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DIRECTED VS REGULAR DIFFUSION STRATEGY: EVOLUTIONARY STABILITY ANALYSIS OF A COMPETITION MODEL AND AN IDEAL FREE PAIR

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Abstract. In this study, we consider a reaction-diffusion competition model describing population dynamics of two competing species and the interactions between them in a heterogeneous environment. The main goal of this paper is to study the impact of different diffusion strategies on the outcome of competition between two populations while the first species is distributed according to the resource function and the second population is following the regular dispersion. We focus on how directed diffusion in the habitat influences selection. The two populations differ in the diffusion strategies they employ as well as in their environmental intensities. We establish the main results which determine that the competing species may either coexist, or one of them may bring the other to extinction. If higher carrying capacity is incorporated for the directed dispersal population then competitive exclusion of a regularly diffusing population is inevitable. We consider the case when both populations manage to coexist and there is an ideal free pair with identical carrying capacity, and the relevant coexistence equilibrium is a global attractor. The coexistence solution is also presented by showing the influence of diffusion coefficients. In a series of examples, the results have been justified and illustrated numerically.

1. Introduction

The modeling of populations is always an important issue in ecology and economy, for instance, to describe the well-known feature such as competitive and cooperative interactions. Reaction-diffusion problems are broadly used as models for spatial effects in ecology. In the past two decades, the Lotka-Volterra model with standard diffusion was considered in the literature [1, 2, 3, 4, 5, 6, 7, 8, 9] and references therein.

In [3], Dockery *et al.* presented an interesting illustrative example of the fact that combined effects of diffusion and spatial heterogeneity is that the slower diffuser always prevails. They considered n phenotypes of species in a heterogeneous environment competing for the resources. If there are only two phenotypes, they proved that the slower diffuser will evolve for the reaction-diffusion model:

$$\begin{cases} u_t = d_1\Delta u(t,x) + u(t,x)\left(K(x) - u(t,x) - v(t,x)\right), t > 0,\ x \in \Omega, \\ v_t = d_2\Delta v(t,x) + v(t,x)\left(K(x) - u(t,x) - v(t,x)\right), t > 0,\ x \in \Omega, \\ \nabla u \cdot n = \nabla v \cdot n = 0,\ x \in \partial\Omega, \\ u(0,x) = u_0(x),\ v(0,x) = v_0(x),\ x \in \Omega. \end{cases} \tag{1.1}$$

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Here $u(t,x)$, $v(t,x)$ represent the population densities of two competing species which are therefore assumed to be no-negative, with corresponding migration rates being d_1, d_2, respectively. The function $K(x)$ represents their common local resource distribution function. The phenotype with the least dispersal coefficient has an evolutional advantage in the perception that the only stable steady state is the one where only this phenotype survives [3].

Hutson *et al.* [10] considered a reaction-diffusion system for two competing species, much like Dockery *et al.* in [3], and the model is defined as follows:

$$\begin{cases} u_t = d_1 \Delta u(t,x) + u(t,x)\left(K(t,x) - u(t,x) - v(t,x)\right), t > 0, \ x \in \Omega, \\ v_t = d_2 \Delta v(t,x) + v(t,x)\left(K(t,x) - u(t,x) - v(t,x)\right), t > 0, \ x \in \Omega, \\ \nabla u \cdot n = \nabla v \cdot n = 0, \ x \in \partial\Omega, \\ u(0,x) = u_0(x), \ v(0,x) = v_0(x), \ x \in \Omega. \end{cases} \tag{1.2}$$

Compared to other studies, they found that in a spatially heterogeneous and temporally constant environment, the faster diffuser will suffer defeat [10]. It is also shown that if the environment varies in both space and time, the faster diffuser can be selected [10].

The regular diffusion combined with the directed movement along the environmental gradient corresponds to the reaction-diffusion-advection model introduced in [2, 11, 12, 13]. If the ratio of the advection to the diffusion coefficients tends to infinity then the solutions tend to be ideally distributed for such models. Dispersal design in [12, 14] introduced by R. S. Cantrell *et al.* was based on the notion of the ideal free distribution, *i.e.* such distribution that any movement in an ideally distributed system will decrease the fitness of moving individuals. An ideal free distribution can be obtained for a particular finite rate of advection in the model considered by R. S. Cantrell *et al.* in [13, 15] and this result was recently investigated and improved by I. Averill *et al.* in [11].

In this paper, we consider Lotka-Volterra models of two interacting species competing in a heterogeneous environment for the same basic resources (water, food, shelter, territory, light or any means to maintain life and reproduce), and the diffusion scenario is different for each individuals. In this model, the movement of one species is affected by diffusion towards a smooth distribution function introduced in [16] by E. Braverman and L. Braverman (for the case $P(x) \equiv K(x)$) and for $P \equiv K$ has an evolutionary advantage [17, 18, 19], while the other species is dispersing regularly.

In reality, species rarely move completely randomly. It is plausible that diffusion combined with directed movement along environmental gradients will help the species maximize its chances of survival [11, 13, 15]. The problem in this paper is addressed in the following way: considering two different diffusion strategies, the first species is dispersing according to a distribution function $P(x)$ whereas the second one is dispersing regularly. Also the carrying capacity of the two species can be different with no-flux boundary conditions:

$$\begin{cases} u_t = d_1 \Delta \left(\frac{u(t,x)}{P(x)} \right) + u(t,x)\left(K(x) - u(t,x) - v(t,x)\right), t > 0,\ x \in \Omega, \\ v_t = d_2 \nabla \cdot \frac{1}{P(x)} \nabla v(t,x) + v(t,x)\left(\gamma(x) - u(t,x) - v(t,x)\right), t > 0,\ x \in \Omega, \\ \nabla(u/P) \cdot n = \nabla v \cdot n = 0,\ x \in \partial\Omega, \\ u(0,x) = u_0(x) > 0,\ v(0,x) = v_0(x) > 0,\ x \in \Omega. \end{cases} \tag{1.3}$$

For positive functions $K(x)$ and $\gamma(x)$, we assume that either $K(x) \not\equiv \gamma(x)$ on a nonempty open domain or $K(x) \equiv \gamma(x)$ for any $x \in \Omega$. The density $K(x) \equiv \gamma(x)$ is the maximum number of populations that the habitat can backing and is known as the environmental carrying capacity. The functions $u(t,x)$ and $v(t,x)$ represent the two competing species with corresponding diffusion rates $d_1 > 0$ and $d_2 > 0$, respectively. Here Ω is a bounded region in $\mathbb{R}^n$ while the smooth boundary is $\partial\Omega$, n denotes the unit normal vector on $\partial\Omega$. The meaning of the no-flux boundary condition is that no individuals cross the boundary. We have the following important assumption throughout the paper:

- smooth distribution function $P(x) \not\equiv const$.

If $P(x) \equiv K(x)$ then this type of dispersal (1.3) has the ideal free distribution as a solution for single species [17]. In [18], a system of equations was investigated by L. Korobenko and E. Braverman for a variety of growth functions when $P(x) \equiv K(x) \equiv \gamma(x)$ in (1.3). They established that the population distributed by the carrying capacity only survives in a heterogeneous environment. The effects of higher or lower carrying capacity are shown by E. Braverman *et al.* in [19] for multiple growth functions when $P(x) \equiv K(x) \not\equiv \gamma(x)$. It is proven that the species incorporated with higher carrying capacity is in advantageous situation. In mathematical biology, the asymptotic behavior of solutions of (1.3) has been extensively investigated to understand coexistence and spatial segregation of two species (see [1, 20] and references therein).

The paper is organized as follows. In section 2, we establish some auxiliary results for species u and v, and these will be used in the rest of the paper. Equilibrium analysis of semi-trivial steady states and coexistence solutions are investigated in section 3.

The characterization $K(x) \not\equiv \gamma(x)$ in the reaction parts of (1.3) is referred to as the *crowdiness effect*, and the two populations have similar physical characteristics. Section 3.1 deals with the effects of crowding tolerance. This section illustrates the dynamics for different distributions of $P(x)$, $K(x)$ and γ. In this case:

1. Let $P(x) \not\equiv const$, $P(x) \not\equiv K(x) \not\equiv const$ and $\gamma \equiv const$. If $K(x) < \gamma$ in a nonempty open domain, the semi-trivial equilibrium $(0, v^*)$ of (1.3) is globally asymptotically stable, independently of diffusion coefficients.

2. If $P(x) \equiv K(x) \not\equiv const$, $\gamma \equiv const$ and $K(x) < \gamma$ for any $x \in \Omega$, the semi-trivial equilibrium $(0, \gamma)$ of (1.3) is globally asymptotically stable.

3. If $P(x) \equiv K(x) \not\equiv const$, $\gamma \equiv const$ and $K(x) > \gamma$ for any $x \in \Omega$, the semi-trivial equilibrium $(K(x), 0)$ of (1.3) is globally asymptotically stable.

The key ingredients of Section 3.2 are to consider the heterogeneous environment with different carrying capacities. In this case, we show that the regularly dispersing population goes to extinction if higher crowdiness tolerance is incorporated with the directed diffusion species.

1. If $P(x)$ and $K(x)$ are proportional, and $K(x) > \gamma(x)$ in a nonempty open domain then the semi-trivial equilibrium $(u^*(x), 0)$ is globally asymptotically stable.

2. For non-constant $K(x) > \gamma(x)$, where $\gamma(x) \equiv \beta P(x)$, $\beta > 0$, the semi-trivial equilibrium $(u^*(x), 0)$ of (1.3) is globally asymptotically stable if $G < H$, where G and H are defined in (3.9) and (3.10), respectively.

3. If either $K(x) > \gamma(x) > P(x)$ or $K(x) > P(x) > \gamma(x)$ in a nonempty open domain then the semi-trivial equilibrium $(0, v^*(x))$ is unstable. Coexistence is also possible (see numerical results in section 4).

Section 3.3 explores the case when the resource function $K(x)$ and the directed distribution function $P(x)$ are linearly independent. In this case, if $K(x) \equiv \alpha P(x) + c$ then there exists a unique ideal free pair $(\alpha P(x), c)$ which is globally asymptotically stable for arbitrary constant diffusion coefficients. In addition, if $P(x) \equiv K(x) + c$, i.e. $P(x) > K(x) \equiv \gamma(x)$ in a nonempty open domain, the semi-trivial steady state $(u^*(x), 0)$ is globally asymptotically stable.

In Section 3.4, we study the effects of diffusion coefficients by considering spatially distributed arbitrary functions. Here, we construct that if d_1, $d_2 < d^*$ then there exists a stable coexistence solution which is globally asymptotically stable. Section 4 involves numerical simulations supporting the theoretical results. Finally, Section 5 presents summary of the results.

2. Preliminary results

First, we describe the following results established in [18, 19] when the first species is distributing ideally while the other is diffusing randomly. In that case, it is observed that only the first population survives since the corresponding species is dispersing along the carrying capacity.

LEMMA 1. [18]*[Theorem 7] If $\gamma(x) \equiv P(x) \equiv K(x) \not\equiv const$ then the steady state $(K(x), 0)$ of (1.3) is globally asymptotically stable.*

LEMMA 2. [19]*[Theorem 6] Suppose that $P(x) \equiv K(x) \not\equiv const$. If $K(x) \geqslant \gamma(x)$ in a nonempty open domain then the steady state $(K(x), 0)$ of (1.3) is globally asymptotically stable.*

Next few results correspond to the stationary solution of the monotone dynamical system (1.3) considering the case of single-species. The function $u^*(x)$ is the solution of the following single-species boundary value problem when the species v is identically equal to zero in (1.3)

$$d_1\Delta\left(\frac{u^*(x)}{P(x)}\right)+u^*(x)\left(K(x)-u^*(x)\right)=0,\ x\in\Omega,\ \nabla(u^*/P)\cdot n=0,\ x\in\partial\Omega. \quad (2.1)$$

Similarly, in absence of species u, let $v^*(x)$ is the unique positive solution of the equation

$$d_2\nabla\cdot\frac{1}{P(x)}\nabla v^*(x)+v^*(x)\left(\gamma(x)-v^*(x)\right)=0,\ x\in\Omega,\ \nabla v^*\cdot n=0,\ x\in\partial\Omega. \quad (2.2)$$

In future, we will need the following four auxiliary results for further analysis of (1.3).

PROPOSITION 1. [21, 22] *Let $u^*(x)$ be a positive solution of (2.1), $P(x)\not\equiv const$ and $P(x)$ and $K(x)$ are linearly independent then*

$$\int_\Omega P(x)\left(u^*(x)-K(x)\right)dx>0. \quad (2.3)$$

PROPOSITION 2. [17] *Suppose that $P(x)\not\equiv const$, $P(x)/K(x)\not\equiv const$ and let $u^*(x)$ is the unique positive solution of (2.1). Then*

$$\int_\Omega K(x)(K(x)-u^*(x))\,dx>0. \quad (2.4)$$

In addition, if $K(x)\leqslant\gamma(x)$ in a nonempty open domain then

$$\int_\Omega \gamma(x)(\gamma(x)-u^*(x))\,dx>0,\ \textit{unless}\ u^*(x)\equiv\gamma(x). \quad (2.5)$$

Proof. The positivity of (2.4) was shown in [17]. To prove (2.5), integrating (2.1) over Ω using the boundary conditions in (2.1) and we obtain

$$0=\int_\Omega u^*(x)(K(x)-u^*(x))\,dx\leqslant\int_\Omega u^*(x)(\gamma(x)-u^*(x))\,dx,\ \text{when}\ K\leqslant\gamma.$$

Now, integrating the equality

$$u^*(x)(\gamma(x)-u^*(x))=(u^*(x)-\gamma(x)+\gamma(x))(\gamma(x)-u^*(x)),$$

over Ω, we have

$$\int_\Omega \gamma(x)(\gamma(x)-u^*(x))\,dx\geqslant\int_\Omega(\gamma(x)-u^*(x))^2\,dx>0,\ \text{unless}\ u^*(x)\equiv\gamma(x)\equiv K(x).$$

If $u^*(x)\equiv\gamma(x)\equiv K(x)$ then $d_1\Delta\left(\frac{K(x)}{P(x)}\right)\equiv 0$, $x\in\Omega$ in (2.1), which is true only when $cP(x)\equiv K(x)$, a contradiction with the assumption $P(x)/K(x)\not\equiv const$. □

PROPOSITION 3. *Suppose that* $P(x) \not\equiv const$, $\gamma(x) \not\equiv const$ *and* $v^*(x)$ *is a positive solution of (2.2) then*

$$\int_\Omega v^*(x)\,dx > \int_\Omega \gamma(x)\,dx. \tag{2.6}$$

We also have the following integral inequality from (2.2) for non-constant $\gamma(x)$

$$\int_\Omega \gamma(x)(\gamma(x) - v^*(x))\,dx > 0. \tag{2.7}$$

Moreover, if $K(x) \geqslant \gamma(x)$ *in a nonempty open domain then*

$$\int_\Omega K(x)\,(K(x) - v^*(x))\,dx > 0. \tag{2.8}$$

Proof. Since $v^*(x) > 0$ for all $x \in \Omega$, dividing the first equation of (2.2) by $v^*(x)$, we obtain

$$d_2\nabla \cdot \frac{1}{P(x)}\frac{\nabla v^*(x)}{v^*(x)} + (\gamma(x) - v^*(x)) = 0,\ x \in \Omega,\ \nabla v^* \cdot n = 0,\ x \in \partial\Omega. \tag{2.9}$$

Integrating (2.9) over the domain Ω using the boundary conditions in (2.9), we have

$$d_2 \int_\Omega \frac{1}{P(x)}\frac{|\nabla v^*|^2}{v^{*2}}\,dx + \int_\Omega (\gamma(x) - v^*(x))\,dx = 0.$$

Thus,

$$\int_\Omega (v^*(x) - \gamma(x))\,dx = \int_\Omega \frac{d_2}{P(x)}\frac{|\nabla v^*|^2}{v^{*2}}\,dx > 0, \text{ unless } v^* \equiv \gamma \equiv const.$$

But, $v^*(x) \equiv \gamma(x)$ is not a solution of (2.2) since $\gamma(x) \not\equiv const$. Hence $\int_\Omega v^*(x)\,dx > \int_\Omega \gamma(x)\,dx$. Rest of the statements (2.7) and (2.8) are justified similarly to proposition 2. □

We now turn our attention to models that describe the dynamics of a system of two variables.

PROPOSITION 4. *Assume that* $(u_s(x), v_s(x))$ *is a strictly positive stationary solution of (1.3) and* $K(x) \geqslant \gamma(x)$ *in a nonempty open domain, then*

$$\int_\Omega K(x)\,(K(x) - u_s - v_s)\,dx \geqslant \int_\Omega (u_s + v_s - K(x))^2\,dx. \tag{2.10}$$

The integral (2.10) is strictly positive unless $u_s + v_s \equiv K$. *Changing* $K(x)$ *by* $\gamma(x)$, *we obtain*

$$\int_\Omega \gamma(x)\,(\gamma(x) - u_s - v_s)\,dx \geqslant \int_\Omega (u_s + v_s - \gamma(x))^2\,dx > 0, \text{ unless } u_s + v_s \equiv \gamma(x).$$

Proof. Assume that there exists a stationary positive solution $(u_s(x), v_s(x))$ and the equilibrium $(u_s(x), v_s(x))$ of (1.3) satisfies

$$\begin{cases} d_1\Delta\left(\frac{u_s(x)}{P(x)}\right) + u_s(x)\left(K(x) - u_s(x) - v_s(x)\right) = 0,\ x \in \Omega, \\ d_2\nabla\cdot\left(\frac{1}{P(x)}\nabla v_s(x)\right) + v_s(x)\left(\gamma(x) - u_s(x) - v_s(x)\right) = 0,\ x \in \Omega, \\ \nabla(u_s/P)\cdot n = \nabla v_s \cdot n = 0,\ x \in \partial\Omega. \end{cases} \tag{2.11}$$

Adding the first two equations of (2.11) and integrating over Ω using boundary conditions in (2.11), we obtain

$$\int_\Omega u_s\left(K - u_s - v_s\right) dx + \int_\Omega v_s\left(\gamma - u_s - v_s\right) dx = 0.$$

If $K(x) \geqslant \gamma(x)$ in a nonempty open domain Ω then $(K - u_s - v_s) \geqslant (\gamma - u_s - v_s)$ and we have

$$\int_\Omega (u_s + v_s)\left(K - u_s - v_s\right) dx \geqslant 0. \tag{2.12}$$

From (2.12), we obtain the following

$$\int_\Omega K(x)\left(K(x) - u_s - v_s\right) dx \geqslant \int_\Omega \left(u_s + v_s - K(x)\right)^2 dx > 0,$$

unless $u_s + v_s \equiv K$ and the proof follows.
The result of the second part is justified similarly and it is noticed that the result is also valid for constant γ. ☐

3. Analysis of steady state solutions

In the following, we will state the results on stability of two semi-trivial steady states of the system (1.3), which are $(u^*(x), 0)$, $(0, v^*(x))$, when only one species survives. If there exists a stationary equilibrium $(u_s(x), v_s(x)$ that is neither a trivial nor a semi-trivial equilibrium and satisfy $u_s > 0$, $v_s > 0$, then we have a coexistence equilibrium.

We let

$$I_p := \alpha \int_\Omega P(x)\, dx > 0,\ \alpha > 0, \tag{3.1}$$

$$I_k := \int_\Omega K(x)\, dx > 0, \tag{3.2}$$

and we will use these notations in further analysis.

In the process of stability analysis of the steady states, first we consider the trivial equilibrium of (1.3).

LEMMA 3. [17, 19] *The trivial equilibrium* $(0,0)$ *of (1.3) is unstable.*

If $(u_s(x), v_s(x))$ is any stationary coexistence solution of (1.3) then the eigenvalue problem of the second equation of (1.3) around $(u^*(x), 0)$ is

$$d_2 \nabla \cdot \frac{1}{P} \nabla \phi(x) + \phi(x)(\gamma(x) - u^*(x)) = \sigma \phi(x),\ x \in \Omega,\ \nabla \phi \cdot n = 0,\ x \in \partial \Omega. \quad (3.3)$$

3.1. Heterogeneous vs homogeneous environment

We now study the case when the species u is living in a heterogeneous environment whereas the surroundings of species v are homogeneous. In this case, we will prove that if somehow the regularly diffusing population carries higher carrying capacity than that of directed dispersing population, only the random diffuser survives.

LEMMA 4. *Suppose that* $P(x)$, $K(x)$ *are non-constant,* $P(x) \not\equiv K(x)$ *and* $\gamma(x) \equiv const$*. If* $0 < K(x) < \gamma$ *in a nonempty open domain then the semi-trivial steady state* $(u^*(x), 0)$ *of (1.3) is unstable.*

Proof. The principal eigenvalue [2] of (3.3) around $(u^*(x), 0)$ is defined as

$$\sigma_1 = \sup_{\phi \neq 0, \phi \in W^{1,2}} \left[-d_2 \int_\Omega \frac{1}{P(x)} |\nabla \phi|^2 \, dx + \int_\Omega \phi^2 (\gamma - u^*(x)) \, dx \right] \Big/ \int_\Omega \phi^2 \, dx.$$

For constant eigenfunction $\phi(x) = \sqrt{\gamma} = const$, the principal eigenvalue σ_1 becomes

$$\sigma_1 \geqslant \frac{\int_\Omega \gamma(\gamma - u^*(x)) \, dx}{\int_\Omega \gamma dx}.$$

Next, integrating the first equation of (2.1) over Ω and applying $K(x) < \gamma$, we obtain

$$0 = \int_\Omega u^*(x)(K(x) - u^*(x)) \, dx < \int_\Omega u^*(x)(\gamma - u^*(x)) \, dx$$

such that $\int_\Omega \gamma(\gamma - u^*(x)) \, dx > \int_\Omega (\gamma - u^*(x))^2 \, dx > 0$ and this integral inequality excludes $\gamma = u^*$. Hence, σ_1 is positive, and the semi-trivial steady state $(u^*(x), 0)$ of (1.3) is unstable. □

LEMMA 5. *Let* $P(x) \not\equiv const$, $P(x) \not\equiv K(x)$ *and* $\gamma(x) \equiv const$*. If* $0 < K(x) < \gamma$ *in a nonempty open domain then the system (1.3) has no coexistence solution* $(u_s(x), v_s(x))$.

Proof. Assume that there exists a positive solution $(u_s(x), v_s(x))$ in (1.3) and we will prove that there is a contradiction. For positive $(u_s(x), v_s(x))$ and for $K(x) < \gamma$ in a nonempty open domain, the proposition 4 is generating the following integral

$$\int_\Omega \gamma(\gamma - u_s - v_s)\, dx > \int_\Omega (u_s + v_s - \gamma)^2\, dx > 0, \tag{3.4}$$

which excludes the possibility of $u_s + v_s \equiv \gamma$.
For $u_s + v_s \not\equiv \gamma$, let us define the eigenvalue problem of the second equation of (1.3)

$$d_2 \nabla \cdot \frac{1}{P(x)} \nabla \phi(x) + \phi(x)(\gamma - u_s - v_s) = \sigma\phi(x),\ x \in \Omega,\ \nabla\phi \cdot n = 0,\ x \in \partial\Omega, \tag{3.5}$$

and the corresponding principal eigenvalue is

$$\sigma_1 = \sup_{\phi \neq 0, \phi \in W^{1,2}} \left[-\int_\Omega \frac{d_2}{P(x)} |\nabla\phi|^2\, dx + \int_\Omega \phi^2 (\gamma - u_s - v_s)\, dx \right] \Big/ \int_\Omega \phi^2\, dx.$$

Choosing $\phi(x) = \sqrt{\gamma} = const$, and designating $I_g = \int_\Omega \gamma dx$, the principal eigenvalue is given by

$$\sigma_1 \geqslant \frac{1}{I_g} \int_\Omega \gamma(\gamma - u_s - v_s)\, dx.$$

Thus, $\sigma_1 > 0$ using (3.4), a contradiction with the zero principal eigenvalue of (3.5) with a positive principal eigenfunction. □

For monotone dynamical system (1.3) if all equilibrium is unstable except one then we can conclude that the remaining steady state is globally asymptotically stable [23, 24]. Next theorem shows that the left semi-trivial equilibrium of (1.3) is globally asymptotically stable regardless of the initial functions. The result is drawing by Lemma 3, Lemma 4, and using Lemma 5.

THEOREM 1. *Suppose that* $P(x) \not\equiv const$, $P(x) \not\equiv K(x)$ *and* $\gamma(x) \equiv const$. *If* $0 < K(x) < \gamma$ *in a nonempty open domain then the semi-trivial equilibrium* $(0, v^*)$ *of* (1.3) *is globally asymptotically stable. Notationally,* $v^* \to \gamma$ *as* $t \to \infty$.

The following two remarks are verified similarly to Theorem 1.

REMARK 1. Suppose that $P(x) \not\equiv const$ and $K(x) \equiv const$, $\gamma(x) \equiv const$. If $K \leqslant \gamma$ in a nonempty open domain then the semi-trivial equilibrium $(0, \gamma)$ of (1.3) is globally asymptotically stable.

REMARK 2. Suppose that $P(x) \equiv K(x) \not\equiv const$, and $\gamma(x) \equiv const$. If $K(x) < \gamma$ in a nonempty open domain then the semi-trivial equilibrium $(0, \gamma)$ of (1.3) is globally asymptotically stable.

Next, let us discuss the case $K(x) > \gamma$ for any $x \in \Omega$, where $P(x) \equiv K(x) \not\equiv const$ and $\gamma \equiv const$. In that case, the Lemma 2, established in [19] is still valid and the steady state $(K(x), 0)$ is globally asymptotically stable while $K(x) > \gamma$; the environment of the second species is homogeneous. In a light observation, we can conclude the following result as a remark.

REMARK 3. Let $P(x) \equiv K(x) \not\equiv const$, and $\gamma(x) \equiv const$. If $P(x) > \gamma$ in a nonempty open domain then the semi-trivial equilibrium $(P(x), 0)$ of (1.3) is the global attractor.

LEMMA 6. *Let $P(x) \not\equiv const$, $K(x) \equiv const$ and $\gamma(x) \equiv const$. If $K > \gamma$ in a nonempty open domain then the semi-trivial steady state $(0, \gamma)$ of (1.3) is unstable.*

Proof. Let us study the eigenvalue problem of (1.3) around $(0, \gamma)$ and we obtain

$$d_1 \Delta \left(\frac{\phi(x)}{P(x)} \right) + \phi(x) (K - \gamma) = \sigma \phi(x), \; x \in \Omega, \; \nabla(\phi/P) \cdot n = 0, \; x \in \partial\Omega. \tag{3.6}$$

According to the variational characterization of the eigenvalues [2], the principal eigenvalue of (3.6) is given by

$$\sigma_1 = \sup_{\phi \neq 0, \phi \in W^{1,2}} \left[-d_1 \int_\Omega |\nabla(\phi/P)|^2 \, dx + \int_\Omega \frac{\phi^2}{P} (K - \gamma) \, dx \right] \Big/ \int_\Omega \frac{\phi^2}{P} \, dx.$$

By considering the eigenfunction $\phi(x) = P(x)$, the principal eigenvalue σ_1 becomes

$$\sigma_1 \geqslant \frac{\alpha}{I_p} \int_\Omega P(x) (K - \gamma) \, dx,$$

where I_p is defined in (3.1). Since $(K - \gamma) > 0$ in a nonempty open domain then the integral $\int_\Omega P(x) (K - \gamma) \, dx > 0$. Thus, σ_1 is positive, and the proof is achieved. □

However, other results can not be extended to this case. In particular, the advantage of directed diffusion is not sufficient to provide competitive exclusion in the case when the other species has a higher carrying capacity.

3.2. Reflection of the non-homogeneous environmental influence

At this stage, let us explore the case when both populations are stayed in a heterogeneous environment as well as their carrying capacities are different.

LEMMA 7. *Assume that $P(x)$, $K(x)$ and $\gamma(x)$ are non-constant and $K(x) \equiv \alpha P(x) + b$, $\alpha > 0$, $b > 0$. If $K(x) \leqslant \gamma(x)$ for any $x \in \Omega$ and $K(x) < \gamma(x)$ in a nonempty open domain, the semi-trivial equilibrium $(u^*(x), 0)$ of (1.3) is unstable.*

Proof. The principal eigenvalue [2] of (3.3) around $(u^*(x),0)$ is defined as

$$\sigma_1 = \sup_{\phi\neq 0, \phi\in W^{1,2}} \left[-d_2 \int_\Omega \frac{1}{P(x)} |\nabla\phi|^2\,dx + \int_\Omega \phi^2\,(\gamma(x)-u^*(x))\,dx \right] \Big/ \int_\Omega \phi^2\,dx$$
$$\geqslant \sup_{\phi\neq 0, \phi\in W^{1,2}} \left[-d_2 \int_\Omega \frac{1}{P(x)} |\nabla\phi|^2\,dx + \int_\Omega \phi^2\,(K(x)-u^*(x))\,dx \right] \Big/ \int_\Omega \phi^2\,dx$$

where $K(x) \leqslant \gamma(x)$ for any $x\in\Omega$.

For eigenfunction $\phi(x) = \sqrt{K(x)-\alpha P(x)} = \sqrt{b} = b_*$, and designating $I_b = \int_\Omega b_*^2 dx$, the principal eigenvalue σ_1 becomes

$$\sigma_1 \geqslant \frac{1}{I_b} \int_\Omega (K(x)-\alpha P(x))\,(K(x)-u^*(x))\,dx$$
$$= \frac{\alpha}{I_b} \int_\Omega P(x)\,(u^*(x)-K(x))\,dx + \frac{1}{I_b}\int_\Omega K(x)\,(K(x)-u^*(x))\,dx.$$

The first integral is non-negative by proposition 1, while the second is positive by proposition 2. Hence, σ_1 is positive, and the semi-trivial steady state $(u^*(x),0)$ of (1.3) is unstable. □

LEMMA 8. *Let $P(x), K(x)$ and $\gamma(x)$ be non-constant. If $K(x)\geqslant\gamma(x)$ for any $x\in\Omega$ and $K(x)>\gamma(x)$ in a nonempty open domain then the equilibrium $(0,v^*(x))$ of (1.3) is unstable for any of the following cases:*
(a) $\gamma(x)\equiv\alpha P(x)+c$, $c>0$, $\alpha>0$,
(b) $K(x)\equiv\alpha P(x)$, $\alpha>0$, and
(c) $\gamma(x)\equiv\beta P(x)$, $\beta>0$.

Proof. Let us study the eigenvalue problem of (1.3) around $(0,v^*(x))$ and we obtain

$$d_1\Delta\left(\frac{\phi(x)}{P(x)}\right) + \phi(x)\,(K(x)-v^*(x)) = \sigma\phi(x),\ x\in\Omega,\ \nabla(\phi/P)\cdot n = 0,\ x\in\partial\Omega. \quad (3.7)$$

The principal eigenvalue of (3.7) is given by

$$\sigma_1 = \sup_{\phi\neq 0, \phi\in W^{1,2}} \left[-d_1 \int_\Omega |\nabla(\phi/P)|^2\,dx + \int_\Omega \frac{\phi^2}{P}\,(K(x)-v^*(x))\,dx \right] \Big/ \int_\Omega \frac{\phi^2}{P}\,dx.$$

Considering $\phi(x) = \sqrt{\alpha}P(x)$ and inviting I_p drafted in (3.1), it is observe that the principal eigenvalue is not less than

$$\sigma_1 \geqslant \frac{1}{I_p}\int_\Omega \alpha P(x)\,(K(x)-v^*(x))\,dx. \quad (3.8)$$

Case (a): If $K(x) \geqslant \gamma(x)$, the principal eigenvalue in (3.8) becomes

$$\begin{aligned}\sigma_1 &\geqslant \frac{1}{I_p}\int_\Omega \alpha P(x)\,(\gamma(x)-v^*(x))\,dx\\ &= \frac{1}{I_p}\int_\Omega (\alpha P(x)-\gamma(x)+\gamma(x))\,(\gamma(x)-v^*(x))\,dx\\ &= \frac{1}{I_p}\int_\Omega \gamma(x)\,(\gamma(x)-v^*(x))\,dx + \frac{c}{I_p}\int_\Omega (v^*(x)-\gamma(x))\,dx,\ \gamma(x)\equiv \alpha P(x)+c.\end{aligned}$$

Since the first term is non-negative using (2.7) and the second is positive by proposition 3. Thus, σ_1 is positive, and this completes the proof.
Case (b): If $K \equiv \alpha P$, $\alpha > 0$ then σ_1 in (3.8) implies

$$\sigma_1 \geqslant \frac{1}{I_p}\int_\Omega K(x)\,(K(x)-v^*(x))\,dx.$$

Next, if $K(x) \geqslant \gamma(x)$ for any $x \in \Omega$ then the integral $\int_\Omega K(x)\,(K(x)-v^*(x))\,dx \geqslant 0$ by using (2.8) in proposition 3 and the inequality is strict when $K \not\equiv const \not\equiv v^*$. Hence $\sigma_1 > 0$ and the proof follows.
Case (c): By considering the fact $\gamma(x) \equiv \beta P$, $\beta > 0$, the structure of σ_1 becomes

$$\sigma_1 \geqslant \frac{\alpha}{\beta I_p}\int_\Omega \gamma(x)\,(K(x)-v^*(x))\,dx \geqslant \frac{\alpha}{\beta I_p}\int_\Omega \gamma(x)\,(\gamma(x)-v^*(x))\,dx,\ K \geqslant \gamma.$$

The positivity of σ_1 is proved as a consequence of the inequality (2.7). □

LEMMA 9. *Let $P(x)$, $K(x)$ and $\gamma(x)$ be non-constant. If $K(x) \equiv \alpha P(x)$, $\alpha > 0$ and $K(x) \geqslant \gamma(x)$ in some nonempty open domain then (1.3) has no coexistence solution.*

Extending the proof of Lemma 5, we can easily prove the result of Lemma 9 and so, the proof is omitted.

The equilibrium $(0, v^*)$ is unstable by Lemma 8(b) and there is no coexistence solution according to Lemma 9 if $K(x) \equiv \alpha P(x)$, $\alpha > 0$ and $K(x) \geqslant \gamma(x)$. Then for monotone dynamical system (1.3), we have the following result.

THEOREM 2. *Let $P(x)$, $K(x)$ and $\gamma(x)$ be non-constant. If $K(x) \equiv \alpha P(x)$, $\alpha > 0$ and $K(x) \geqslant \gamma(x)$ in a nonempty open domain, the semi-trivial equilibrium $(u^*, 0)$ of (1.3) is globally asymptotically stable.*

Define the integral G for non-proportional functions $K(x)$ and $\gamma(x)$

$$G := \beta d_1 \int_\Omega \left|\sqrt{\frac{K}{\gamma}}\right|^2 dx > 0,\ \beta > 0. \tag{3.9}$$

and

$$H := \int_\Omega K(x)(K(x) - u_s - v_s)\,dx. \tag{3.10}$$

In the next result, it is also shown that H is positive if $K(x) > \gamma(x)$.

LEMMA 10. *Assume that $K(x)$ and $\gamma(x)$ are non-constant, $\gamma(x) \equiv \beta P(x)$, $\beta > 0$ and $K(x) > \gamma(x)$ in a nonempty open domain. If there exist K and γ such that $H > G$ then the problem (1.3) has no coexistence solution $(u_s(x), v_s(x))$.*

Proof. Assume that (u_s, v_s) is a coexistence equilibrium of (1.3) and for a stationary solution (u_s, v_s) with $\gamma(x) \equiv \beta P(x)$, the system (1.3) can be written as

$$\begin{cases} \beta d_1 \Delta\left(\dfrac{u_s(x)}{\gamma(x)}\right) + u_s(x)\,(K(x) - u_s(x) - v_s(x)) = 0,\ x \in \Omega, \\ \beta d_2 \nabla \cdot \left(\frac{1}{\gamma(x)} \nabla v_s(x)\right) + v_s(x)\,(\gamma(x) - u_s(x) - v_s(x)) = 0,\ x \in \Omega, \\ \nabla(u_s/\gamma)\cdot n = \nabla v_s \cdot n = 0,\ x \in \partial\Omega. \end{cases} \tag{3.11}$$

Introducing the inequality $K(x) > \gamma(x)$ in (3.11) and according to the proposition 4, we obtain

$$H := \int_\Omega K(x)\,(K(x) - u_s - v_s)\ dx > 0, \tag{3.12}$$

such that $u_s(x) + v_s(x) \not\equiv K(x)$.

Next, we define the eigenvalue problem of the first equation of (3.11)

$$\beta d_1 \Delta\left(\frac{\phi(x)}{\gamma(x)}\right) + \phi(x)\,(K(x) - u_s - v_s) = \sigma\phi(x),\ x \in \Omega, \nabla(\phi/\gamma)\cdot n = 0,\ x \in \partial\Omega. \tag{3.13}$$

The principal eigenvalue σ_1 of (3.13) is defined by

$$\sigma_1 = \sup_{\phi \neq 0, \phi \in W^{1,2}} \left[-\beta d_1 \int_\Omega |\nabla(\phi/\gamma)|^2\,dx + \int_\Omega \frac{\phi^2}{\gamma}\,(K(x) - u_s - v_s)\ dx \right] \Big/ \int_\Omega \frac{\phi^2}{\gamma}\,dx.$$

Substituting $\phi(x) = \sqrt{K(x)\gamma(x)}$, and using the notation I_k defined in (3.2), σ_1 becomes

$$\sigma_1 \geqslant \frac{1}{I_k}\left[-\beta d_1 \int_\Omega |\sqrt{K/\gamma}|^2\,dx + \int_\Omega K(x)\,(K(x) - u_s - v_s)\ dx \right] = \frac{-G+H}{I_k}.$$

But, the integral H is positive by (3.12) and the numerator of σ_1 is strictly positive as long as $H > G$ and the proof follows. □

Lemmata 8(c) and 10 due to the following result when $K(x) > \gamma(x)$, $\gamma(x)/P(x) \equiv$ *const* and $H > G$.

THEOREM 3. *Assume that $K(x)$ and $\gamma(x)$ are non-constant, $\gamma(x) \equiv \beta P(x)$, $\beta > 0$ and $K(x) > \gamma(x)$ in a nonempty open domain. If there exist K and γ such that $H > G$ then the semi-trivial equilibrium $(u^*, 0)$ of (1.3) is globally asymptotically stable.*

Proof. The instability of $(0, v^*)$ is proven in Lemma 8(c) and we need not to impose the additional condition $H > G$. Next, it is possible to find some functions K and γ such that $K > \gamma$ and we have $H > G$, which shows that there are no stable positive equilibrium solutions. The trivial equilibrium is unstable and still valid. Therefore, for a monotone dynamical system (1.3), the remaining equilibrium $(u^*, 0)$ is the global attractor regardless of initial densities. □

PROPOSITION 5. *Suppose that $P(x) \not\equiv const$, $\gamma(x) \not\equiv const$, $P(x) \geqslant \gamma(x)$ for any $x \in \Omega$ and $v^*(x)$ is a positive solution of (2.2) then*

$$\int_\Omega P(x)\,(P(x) - v^*(x))\,dx \geqslant \int_\Omega (v^*(x) - P(x))^2\,dx > 0. \tag{3.14}$$

Proof. Since $v^*(x)$ is the solution of (2.2), integrating the first equation in (2.2) over Ω and for $P(x) \geqslant \gamma(x)$, we obtain

$$0 = \int_\Omega v^*(x)\,(\gamma(x) - v^*(x))\,dx \leqslant \int_\Omega v^*(x)\,(P(x) - v^*(x))\,dx. \tag{3.15}$$

Integrating $v^*(x)\,(P(x) - v^*(x)) = (v^*(x) - P(x))\,(P(x) - v^*(x)) + P(x)\,(P(x) - v^*(x))$ over Ω using the integral inequality (3.15), we obtain

$$0 \leqslant \int_\Omega (v^*(x) - P(x))\,(P(x) - v^*(x)) + \int_\Omega P(x)\,(P(x) - v^*(x)).$$

Consequently,

$$\int_\Omega P(x)\,(P(x) - v^*(x))\,dx \geqslant \int_\Omega (v^*(x) - P(x))^2\,dx > 0, \tag{3.16}$$

as long as $v^* \not\equiv P$. In (3.16), equality is attained only for $\gamma(x) \equiv P(x)$ and $v^*(x) \equiv \gamma(x) \equiv P(x)$ is not a solution of (2.2) while $P(x) \equiv \gamma(x) \not\equiv const$. □

LEMMA 11. *Assume that $P(x)$, $K(x)$ and $\gamma(x)$ are non-constant and $\gamma(x) \leqslant P(x) \leqslant K(x)$ for any $x \in \Omega$. Then the semi-trivial steady state $(0, v^*(x))$ of (1.3) is unstable.*

Proof. The analysis is straightforward for $\gamma(x) = P(x) = K(x)$ and so we are interested to consider the case $\gamma(x) \leqslant P(x) < K(x)$ only. By considering the eigenfunction $\phi(x) = \sqrt{\alpha}P(x)$, recall the principal eigenvalue of Lemma 8 and we obtain

$$\begin{aligned}\sigma_1 &\geqslant \frac{1}{I_p} \int_\Omega \alpha P(x)\,(K(x) - v^*(x))\,dx \\ &> \frac{\alpha}{I_p} \int_\Omega P(x)\,(P(x) - v^*(x))\,dx, \text{ where } P(x) < K(x).\end{aligned} \tag{3.17}$$

But if $P(x) \geqslant \gamma(x)$ for any $x \in \Omega$ then we have

$$\int_\Omega P(x)\,(P(x)-v^*(x))\,dx > 0, \tag{3.18}$$

since the integral (3.18) is extracted from (3.14) in proposition 5 when $\gamma(x) \leqslant P(x)$ for all $x \in \Omega$ and hence $\sigma_1 > 0$. □

3.3. An ideal free pair and significance of directed movements

The following portion presents the main steps in analyzing the stability of the unique coexistence steady state for non-proportional positive functions $P(x)$ and $K(x)$ when the two resource distribution functions are identical, *i.e.* $K(x) \equiv \gamma(x)$. We will also show that the species distributed along a directed function is the sole winner independently of the diffusion coefficients.

Lemmata 7 and 8(a) due to the following result as long as $K(x) \equiv \gamma(x)$.

LEMMA 12. *Let $P(x)$ and $K(x)$ are non-constant. If $K(x) \equiv \gamma(x) \equiv \alpha P(x) + c$, $\alpha > 0$, $c > 0$, both semi-trivial steady states $(u^*(x), 0)$ and $(0, v^*(x))$ of (1.3) are unstable.*

LEMMA 13. *If $P(x) \not\equiv const$ and $K(x) \equiv \gamma(x) \equiv \alpha P(x) + c$, $\alpha > 0$, $c > 0$ then the system (1.3) has a unique positive coexistence equilibrium $(u_s, v_s) \equiv (\alpha P(x), c)$.*

Proof. For a stationary solution (u_s, v_s), the system (1.3) can be written as

$$\begin{cases} d_1 \Delta \left(\dfrac{u_s(x)}{P(x)} \right) + u_s(x)\,(K(x) - u_s - v_s) = 0, \; x \in \Omega, \\ d_2 \nabla \cdot \left(\frac{1}{P(x)} \nabla v_s(x) \right) + v_s(x)\,(K(x) - u_s - v_s) = 0, \; x \in \Omega, \\ \nabla (u_s/P) \cdot n = \nabla v_s \cdot n = 0, \; x \in \partial\Omega. \end{cases} \tag{3.19}$$

By direct substitution it is easy to check that $(\alpha P(x), c)$ is a coexistence stationary solution of (3.19). To show the uniqueness, assume that (u_s, v_s) is a coexistence equilibrium of (3.19) except $(\alpha P(x), c)$.

Since $v_s > 0$, dividing the second equation of (3.19) by v_s and integrating over Ω, we obtain

$$\int_\Omega (u_s + v_s - K(x))\,dx = \int_\Omega \frac{d_2}{P} \frac{|\nabla v_s|^2}{v_s^2}\,dx \geqslant 0. \tag{3.20}$$

The equality is attained in (3.20) only when $v_s \equiv const$.

Let us prove that $u_s(x) + v_s(x) \equiv K(x)$.

Assume to the contrary that $u_s(x) + v_s(x) \not\equiv K(x)$ and, we define the eigenvalue problem

$$d_1 \Delta \left(\frac{\phi(x)}{P(x)} \right) + \phi(x)\,(K(x) - u_s - v_s) = \sigma \phi(x), \; x \in \Omega, \nabla(\phi/P) \cdot n = 0, \; x \in \partial\Omega. \tag{3.21}$$

The principal eigenvalue σ_1 of (3.21) is defined by

$$\sigma_1 = \sup_{\phi\neq 0, \phi\in W^{1,2}} \left[-d_1 \int_\Omega |\nabla(\phi/P)|^2 \, dx + \int_\Omega \frac{\phi^2}{P} (K(x) - u_s - v_s) \, dx \right] \Big/ \int_\Omega \frac{\phi^2}{P} \, dx$$

and $\sigma_1 \geqslant \frac{1}{I_p} \int_\Omega \alpha P (K(x) - u_s - v_s) \, dx$ by substituting $\phi(x) = \sqrt{\alpha} P(x)$, where I_p is as in (3.1). Thus

$$\begin{aligned} \sigma_1 &\geqslant \frac{1}{I_p} \int_\Omega (\alpha P(x) - K(x) + K(x)) (K(x) - u_s - v_s) \, dx \\ &= \frac{c}{I_p} \int_\Omega (u_s + v_s - K(x)) \, dx + \frac{1}{I_p} \int_\Omega K(x) (K(x) - u_s - v_s) \, dx > 0 \end{aligned}$$

using (3.20) and by proposition 4. The zero principal eigenvalue of (3.21) contradicts $\sigma_1 > 0$ and thus $u_s(x) + v_s(x) \equiv K(x)$.

Now, if $u_s(x) + v_s(x) \equiv K(x)$ then by the Maximum Principle [25], $w_s = const$ and $v_s = const$ in (3.19), where $u_s/P = w_s$. Therefore, $P(x)w_s + v_s \equiv K(x) \equiv \alpha P(x) + c$ implies that $w_s = \alpha$ and $v_s = c$. Hence the unique solution of (1.3) is $(u_s, v_s) = (\alpha P(x), c)$. $\square$

For non-constant arbitrary functions $K(x)$ and $P(x)$, if $K(x) \equiv \gamma(x) \equiv \alpha P(x) + c$, $c > 0$, $\alpha > 0$, both semi-trivial equilibria $(u^*, 0)$ and $(0, v^*)$ of (1.3) are unstable by Lemma 12. Uniqueness of coexistence solution is verified in Lemma 13. Hence the following result shows that the coexistence equilibrium (u_s, v_s) of (1.3) remains globally asymptotically stable regardless of the initial functions.

THEOREM 4. *Let $P(x) \not\equiv const$ and $K(x) \equiv \gamma(x) \equiv \alpha P(x) + c$, $c > 0$, $\alpha > 0$. Then there exists a unique coexistence solution $(u_s, v_s) \equiv (\alpha P(x), c)$ of (1.3) which is globally asymptotically stable.*

If $K(x) \equiv P(x)$ then $(K(x), 0)$ is globally asymptotically stable and it was proven in [18], (see Lemma 1 for details). Now, we will observe that for small variation of distribution function, $P(x)$ and carrying capacity, $K(x)$, how the dynamic changes. If $0 < P(x) < K(x)$ and there is a small deviation between the carrying capacity and the distribution function, mathematically, $P(x) \equiv K(x) - \varepsilon$, $\varepsilon > 0$, we have the following remark.

REMARK 4. Let $P(x) \not\equiv const$, $K(x) \equiv \gamma(x)$ and $P(x) \equiv K(x) - \varepsilon$, ε is positive and small enough. Then the unique coexistence solution $(P(x), \varepsilon)$ of (1.3) is globally asymptotically stable.

If the distribution function $P(x) > K(x)$ in a nonempty open domain, different scenarios can be happened and the following analysis is of particular interest for that type of case.

Let us define

$$c^* = \frac{\int\limits_\Omega K(x)\,(K(x)-v^*(x))\,dx}{\int\limits_\Omega (v^*(x)-K(x))\,dx}, \tag{3.22}$$

and

$$C^* = \frac{\int\limits_\Omega K(x)\,(K(x)-u_s-v_s)\,dx}{\int\limits_\Omega (u_s+v_s-K(x))\,dx}. \tag{3.23}$$

If $K(x)\equiv\gamma(x)$, it is noted that $c^*>0$ by proposition 3 and C^* is positive by equation (2.10) in proposition 4 and by equation (3.20) in Lemma 13.

LEMMA 14. *Let $P(x)$ be non-constant and $K(x)\equiv\gamma(x)$. If $P(x)\equiv K(x)+c$ for any $x\in\Omega$ such that $0<c<c^*$, where c^* is defined in (3.22) then the equilibrium $(0,v^*(x))$ of (1.3) is unstable.*

Proof. It is remarked that $K(x)\not\equiv const$ is not a solution of single species equation of v as long as $P\equiv K+c$, $c>0$. Next, let us study the eigenvalue problem of (1.3) around $(0,v^*(x))$ and we obtain

$$d_1\Delta\left(\frac{\phi(x)}{P(x)}\right)+\phi(x)\,(K(x)-v^*(x))=\sigma\phi(x),\ x\in\Omega,\ \nabla(\phi/P)\cdot n=0,\ x\in\partial\Omega. \tag{3.24}$$

According to the variational characterization of the eigenvalues [2], the principal eigenvalue of (3.7) is given by

$$\sigma_1=\sup_{\phi\neq0,\phi\in W^{1,2}}\left[-d_1\int\limits_\Omega|\nabla(\phi/P)|^2\,dx+\int\limits_\Omega\frac{\phi^2}{P}\,(K(x)-v^*(x))\,dx\right]\Bigg/\int\limits_\Omega\frac{\phi^2}{P}\,dx.$$

Considering $\phi(x)=P(x)$ and inviting I_p drafted in (3.1), it is observe that the principal eigenvalue is at least

$$\begin{aligned}\sigma_1&\geqslant\frac{\alpha}{I_p}\int\limits_\Omega P(x)\,(K(x)-v^*(x))\,dx\\&=\frac{\alpha}{I_p}\int\limits_\Omega(K(x)+c)\,(K(x)-v^*(x))\,dx,\ \text{since } P\equiv K+c\\&=\frac{\alpha}{I_p}\left[\int\limits_\Omega K(x)\,(K(x)-v^*(x))\,dx+c\int\limits_\Omega(K(x)-v^*(x))\,dx\right].\end{aligned}$$

Finally, we have to show that $\sigma_1>0$ and it is true only when $c<c^*=\frac{\int_\Omega K(K-v^*)\,dx}{\int_\Omega(v^*-K)\,dx}$ and c^* is strictly positive by proposition 3. Thus, σ_1 is positive, and the semi-trivial equilibrium $(0,v^*(x))$ of (1.3) is unstable. □

LEMMA 15. *Let $P(x)$ be non-constant and $K(x) \equiv \gamma(x)$. If $P(x) \equiv K(x) + c$ for any $x \in \Omega$ such that $0 < c < C^*$, where C^* is defined in (3.23) then the system (1.3) has no coexistence solution $(u_s(x), v_s(x))$.*

Proof. According to proposition 4 if $K(x) \equiv \gamma(x)$ then we have

$$\int_\Omega K(x)\,(K(x) - u_s - v_s)\,dx = \int_\Omega (K(x) - u_s - v_s)^2\,dx > 0, \text{ unless } u_s + v_s \equiv K(x)$$

and similarly from equation (3.20) in Lemma 13, we have the following integral

$$\int_\Omega (u_s + v_s - K(x))\,dx = \int_\Omega \frac{d_2}{P}\frac{|\nabla v_s|^2}{v_s^2}\,dx > 0, \text{ unless } v_s = const.$$

Let us assume that there is a coexistence solution $(u_s(x), v_s(x))$ of (1.3) and we study the eigenvalue problem around $(u_s(x), v_s(x))$ and obtain

$$d_1 \Delta\left(\frac{\phi(x)}{P(x)}\right) + \phi(x)\,(K(x) - u_s - v_s) = \sigma\phi(x),\ x \in \Omega,\ \nabla(\phi/P)\cdot n = 0,\ x \in \partial\Omega. \quad (3.25)$$

The principal eigenvalue of (3.25) is given by

$$\sigma_1 = \sup_{\phi \neq 0, \phi \in W^{1,2}} \left[-d_1 \int_\Omega |\nabla(\phi/P)|^2\,dx + \int_\Omega \frac{\phi^2}{P}\,(K(x) - u_s - v_s)\,dx\right] \Big/ \int_\Omega \frac{\phi^2}{P}\,dx.$$

First, it is assume that $u_s + v_s \not\equiv K(x)$. Choosing $\phi(x) = P(x)$, using the equality $P \equiv K + c$ and inviting I_p drafted in (3.1), it is observe that the principal eigenvalue is

$$\begin{aligned}
\sigma_1 &\geqslant \frac{\alpha}{I_p}\int_\Omega P(x)\,(K(x) - u_s - v_s)\,dx \\
&= \frac{\alpha}{I_p}\int_\Omega (K(x) + c)\,(K(x) - u_s - v_s)\,dx \\
&= \frac{\alpha}{I_p}\left[\int_\Omega K(x)\,(K(x) - u_s - v_s)\,dx + c\int_\Omega (K(x) - u_s - v_s)\,dx\right].
\end{aligned}$$

It is seen that the principal eigenvalue $\sigma_1 > 0$ as long as $c < C^* = \frac{\int_\Omega K(K - u_s - v_s)\,dx}{\int_\Omega (u_s + v_s - K)\,dx}$ and $C^* > 0$ by equation (2.10) in proposition 4 and by equation (3.20) in Lemma 13. Therefore, there is no coexistence of (1.3) and the equilibrium $(u_s(x), v_s(x))$ is unstable.

However, if $u_s + v_s = K(x)$, by the Maximum Principle $u_s = P(x)$ and $v_s = c = const$ (see e.g. [26, Theorem 3.6]) such that $u_s + v_s = P(x) + c = K(x)$, a contradiction of our assumption, $P(x) = K(x) + c$. □

Note that once the trivial equilibrium is a repeller, there is no coexistence equilibrium and one of the two semi-trivial equilibrium solutions is unstable, the other one is globally asymptotically stable. Using Lemmata 14 and 15, we have the following result.

THEOREM 5. *Let $P(x)$ be non-constant and $K(x) \equiv \gamma(x)$. If $P(x) \equiv K(x)+c$ for any $x \in \Omega$ then there exists a positive constant $c_* = \min\{c^*, C^*\}$ such that for $0 < c < c_*$, the semi-trivial equilibrium $(u^*(x),0)$ of (1.3) is globally asymptotically stable.*

3.4. Influence of diffusion coefficients

The outline of main steps in this section is to analyze the stability of semi-trivial equilibria and coexistence steady state due to the effects of diffusion coefficients in a heterogeneous environment, $\gamma(x) \equiv K(x)$.

For simplicity, we let

$$E_u = \int_\Omega K(x)\,(K(x) - u^*(x))\,dx, \tag{3.26}$$

and

$$E_v = \int_\Omega K(x)\,(K(x) - v^*(x))\,dx. \tag{3.27}$$

We know that both E_u and E_v are positive according to (2.4) and (2.7), respectively.

LEMMA 16. *Suppose that $P(x)$ and $K(x)$ are linearly independent, where $K(x) \equiv \gamma(x)$. Then there exists positive d_2^* such that for $d_2 < d_2^*$, the semi-trivial steady state $(u^*(x),0)$ of (1.3) is unstable.*

Proof. The principal eigenvalue of (3.3) is defined as

$$\sigma_1 = \sup_{\phi \neq 0, \phi \in W^{1,2}} [-d_2 \int_\Omega \frac{1}{P(x)} |\nabla \phi|^2\,dx + \int_\Omega \phi^2 (K(x) - u^*(x))\,dx] / \int_\Omega \phi^2\,dx.$$

Choosing the eigenfunction $\phi(x) = \sqrt{K(x)}$, and using the notation I_k defined in (3.2), we have

$$\sigma_1 \geqslant \frac{1}{I_k}\left[-d_2 \int_\Omega P^{-1} |\nabla \sqrt{K(x)}|^2\,dx + \int_\Omega K(x)(K(x) - u^*(x))\,dx\right]. \tag{3.28}$$

Using the integral mathematics E_u from (3.26) and constant $d_2 < d_2^*$, we obtain

$$\sigma_1 > \frac{1}{I_k}\left[-d_2^* \int_\Omega P^{-1} |\nabla \sqrt{K(x)}|^2\,dx + E_u\right] > 0$$

for $d_2 < d_2^* = E_u / \int_\Omega P^{-1} |\nabla \sqrt{K(x)}|^2\,dx$. □

LEMMA 17. *Suppose that* $K(x) \equiv \gamma(x)$ *and* $P(x)$ *and* $K(x)$ *are linearly independent. Then there exists positive* d_1^* *such that for* $d_1 < d_1^*$*, the semi-trivial steady state* $(0, v^*(x))$ *of (1.3) is unstable.*

Proof. The proof is similar to the proof of Lemma 16. It is verified that $d_1 < d_1^* = E_v / \int_\Omega |\nabla \sqrt{(}K/P)|^2\, dx$, where the integral E_v is defined in (3.27). □

THEOREM 6. *Let* $P(x)$ *and* $K(x)$ *are linearly independent, where* $K(x) \equiv \gamma(x)$*. Then there exists positive* $d^* = \min\{d_1^*, d_2^*\}$ *such that for* $d_1 < d^*$ *and* $d_2 < d^*$*, there is at least one stable coexistence equilibrium of (1.3).*

Proof. Recalling d_2^* from Lemma 16 and d_1^* from Lemma 17, it is justified that

$$d^* = \min\{d_1^*, d_2^*\} = \min\left\{ E_v / \int_\Omega |\nabla \sqrt{(}K/P)|^2\, dx,\, E_u / \int_\Omega P^{-1} |\nabla \sqrt{K(x)}|^2\, dx \right\}$$

and then both semi-trivial equilibria $(u^*, 0)$ and $(0, v^*)$ are unstable for $d_1, d_2 < d^*$. □

4. Numerical examples

The goal of this section is to present the numerical simulations results that complement theoretical results of previous sections. The simulations reported competitive exclusion, the elimination of one species by another and coexistence of both populations.

The following example illustrates that the coexistence equilibrium $(P(x), c)$ known as ideal free pair [11, 13] is attracting when $t \to \infty$.

EXAMPLE 1. In this example, we consider $d_1 = d_2 = 0.25$, $P = 1.7 + \cos(\pi x)$, $K = 2.5 + \cos(\pi x)$ with $K = P + c$, $c = 0.8 > 0$. It is seen in Fig. 1 that the solution tends to the ideal pair $(P(x), c)$ regardless of initial values, a confirmation of Theorem 4.

In the next example, we consider a non-constant positive function $h(x)$ for any $x \in \Omega$ due to $K(x) - P(x)$ such that $K(x) - P(x) = h(x) > 0$. Rewrite $K = P + h$ into the form $K = \alpha P + \beta$, where $\alpha > 0$ and $0 \not\equiv \beta \in \mathbb{R}$. If $\beta > 0$ then the unique coexistence solution is globally asymptotically stable, see corresponding Theorem 4 and Remark 4. However, if $\beta < 0$ then the equilibrium $(u^*, 0)$ is globally asymptotically stable.

EXAMPLE 2. Consider (1.3) with $d_1 = d_2 = 0.25$ and $K = \gamma = 2.5 + \cos(\pi x)$. If $P = 1.5 + 0.5\cos(\pi x)$ then $K - P = h = 1.0 + 0.5\cos(\pi x) > 0$ for any $x \in \Omega$. Rewrite $K - P = h$ and we have $K = 2P - 0.5$, where $\alpha = 2$, $\beta = -0.5$ and it is seen in Fig. 2 (left) that $(u^*, 0)$ is globally asymptotically stable. The fact is $\alpha P = 2P = 3 + \cos(\pi x) > K$ in some nonempty open domain.

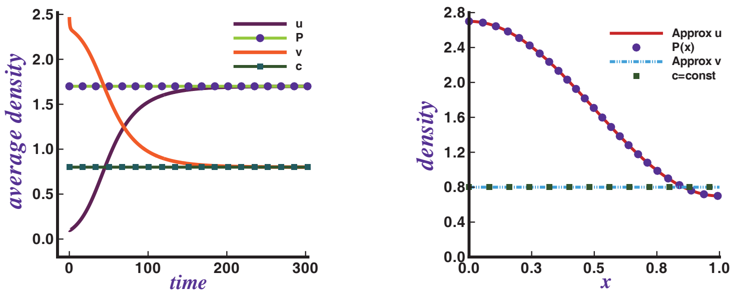

Figure 1: Average solutions of (1.3) (left) and stationary solution at $t = 300$ (right) for $P = 1.7 + \cos(\pi x)$, $K = \gamma = 2.5 + \cos(\pi x)$, $d_1 = d_2 = 0.25$, $\Omega = (0,1)$, $(u_0, v_0) = (0.1, 2.5)$ with $K - P = c$, where $c = 0.8$.

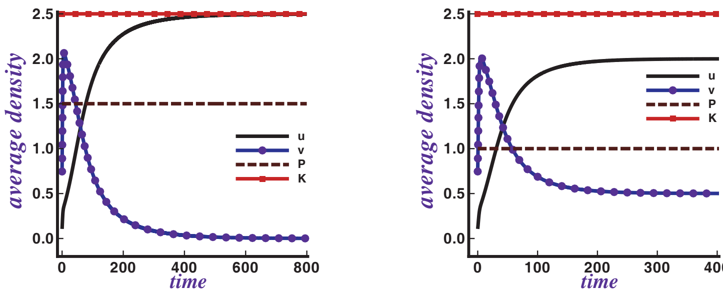

Figure 2: Average solutions of (1.3) for $K = \gamma = 2.5 + \cos(\pi x)$, $d_1 = d_2 = 0.25$, $(u_0, v_0) = (0.1, 0.7)$, $\Omega = (0,1)$ with (left) $P = 1.5 + 0.5\cos(\pi x)$ and (right) $P = 1.0 + 0.5\cos(\pi x)$.

Similarly, if we consider $P = 1.0 + 0.5\cos(\pi x)$ then $K - P = h > 0$ for all $x \in \Omega$. Rearranging K, we obtain $K = 2P + 0.5$, where $\alpha = 2$, $\beta = 0.5$ and the Fig. 2 (right) displayed that the coexistence solution is globally asymptotically stable. Fig. 2 (right) showed that both semi-trivial equilibriums $(u^*, 0)$ and $(0, v^*)$ are unstable while at least one coexistence solution is stable, (see Lemmata 7, 8(a) and Lemma 12 for details).

Next, let us illustrate the fact that the small difference of two carrying capacities provide coexistence steady states with equal diffusion rates.

EXAMPLE 3. Consider (1.3) with $d_1 = d_2 = 1$ and $K > P$, $\gamma > P$ for any $x \in \Omega$. If there is a small deviation between K and γ, i.e. $|K(x) - \gamma(x)| < \varepsilon$, here $\varepsilon \leqslant 0.1$, then there is a attractive coexistence solution as $t \to \infty$.

In Fig. 3, $K > \gamma$ for any $x \in \Omega$ and vice-versa in Fig. 4 with fixed $P = 1.45 + \cos(\pi x)$. Both figures 3 and 4 displayed that all positive solutions converge to the coexistence equilibrium (u_s, v_s) independently of non-negative and non-trivial initial values.

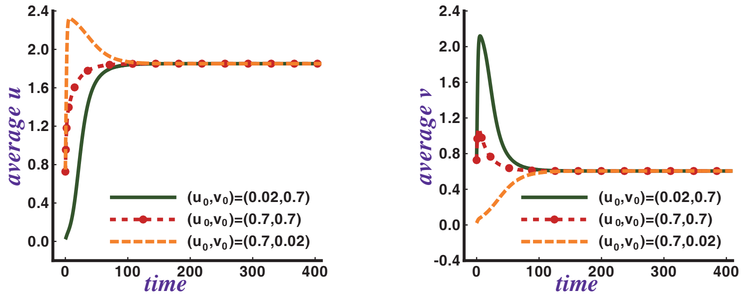

Figure 3: Average solutions of (1.3) for $P = 1.45 + \cos(\pi x)$, $K = 2.5 + \cos(\pi x)$, $\gamma = 2.4 + \cos(\pi x)$, $d_1 = d_2 = 1$, $\Omega = (0,1)$ with initial values $(u_0, v_0) = (0.02, 0.7), (0.7, 0.7), (0.7, 0.02)$.

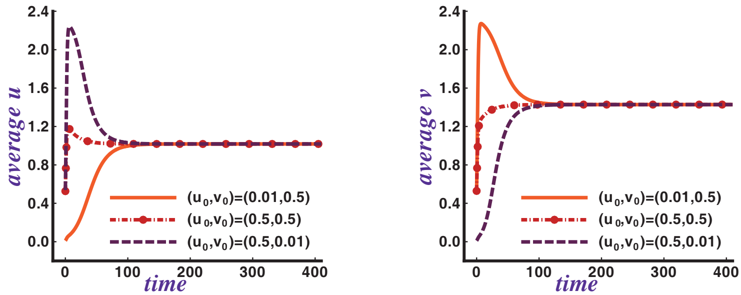

Figure 4: Average solutions of (1.3) for $P = 1.45 + \cos(\pi x)$, $K = 2.4 + \cos(\pi x)$, $\gamma = 2.5 + \cos(\pi x)$, $d_1 = d_2 = 1$, $\Omega = (0,1)$ with initial values $(u_0, v_0) = (0.01, 0.5), (0.5, 0.5), (0.5, 0.01)$.

5. Summary and discussion

The dynamics of a reaction-diffusion-advection model for two competing species in a spatially heterogeneous environment were studied in [11, 13]. It was assumed that the two species have the same population dynamics but different diffusion parameters: both species diffuse by regular dispersion and advection along the environmental gradient, with different diffusion coefficients and advection rates. It was exhibited that both competitive exclusion and coexistence are possible. In this paper, we investigated a reaction-diffusion system that models two competing species concerning the dynamics of different diffusion strategies: one disperses along a smooth distribution function and the other diffuses randomly.

We have characterized the global dynamics of the problem in a heterogeneous (or homogeneous) environment and established several results. If the carrying capacity coincides with the directed distribution function then there is no coexistence solution, and the strategy leading to the ideal free distribution has the advantage of evolutionary stability. The population diffusing with directed function survives whereas the regular diffusing population goes to extinction if the ratio of the resource function and the distribution function is constant, supporting the results established in [17].

We have illustrated the outcome of the combined effort of competition and collaboration, independently of the constant diffusion coefficients. Cooperative event occurs for arbitrary functions and a unique ideal free solution is globally asymptotically stable independently of the diffusion coefficients. If the environment is homogeneous then the random diffusion strategy is advantageous for universal (common) carrying capacity and the corresponding population has an evolutionary advantage.

We have studied the system (1.3) involving the case of two different carrying capacities. With a heterogeneous environment, if P and $K(>\gamma)$ are proportional then the global stability is guaranteed for the species driven by the distribution function. For various resource functions, the first population faces extinction if the second population stays in a homogeneous environment and carries higher carrying capacity. When either $K(x) > P(x) > \gamma(x)$ or $K(x) > \gamma(x) > P(x)$ holds in a nonempty open domain, it is proved that the semi-trivial steady state $(0, v^*(x))$ is unstable. However, only these conditions are not enough to analyze the coexistence of both populations and it remains an open problem to be investigated. When it comes to the effect of crowdedness, illustrated via numerical result, the outcome is that there are competitive exclusions and that coexistence is possible if deviation between K and γ is small enough. If both $K(x)$ and $\gamma(x)$ are greater than $P(x)$ for any $x \in \Omega$ and $|K-\gamma| < \varepsilon$, where $\varepsilon > 0$ and small enough, then the coexistence equilibrium $(u_s(x), v_s(x))$ is globally asymptotically stable.

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Conflict of Interest

The author(s) declare(s) that there is no conflict of interest regarding the publication of this paper.

REFERENCES

[1] Y. Morita and K. Tachibana, *An entire solution to the Lotka-Volterra competition-diffusion equations*, SIAM J. Math. Anal., **40**, 6 (2009), 2217–2240.

[2] R. S. Cantrell and C. Cosner, *Spatial Ecology via Reaction-diffusion Equations*, Wiley Series in Mathematical and Computational Biology, John Wiley & Sons, Chichester, 2003.

[3] J. Dockery, V. Hutson, K. Mischaikow, M. Pernarowski, *The evolution of slow dispersal rates: a reaction diffusion model*, J. Math. Biol., **37**, 1 (1998), 61–83.

[4] S. Williams and P. Chow, *Nonlinear reaction-diffusion models for interacting populations*, J. Math. Anal. Appl., **62** (1978), 157–159.

[5] A. Leung, *Limiting behaviour for a prey-predator model with diffusion and crowding effects*, J. Math. Biol., **6** (1978), 87–93.

[6] X. Q. HE AND W. M. NI, *The effects of diffusion and spatial variation in Lotka-Volterra competition-diffusion system I: Heterogeneity vs. homogeneity*, J. Differential Equations, **254**, 2 (2013), 528–546.
[7] K. KISHIMOTO AND H. F. WEINBERGER, *The spatial homogeneity of stable equilibria of some reaction-diffusion systems on convex domains*, J. Differential Equations, **58** (1985), 15–21.
[8] M. MIMURA, S. I. EI AND Q. FANG, *Effect of domain-shape on the coexistence problems in a competition-diffusion system*, J. Math. Biol., **29** (1991), 219–237.
[9] K. Y. LAM AND W. M. NI, *Uniqueness and complete dynamics in heterogeneous competition-diffusion systems*, SIAM J. Appl. Math. **72** (2012), 1695–1712.
[10] V. HUTSON, K. MISCHAIKOW, AND P. POLACIK, *The evolution of dispersal rates in a heterogeneous time-periodic environment*, J. Math. Biol., **43**, 6 (2001), 501–533.
[11] I. AVERILL, Y. LOU, AND D. MUNTHER, *On several conjectures from evolution of dispersal*, J. Biol. Dyn., **6**, 2 (2012), 117–130.
[12] R. S. CANTRELL, C. COSNER, Y. LOU, *Approximating the ideal free distribution via reaction-diffusion-advection equations*, J. Differential Equations, **245**, 12 (2008), 3687–3703.
[13] R. S. CANTRELL, C. COSNER, Y. LOU, *Evolution of dispersal and the ideal free distribution*, Math. Biosci. Eng., **7**, 1 (2010), 17–36.
[14] R. S. CANTRELL, C. COSNER, D. L. DEANGELIS AND V. PADRON, *The ideal free distribution as an evolutionarily stable strategy*, J. Biol. Dyn., **1**, 3 (2007), 249–271.
[15] R. S. CANTRELL, C. COSNER, Y. LOU , *Evolutionary stability of ideal free dispersal strategies in patchy environments*, J. Math. Biol., **65**, 5 (2012), 943–965.
[16] E. BRAVERMAN AND L. BRAVERMAN, *Optimal harvesting of diffusive models in a non-homogeneous environment*, Nonlin. Anal. Theory Meth. Appl., **71** (2009), e2173–e2181.
[17] L. KOROBENKO AND E. BRAVERMAN, *On logistic models with a carrying capacity dependent diffusion: stability of equilibria and coexistence with a regularly diffusing population*, Nonlinear Anal. B: Real World Appl., **13**, 6 (2012), 2648–2658.
[18] L. KOROBENKO AND E. BRAVERMAN, *On evolutionary stability of carrying capacity driven dispersal in competition with regularly diffusing populations*, J. Math. Biol., **69**, 5 (2014), 1181.
[19] E. BRAVERMAN, MD. KAMRUJJAMAN AND L. KOROBENKO, *Competitive spatially distributed population dynamics models: does diversity in diffusion strategies promote coexistence?*, Math. Biosci., **264** (2015), 63–73.
[20] PIERO DE MOTTONI, *Qualitative analysis for some quasilinear parabolic systems*, Inst. Math. Polish Acad. Sci., (1979).
[21] E. BRAVERMAN AND MD. KAMRUJJAMAN, *Competitive–cooperative models with various diffusion strategies*, Comp. Math. with Appl., **72** (2016), 653–662.
[22] E. BRAVERMAN AND MD. KAMRUJJAMAN, *Lotka systems with directed dispersal dynamics: Competition and influence of diffusion strategies*, Math. Biosci., **279** (2016), 1–12.
[23] S. B. HSU, H. L. SMITH AND P. WALTMAN, *Competitive exclusion and coexistence for competitive systems on ordered Banach spaces*, Trans. Amer. Math. Soc., **348**, 10 (1996), 4083–4094.
[24] K. - Y. LAM AND D. MUNTHER, *A remark on the global dynamics of competitive systems on ordered Banach spaces*, Proc. Amer. Math. Soc., **144** (2015), 1153–1159.
[25] M. H. PROTTER, H. F. WEINBERGER, *Maximum Principles in Differential Equations*, Prentice-Hall, Inc., Englewood Cliffs, N.J. (1967).
[26] D. GILBARG, N. S. TRUDINGER, *Elliptic Partial Differential Equations of Second Order*, second edition, Springer-Verlag, Berlin, (1983).

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