delta \left(\frac{u}{K_1} \right) + r_1 u \left(1 - \left(\frac{u+v}{K_1} \right)^{\theta} \right), & t > 0, x \in \Omega, \\ \frac{\partial v(t, x)}{\partial t} = \nabla \cdot \left(\frac{D_2}{K_2} \nabla v \right) + r_2 v \left(1 - \left(\frac{u+v}{K_2} \right)^{\theta} \right), & t > 0, x \in \Omega, \\ \frac{\partial (u/K_1)}{\partial n} = \frac{1}{K_2(x)} \frac{\partial v}{\partial n} = 0, & x \in \partial \Omega. \end{cases} \tag{5.2}$$

First, let us consider the case of equal carrying capacities. The following example shows that in the case of space-dependent growth rates the conclusion of Theorem 6 is no longer valid, and the second population may survive, coexistence is possible.

Example 1. Consider (5.1), where $\Omega = (0, \pi)$, $K(x) = K_1(x) = K_2(x) = 2 + \cos(x) \neq \text{const}$, $D = D_1 = D_2 = 1$, $r_1(x) = (x + 0.1)^3$ and $r_2(x) = 2/(Kv^*)$ which has the semitrivial equilibria $(K_1, 0)$ and $(0, v^*)$ with $v^* = \frac{7}{4} + \frac{1}{2} \cos(x)$. The numerical simulations show that in this situation the two species can coexist, see Fig. 1, left, we can also proportionally change r_1 , see Fig. 1, middle and right.

The step in the proof that fails in this case is the inequality (4.1). More precisely, we still have the estimate $\int_{\Omega} r_2(x)g(x, 0, v^*, K_1)K_1(x) dx > 0$, however, one can check that the inequality we need in the proof of Theorem 4 is $\int_{\Omega} r_1(x)g(x, 0, v^*, K_1)K_1(x) dx > 0$ which does not hold for r_1, g and K_1 as above.

Fig. 1 (left) illustrates that the semi-trivial equilibrium $(0, v^*)$ is unstable, while according to Fig. 1 (right) the equilibrium $(K(x), 0)$ is neither a local nor a global attractor.

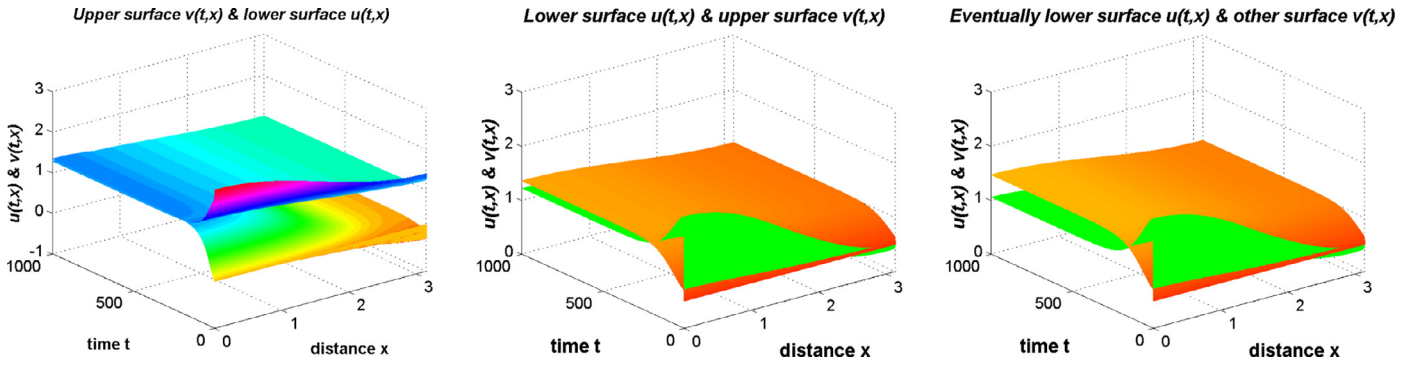


Fig. 1. Solutions of (5.1) for $K(x) = K_1(x) = K_2(x) = 2 + \cos(x)$, $D_1 = D_2 = 1$, $r_2 = 2/(Kv^*)$, where $v^* = 7/4 + 0.5 \cos(x)$, $\Omega = (0, \pi)$, and (left) $r_1 = (x + 0.1)^3$, (middle) $r_1 = 1.5(0.1 + x)^3$ and (right) $r_1 = 0.8(0.1 + x)^3$.

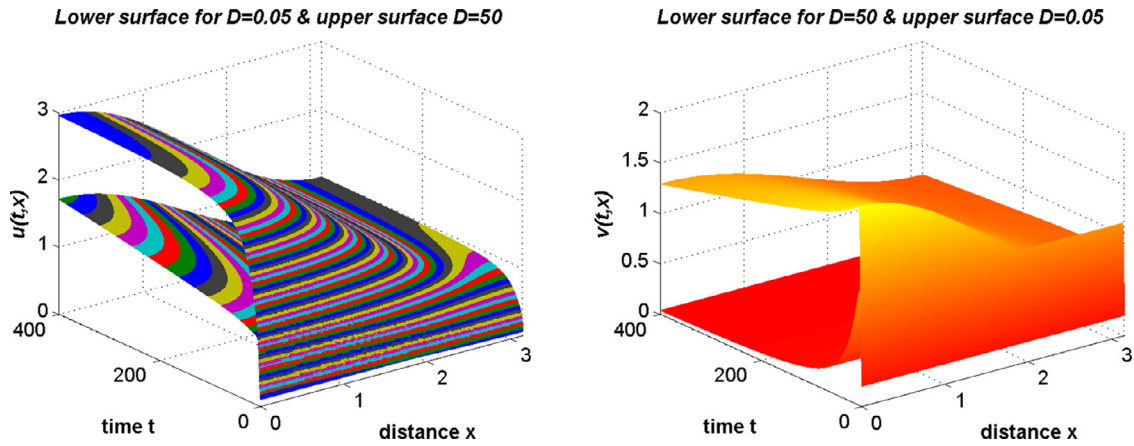


Fig. 2. Solutions of (5.1) for $K_1 = K_2 = 2 + \cos(x)$, $r_1 = r_2 = 1$, the initial values $(u_0, v_0) = (0.1, 0.2)$, $D = 0.05$ and $D = 50$. Higher diffusion coefficients lead to faster convergence to the stable equilibrium.

Here lower growth rates are observed in the areas of small x with larger K , especially for the carrying capacity oriented population, which gives some advantage to the strategy of random dispersal.

In the next example, we outline the effect of the diffusion coefficient.

Example 2. Consider (5.1) with $K_1 \equiv K_2 \equiv K$ and constant r_1, r_2 . According to Theorem 6, the value of u should tend to K while v tends to zero as $t \rightarrow \infty$. As long as we increase the diffusion coefficient, there is a faster convergence to the limit state, see Fig. 2. For the same initial values and $t > 0$, we have smaller values of v and greater values of u as D increases.

Next, consider the case when the growth rates are constant but the carrying capacities are different.

Example 3. Consider logistic growth model (5.1) with different carrying capacities. If the carrying capacities are different but the one for the species choosing the carrying-capacity driven diffusion strategy is less or equal than the other carrying capacity everywhere, there are two possible scenarios: the species with a higher carrying capacity sustains and the other goes extinct and coexistence, see Fig. 3. Coexistence is observed when carrying capacities are relatively close, while in the limit case of the equal carrying capacities the regularly diffusing population goes extinct while the other species sustains. If $K_1 = \beta K_2$ with $\beta \in (0, 1]$, then there is β_0 such that there is a competitive exclusion (the second species survives only) for $\beta \in (0, \beta_0)$ and coexistence for $\beta \in (\beta_0, 1)$, where only the first species survives for $\beta = 1$, see Fig. 3. However, the average eventual population levels of u increase and of v decrease as $\beta > \beta_0$ grows and approaches one, see Fig. 4.

Consider the case of time-variable carrying capacities and explore the dependency of the coexistence equilibrium on the relation between the growth rates.

Example 4. Consider (5.1) with time-variable $K_1 = K_2 = (1.2 + \cos(x))(1.1 + \sin(t))$, $D_1 = D_2 = 1$ and stationary $r_2 = 1.1 + 0.5 \cos(x)$. Fig. 5 demonstrates the established regime (the time is between 450 and 600), where the higher relative growth rates r_1 lead to higher average population levels achieved in the competition.

In addition to the periodicity with the same period as K has, there are also slower amplitude oscillations with a period depending on the ratio $r_1 : r_2$.

The following example illustrates the dependency of the average growth rates on the ratio or $r_1 : r_2$ in the case of stationary carrying capacities and Gilpin–Ayala growth rate.

Example 5. Consider Eq. (5.2) representing Gilpin–Ayala growth system with $D_1 = D_2 = 1$, $\theta = 0.5$, $K_1 = 1.45 + 0.95 \cos(x) < K_2 = 1.5 + \cos(x)$, and proportional intrinsic growth rates. For all chosen ratios $r_1 : r_2$ the two species coexist, and the average population levels depend on the ratio. Here the advantage of a higher carrying capacity of the second population is alleviated by a more advanced diffusion type chosen by the first population.

In Fig. 6 we observe coexistence, and average population levels of u increase, while of v decrease with the growth of $r_1 : r_2$. Thus reduction of reproduction rates of the invading population can really reduce invasion of species with a higher carrying capacity, compare to [18].

Let us note that even for the same (or proportional) growth rates and the same carrying capacity, time dependency of the carrying

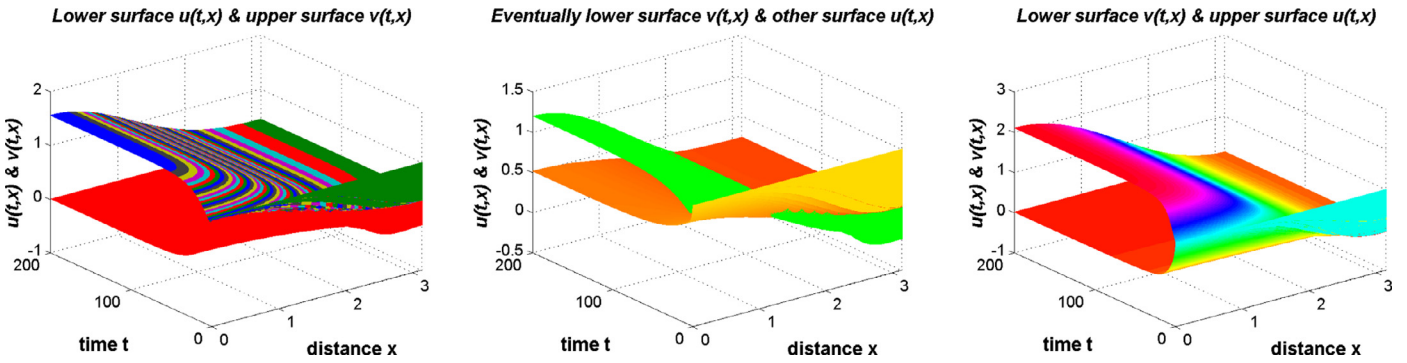


Fig. 3. Solutions of (5.1) for $K_2 = 1.1 + \cos(x)$, $D = 1$, $r_1 = r_2 = 1$, $u_0 = v_0 = 1.0$ with (left) $K_1 = 0.75K_2$, (middle) $K_1 = 0.85K_2$ and (right) $K_1 = K_2$.

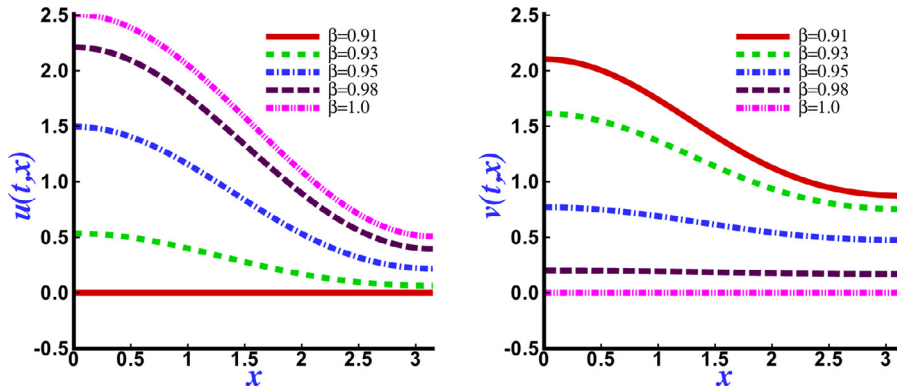


Fig. 4. Solutions of (5.1) for $K_2 = 1.5 + \cos(x)$, $D_1 = D_2 = 1$, $r_1 = r_2 = 1.0$, $u_0 = v_0 = 0.6$ with $K_1 = \beta K_2$ and for $\beta \geq 0.91$ at time $t = 600$. The average eventual population levels of u increase and of v decrease as $\beta \geq 0.91$ grows up to one.

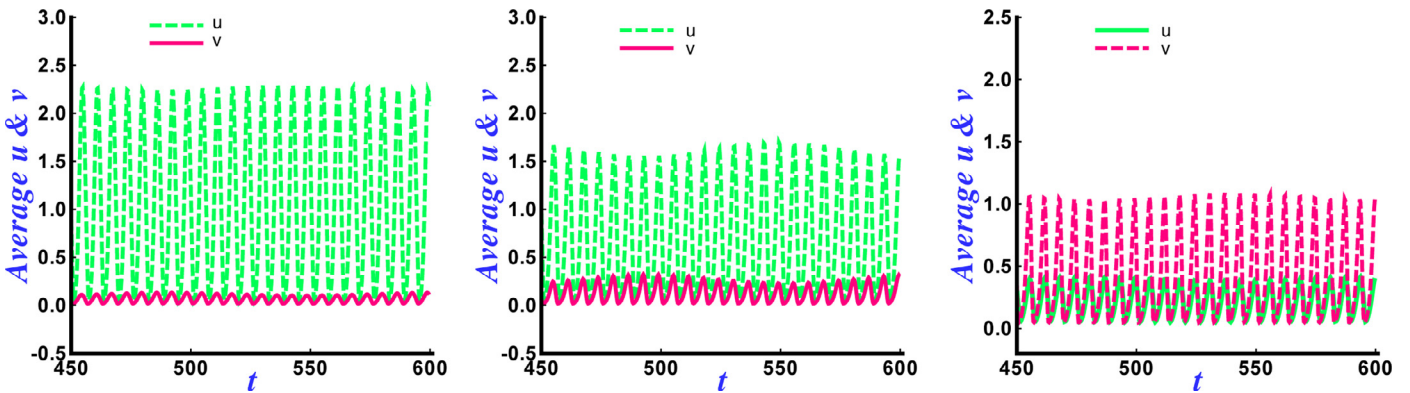


Fig. 5. Solutions of (5.1) for $D_1 = D_2 = 1$, $K_1 = K_2 = (1.2 + \cos(x))(1.1 + \sin(t))$, $r_2 = 1.1 + 0.5 \cos(x)$, $u_0 = v_0 = 0.5$ with (left) $r_1 = 1.5r_2$, (middle) $r_1 = r_2$ and (right) $r_1 = 0.5r_2$ for time $t = 600$.

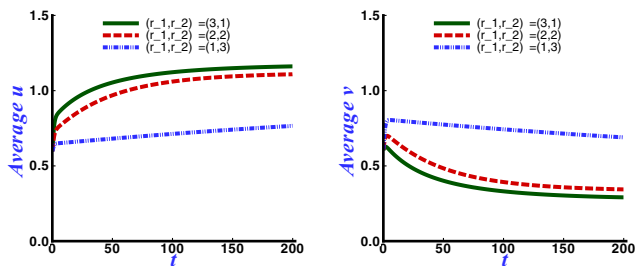


Fig. 6. Solutions of (5.2) for $D_1 = D_2 = 1$, $\theta = 0.5$, $K_1 = 1.45 + 0.95 \cos(x) < K_2 = 1.5 + \cos(x)$, $u_0 = v_0 = 0.6$ with growth rates $(r_1, r_2) = \{(3, 1), (2, 2), (1, 3)\}$.

capacity can lead to coexistence. The following example illustrates it, as well as explores how the average population rates depend on the growth rate.

Example 6. Consider (5.2) where the carrying capacity $K = K_1 = K_2 = e^{-Dt} \cos(x) + 2.5$ is variable in both space and time, $\theta = 0.1$ and different constant intrinsic growth rates r_1 and r_2 . The average carrying capacity tends to 2.5 as $t \rightarrow \infty$. Fig. 7 illustrates average solutions for $t \in [0, 600]$. There is coexistence, and the average population level increases with the increase of the intrinsic growth rate relative to the one of the other species.

Next, let us illustrate the fact that for time-variable carrying capacities the relation between the average population levels at coexistence may depend on the diffusion rate as well, even in the case when these diffusion rates are equal.

Example 7. Consider (5.2) for $\theta = 0.75$ and time-variable $r_1 = r_2 = 2(1.5 + \cos(t))/(1.5 + \sin(t))$ and $K_1 = K_2 = (1.2 + \cos(x))(2 + 0.5 \sin(t))$ with different diffusion rates.

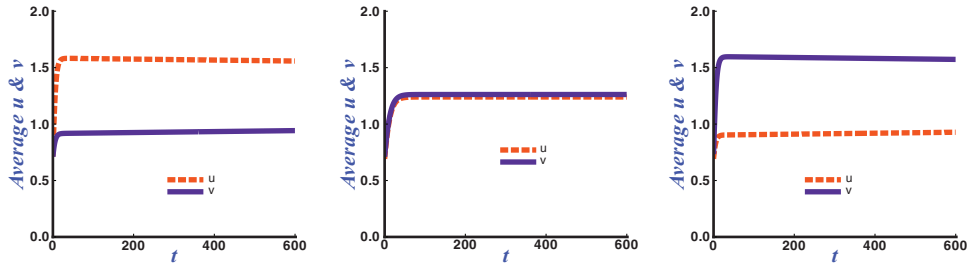


Fig. 7. Solutions of (5.2) for $D = D_1 = D_2 = 1.0$, $\theta = 0.1$, $K_1 = K_2 = e^{-Dx} \cos(x) + 2.5$, $u_0 = v_0 = 0.7$ with (left) $r_1 = 3 > r_2 = 1$, (middle) $r_1 = r_2 = 1$ and (right) $r_1 = 1 < r_2 = 3$.

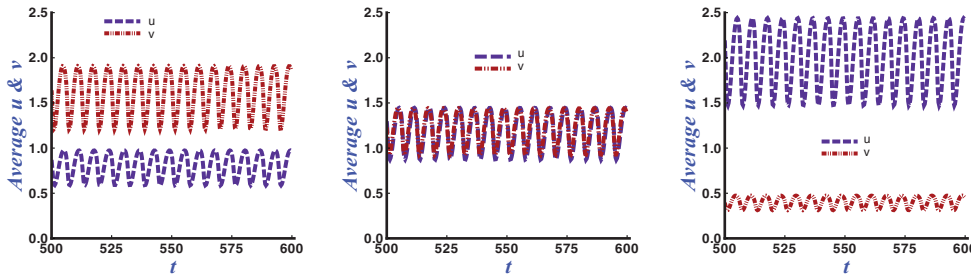


Fig. 8. Solutions of (5.2) for $\theta = 0.75$, $r_1 = r_2 = 2(1.5 + \cos(t))/(1.5 + \sin(t))$, $K_1 = K_2 = (1.2 + \cos(x))(2 + 0.5 \sin(t))$, $u_0 = v_0 = 0.7$ with (left) $D_1 = D_2 = 0.1$, (middle) $D_1 = D_2 = 0.19$ and (right) $D_1 = D_2 = 0.5$.

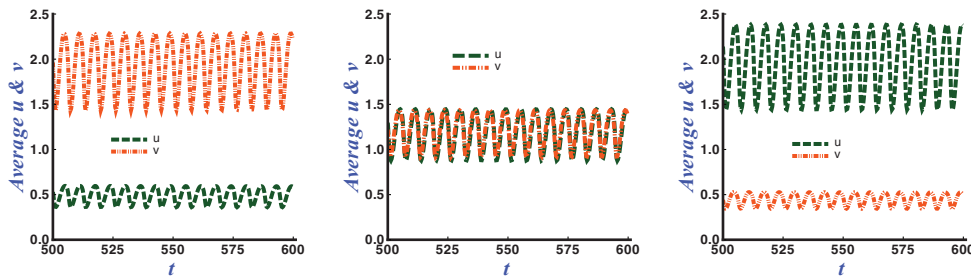


Fig. 9. Solutions of (5.2) for $\theta = 0.75$, $r_1 = r_2 = 2(1.5 + \cos(t))/(1.5 + \sin(t))$, $K_1 = K_2 = (1.2 + \cos(x))(2 + 0.5 \sin(t))$, $D_1 = 5.0$, $u_0 = v_0 = 0.7$ with (left) $D_2 = 0.1$, (middle) $D_2 = 0.3$ and (right) $D_2 = 0.5$.

There is coexistence for the chosen diffusion rates of 0.1, 0.19 and 0.5, and, as can be seen in Fig. 8, for slow dispersion, the average rate of v is greater than the average rate of u (left). As the dispersion rate D increases, for a certain value of $D \approx 0.19$ both populations coincide (Fig. 8, middle), and $u_{ave} > v_{ave}$ for larger D (Fig. 8, right).

Let us note that the relative population densities depend on the diffusion coefficient D_2 , see Fig. 9 for $D_1 = 5$ and $D_2 = 0.1, 0.3, 0.5$. Fig. 9 confirms the conclusion of [12] that for regularly diffusing populations, a higher diffusion rate leads to a disadvantage: for $D_2 = 0.1$, average population levels of a regularly diffusing population are higher than for species with a carrying capacity driven diffusion (Fig. 9, left), become equal for $D_2 = 0.3$ (Fig. 9, middle) and are smaller for $D_2 = 0.5$ (Fig. 9, right).

Numerical runs show that for this example, whenever D_2 is fixed, the relation of eventual population levels does not depend on D_1 .

Finally, we show that for steep enough variations of carrying capacities, the population with directed diffusion strategy can form a refuge-type area with higher average density than the regularly diffusing population with a higher carrying capacity everywhere.

Example 8. Consider (5.1) representing logistic growth system with $D_1 = 0.1$, $r_1 = r_2 = 1$, stationary

$$K_1(x) = 500e^{-12.5(x-\pi/2)^2} - 5e^{-50(x-\pi/2)^2} + 1, \tag{5.3}$$

either $K_2 = 1.1K_1$ or $K_2 = 1.6K_1$ and various diffusion rates D_2 of v . Here the carrying capacity for regularly diffusing species v is 1.6 times

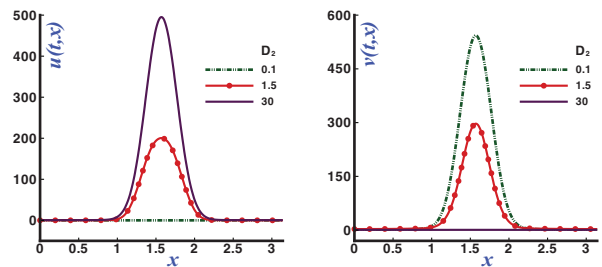


Fig. 10. Solutions of (5.1) for $K_1(x)$ as in (5.3), $K_2(x) = 1.1K_1(x)$, $D_1 = 0.1$, $\Omega = (0, \pi)$, $r_1 = 1 = r_2$, $u_0 = v_0 = 0.5$ for various $D_2 = 0.1, 1.5, 30$ at time $t = 400$.

higher than for those with a directed diffusion strategy (Figs. 12 and 13, right). Still, this strategy allows to form a refuge (at the middle of $[0, \pi]$) where the population survives and thrives, especially for higher diffusion rates for randomly diffusing species, see Fig. 10 for the relation between the two and density profiles for various D_2 for a large running time (it is a limit profile, see Fig. 11). If $D_2 = 0.1$, the profile of a regularly diffusing population is similar to the profile of the carrying capacity, and the average is high, the population with directed diffusion strategy is suppressed (its potential refuge is still overpopulated). As D_2 grows, the profile of v flattens, tending to be constant, with a decreasing average, and u gradually builds a refuge in the area of abundant resources.

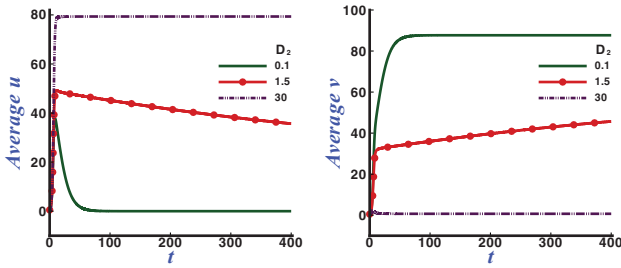


Fig. 11. Solutions of (5.1) for $K_1(x)$ as in (5.3), $K_2(x) = 1.1K_1(x)$, $D_1 = 0.1$, $r_1 = 1 = r_2$, $u_0 = v_0 = 0.5$ for various $D_2 = 0.1, 1.5, 30$.

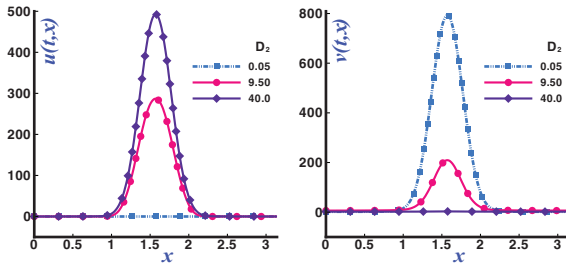


Fig. 12. Solutions of (5.1) for $K_1(x)$ as in (5.3), $K_2(x) = 1.6K_1(x)$, $D_1 = 0.05$, $\Omega = (0, \pi)$, $r_1 = 1 = r_2$, $u_0 = v_0 = 0.7$ for various $D_2 = 0.05, 9.5, 40$ at time $t = 400$.

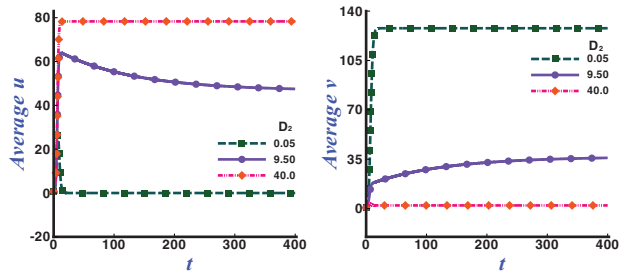


Fig. 13. Solutions of (5.1) for $K_1(x)$ as in (5.3), $K_2(x) = 1.6K_1(x)$, $D_1 = 0.05$, $\Omega = (0, \pi)$, $r_1 = 1 = r_2$, $u_0 = v_0 = 0.7$ for various $D_2 = 0.05, 9.5, 40$.

The asymptotical convergence of population averages for $K_2 = 1.1K_1$ is illustrated in Fig. 11.

Similarly, Figs. 12 and 13 show the limit behavior and the asymptotics in the case of $K_2(x) = 1.6K_1(x)$.

We observe that for high enough diffusion rate of the regularly diffusing population, the population choosing directed diffusion can survive, form a refuge and flourish there, even for a lower carrying capacity anywhere.

6. Summary and discussion

In the present paper we have considered the case when the two competing spatially distributed species choose different dispersal strategy, and studied separately the influence of different growth rates and carrying capacities corresponding to crowding tolerance. If the carrying capacities are equal and the growth rates are spatially homogeneous (proportional) for both populations, the situation is the same as in the case of equal growth rates: there is a competitive exclusion of a randomly diffusing species. If the growth rates are spatially different, the two populations can coexist, as a numerical example demonstrates. In the case of different crowding tolerances, the following three scenarios can occur. If the crowding tolerance of a species diffusing according to the carrying capacity is not less than the other one, a randomly diffusing population goes extinct. If

the crowding tolerance of a randomly diffusing population is higher, this provides its survival; when the difference between the crowding tolerances is not large, the two populations coexist. This means that the judicious choice of diffusion can alleviate the disadvantage of higher sensitivity to crowding effects when the two sensitivities are still close to each other. If the crowding tolerance of a randomly diffusing population is much higher than the second one, this brings the population with a lower crowding tolerance to extinction. In all the numerical simulations we have not observed any dependence of the asymptotic behavior on the initial conditions. Whenever the growth rates are proportional, their relation also does not influence the scenario in general, however, in the coexistence case, higher growth rates led to higher population levels. Similarly, the diffusion coefficient contributed not to the asymptotic behavior but to the convergence rate. Also, depending on the relation between the growth rates and the carrying capacities, competitive exclusion or coexistence can occur; so far we observed only one coexistence equilibrium but have not justified that this is the only possibility.

If the two populations have differential consumption of resources and the space-dependent consumption rates are proportional, we have proved that the regularly diffusing population would become extinct. However, the initial numerical simulations demonstrate that this situation sustains for a wider range of the ratios $K_1(x) : K_2(x)$ than just being a constant, but so far we have not succeeded in proving this result analytically; this part should be further investigated, for example, the general Lotka-type system as in [27] where in addition different diffusion types are chosen.

The diffusion coefficients and the relation between proportional growth rates do not influence the asymptotics but the transient behavior significantly depends on these parameters, as numerical examples illustrated. The results of the present paper can be applied to the case of a symmetric competition when both species distribute according to some positive function [25], demonstrating the advantage of choosing the carrying capacity as this distribution target.

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Appendix A.

In this section we present auxiliary results which were used earlier in proofs. The next theorem from [28] deals with the time-dependent solution of the system of the form

$$\frac{\partial u_i}{\partial t} - L_i u_i = f_i(x, u_1, u_2), \quad t > 0, x \in \Omega, \tag{A.1}$$

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

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

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

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

$$\lambda |\xi|^2 \leq \sum_{ij=1}^n a_{ij}(t, x) \xi_i \xi_j \leq \Lambda |\xi|^2, \quad (t, x) \in [0, T] \times \bar{\Omega}. \tag{A.3}$$

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 $\rho = (\rho_1, \rho_2) \in \mathbb{R}_+^2$ define

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

Theorem 8. [28, Theorem 8.7.2] *Let (f_1, f_2) be a quasimonotone non-increasing Lipschitz function in \mathbf{S}_ρ and let (f_1, f_2) satisfy*

$$f_1(t, x, \rho_1, 0) \leq 0 \leq f_1(t, x, 0, \rho_2), f_2(t, x, 0, \rho_2) \leq 0 \leq f_2(t, x, \rho_1, 0) \quad (\text{A.4})$$

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

The next lemma [4] implies the monotonicity property for solutions of (A.1).

Lemma 5. *Let $(u_i(t, x), v_i(t, x))$, $i = 1, 2$, be two solutions of system (A.1), where $u_1(0, x) \geq u_2(0, x)$ and $v_1(0, x) \leq v_2(0, x)$ for any $x \in \Omega$. Then $u_1(t, x) \geq u_2(t, x)$ and $v_1(t, x) \leq v_2(t, x)$ for any $x \in \Omega$ and any $t > 0$. Moreover, if $(u_1(0, x), v_1(0, x)) \neq (u_2(0, x), v_2(0, x))$, 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 [4] Theorem 1.20 and remarks thereafter. The final statement of the lemma follows from the strong maximum principle for parabolic equations [29] applied to the differences $u_1 - u_2$ and $v_2 - v_1$.

The next result [20] classifies all possible equilibria for a monotone dynamical system. We will present a particular case of Theorem B [20]. Denote $X^+ = C_+(\bar{\Omega}) \times C_+(\bar{\Omega})$, where $C_+(\bar{\Omega})$ is the class of all nonnegative functions from $C(\bar{\Omega})$; $I = \langle 0, \tilde{u}_1 \rangle \times \langle 0, \tilde{u}_2 \rangle$, where $(\tilde{u}_1, 0)$ and $(0, \tilde{u}_2)$ are the semi-trivial equilibria of (A.1). Here $\langle \cdot, \cdot \rangle$ is as in the proof of Theorem 1.

Theorem 9. *Let operator T_t be defined as $T_t(\mathbf{u}_0) = \mathbf{u}$, where $\mathbf{u}_0 \equiv (u_{1,0}, u_{2,0})$ and $\mathbf{u} \equiv (u_1, u_2) = (T_t(u_{1,0}), T_t(u_{2,0}))$ is a solution of (A.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 neighborhood 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 (A.1).
- (b) $(u_1, u_2) \rightarrow (\tilde{u}_1, 0)$ as $t \rightarrow \infty$ for every $(u_{1,0}, u_{2,0}) \in I$.
- (c) $(u_1, u_2) \rightarrow (0, \tilde{u}_2)$ as $t \rightarrow \infty$ for every $(u_{1,0}, u_{2,0}) \in I$.

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

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