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A REVIEW ON THE DYNAMICS OF TWO SPECIES COMPETITIVE ODE AND PARABOLIC SYSTEMS

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Abstract This paper is devoted to a review on the dynamics of two species competition systems including the classical ODE, reaction-diffusion as well as reaction-diffusion-advection models. The primary purpose is to illustrate the effect of competition intensity, movement (diffusion and/or advection) and spatial variation on the population dynamics. Specific topics include Lotka-Volterra competition models in heterogeneous environments and in advective environments, linear second order eigenvalue problems, and the evolution of movement strategy. Several fundamental tools such as the monotone theory, the principal eigenvalue theory (for single equations or systems) and some technical approaches are introduced. Some recent developments are discussed and also several problems that deserve future investigation are proposed.

Keywords Lotka-Volterra competition, monotone theory, linear eigenvalue problems, steady state, global stability.

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1. Introduction

In the past half-century, there is a great deal of research, by both mathematicians and ecologists, devoted to the investigation of competition between two populations. The mathematical models are studied in various different types such as ordinary differential equations, difference equations, partial differential equations, or differential equations with time delays. See, e.g., the monographs by Cantrell and Cosner [13], Hirsch and Smith [57], Ni [113], Smith [121] and references therein.

Ecologically, a fundamental concept in this research area is the so-called "competitive exclusion principle" [47] (sometimes also referred to as Gause' law [117]), which has been predicted by theoretical models such as the Lotka-Volterra competition systems. However, for poorly understood reasons, competitive exclusion is rarely observed in natural ecosystems, and many biological communities appear to violate Gause' law. A possible solution to this paradox lies in raising the dimensionality of the system, as spatial variations, resource competition and lag may prevent exclusion, but systems incorporating these factors tend to be analytically intractable.

In this paper, focusing on the situation of two competing species, we aim to give a review on the dynamics of several types of competitive systems, including the

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classical ODE, reaction-diffusion (R-D), and reaction-diffusion-advection (R-D-A) models. For these models, we shall discuss them in various different environmental situations (e.g., spatially homogeneous or heterogeneous environments, or advective environments), introduce relevant study and recent development, and try to illustrate some interesting and perhaps surprising phenomena incurred by the (joint) action of movement, spatial variation, and competition intensity. Several fundamental approaches which are useful to analyze these models are also introduced.

We mention here that there are also some other types of competitive models, e.g., competitive patch models (a system of ODEs), competitive non-local models (non-local dispersal or non-local reaction terms). For the purpose of saving space, we do not discuss these models in details in the main body but include some related works in the last discussion section.

The remainder of this paper is organized as follows.

In section 2, we primarily recall some well known results on the classical two species competitive ODE system (autonomous).

In section 3, focusing on the competitive R-D systems, we introduce several classical results and some recent development in, respectively, spatially homogeneous, spatially heterogeneous, and both spatially and temporally heterogeneous environments.

In section 4, we mainly discuss the development on competitive R-D-A systems. See subsection 4.1 for models with resource gradient, subsection 4.2 for models arising from river ecology and subsection 4.3 for general R-D-A models.

Section 5 is devoted to the introduction of several mathematical approaches, including the monotone theory in subsection 5.1, the principal eigenvalue theory for single equation and system in subsections 5.2 and 5.3, and some analytical approaches in subsection 5.4.

In the discussion section 6, we make some comments on the strategies and arguments used in the study of competitive R-D and R-D-A systems, propose several problems that deserve future investigation, and also mention some works on other types of competitive models.

2. ODE systems

We start with the following classical Lotka-Volterra competitive ODE system

$$\begin{cases} u_t = u[r_1 - u - bv], & t > 0, \\ v_t = v[r_2 - cu - v], & t > 0, \\ u(0) = u_0 > 0, \quad v(0) = v_0 > 0, \end{cases} \tag{2.1}$$

where $u(t)$ and $v(t)$, respectively, denote the population numbers of two competing species at time $t > 0$. The positive constants r_1 and r_2 stand for the intrinsic growth rates of two populations. The positive numbers b and c are used to measure the inter-specific competition intensities while the intra-specific competition coefficients have been normalized by 1.

It is well known that system (2.1) can be classified into the following several cases by specifying values of b and c:

(i) weak competition case: $0 < b < \frac{r_1}{r_2}$ and $0 < c < \frac{r_2}{r_1}$;

(ii) strong-weak competition case:

$(ii.1)$ $0 < b < \frac{r_1}{r_2}$ and $c > \frac{r_2}{r_1}$ (u-strong and v-weak);
$(ii.2)$ $b > \frac{r_1}{r_2}$ and $0 < c < \frac{r_2}{r_1}$ (u-weak and v-strong);

(iii) strong competition case: $b > \frac{r_1}{r_2}$ and $c > \frac{r_2}{r_1}$.

For each of the above cases, the global dynamics of system (2.1) can be completely determined. Precisely, let us denote all possible equilibria of problem (2.1) by

$$(0,0), \quad (r_1,0), \quad (0,r_2), \quad (u^+,v^+) = \Big(\frac{\frac{r_1}{r_2}-b}{1-bc}\cdot r_2, \frac{\frac{r_2}{r_1}-c}{1-bc}\cdot r_1\Big).$$

Then the following results are standard (see, e.g., [62]):

- ($\bullet$) For the weak competition case (i), (u^+,v^+) is globally asymptotically stable—coexistence;
- ($\bullet$) For the strong-weak competition case $(ii.1)$, $(r_1,0)$ is globally asymptotically stable—competitive exclusion; and symmetrically, for case $(ii.2)$, $(0,r_2)$ is globally asymptotically stable—competitive exclusion;
- ($\bullet$) For the strong competition case (iii): both $(r_1,0)$ and $(0,r_2)$ are locally stable—bistability, and (u^+,v^+) is unstable (a saddle). Moreover, there is a function $v = h(u)$ such that

$$\lim_{t\longrightarrow\infty}(u(t),v(t)) = (r_1,0) \qquad \text{provided} \quad v(0) < h(u(0)),$$
$$\lim_{t\longrightarrow\infty}(u(t),v(t)) = (0,r_2) \qquad \text{provided} \quad v(0) > h(u(0)),$$
$$\lim_{t\longrightarrow\infty}(u(t),v(t)) = (u^+,v^+) \qquad \text{provided} \quad v(0) = h(u(0)).$$

The curve $v = h(u)$ is called the *separatrix*.

3. R-D systems

Taking migration into consideration, one can generalize the kinetic system (2.1) to the following spatially homogeneous reaction-diffusion system

$$\begin{cases} u_t = d_1\triangle u + u[r_1 - u - cv], & x\in\Omega,\ t>0,\\ v_t = d_2\triangle v + v[r_2 - bu - v], & x\in\Omega,\ t>0,\\ \dfrac{\partial u}{\partial\nu} = \dfrac{\partial v}{\partial\nu} = 0, & x\in\partial\Omega,\ t>0,\\ u(x,0) = u_0(x) \geq,\not\equiv 0, & x\in\Omega,\\ v(x,0) = v_0(x) \geq,\not\equiv 0, & x\in\Omega, \end{cases} \tag{3.1}$$

where, Ω, the habitat, is a bounded smooth domain in $\mathbb{R}^N$, $1 \leqslant N \in \mathbb{Z}$; $u(x,t)$ and $v(x,t)$ represent the population densities of two competing species at location $x\in\Omega$ and time $t > 0$, respectively; $\triangle = \sum_{i=1}^N \frac{\partial^2}{\partial x_i^2}$, the usual Laplace operator, is used to describe the random movements with dispersal rates of two species denoted by $d_1, d_2 > 0$; and ν signifies the outward unit normal vector on the boundary $\partial\Omega$. The homogeneous Neumann (no-flux) boundary conditions mean that no individuals can move in or out through the boundary of the habitat.

It turns out that for the above weak and strong-weak competition cases (i) and (ii), the globally stable equilibrium of system (2.1) is also globally stable as a solution of system (3.1) (see, e.g., [1, 31, 87, 97]). In sharp contrast, the dynamics of the strong competition case (iii) is more delicate. One of the remarkable results is due to Kishimoto and Weinberger [69], which says that there are no stable non-constant steady states if the domain Ω is convex. But, if Ω is non-convex, there may appear a stable spatially heterogeneous steady state corresponding to the habitat segregation phenomenon (see, e.g., Matano and Mimura [107] and Mimura et al. [110]). We also refer to Iida et al. [62] for the diffusion-induced extinction of a superior species and Jiang et al. [67] for the existence of a one-codimensional C^1-separatrix which separates the basins of attraction of the two semi-trivial steady states.

We note here that for the strong competition case (iii), generally it is very hard to give a clear picture on the global dynamics even for the very simple situation as shown in system (3.1). For the Dirichlet problem, a remarkable work by Gui and Lou [42] used the bifurcation approach to show that for a special case of system (3.1), there may appear many positive steady states in the strong competition case.

A more general and reasonable situation than system (3.1) is to consider the spatially heterogeneous environments, e.g., the spatial distribution of resource may vary from point to point. This leads us to consider the following system

$$\begin{cases} u_t = d_1 \triangle u + u[r_1(x) - u - bv], & x \in \Omega,\ t > 0, \\ v_t = d_2 \triangle v + v[r_2(x) - cu - v], & x \in \Omega,\ t > 0, \\ \dfrac{\partial u}{\partial \nu} = \dfrac{\partial v}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0, \\ u(x,0) = u_0(x) \geq, \not\equiv 0, & x \in \Omega, \\ v(x,0) = v_0(x) \geq, \not\equiv 0, & x \in \Omega, \end{cases} \tag{3.2}$$

where $r_1(x)$ and $r_2(x)$ are positive non-constant functions.

Problem (3.2) has been extensively studied in the past several decades. For example, one widely accepted result on the evolution of dispersal is due to Hastings [48] and Dockery et al. [34], where by considering

$$b = c = 1 \quad \text{and} \quad r_1(x) = r_2(x) := r(x),$$

that is,

$$\begin{cases} u_t = d_1 \triangle u + u[r(x) - u - v], & x \in \Omega,\ t > 0, \\ v_t = d_2 \triangle v + v[r(x) - u - v], & x \in \Omega,\ t > 0, \\ \dfrac{\partial u}{\partial \nu} = \dfrac{\partial v}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0, \\ u(x,0) = u_0(x) \geq, \not\equiv 0, & x \in \Omega, \\ v(x,0) = v_0(x) \geq, \not\equiv 0, & x \in \Omega, \end{cases} \tag{3.3}$$

the authors proved that species with slower dispersal rate will wipe out completely the faster one, i.e., "slower diffuser prevails". To further understand this phenomenon, Lou [92] (see also [60, 82]) adopted the strategy of weak competition approach, i.e.,

$$0 < b < 1 \quad \text{and} \quad 0 < c < 1,$$

and observed that two weakly competing species may not coexist eventually; indeed, one species could drive its competitor to extinction by taking suitable diffusion rates, which is in sharp contrast to the coexistence phenomenon observed in the

ODE system (2.1) or the homogeneous R-D system (3.1). In other words, diffusion and spatial variations could effectively change the nature of weak competition.

To further understand the joint action of movements and spatial variations, based on system (3.2), He and Ni published a series of works [49–53]. In particular, they made an important breakthrough in [51], where, by assuming

$$(b, c) \in \big\{(b, c) \in \mathbb{R}^+ \times \mathbb{R}^+ : 0 < b \cdot c \leqslant 1\big\},$$

a complete classification in terms of d_1 and d_2 on the possible long time behaviors of system (3.2) is established (in some cases the upper bound 1 could be relaxed). The key point is to make the a priori estimate on the linear stability of all positive steady states, which, together with the theory of monotone dynamical systems (see Proposition 9.1 and Theorem 9.2 in [55]), implies that either system (3.2) has a unique positive steady state that is globally asymptotically stable, or there are no positive steady states and one of the two semi-trivial steady states is globally asymptotically stable while the other one is unstable. These ideas are also developed in [43, 44] to treat more general intrinsic growth rate and carrying capacity.

The more complex situation involving both temporal and spatial variations is much more challenging to treat mathematically. A natural as well as a simple way is to consider the periodic-in-time case first. Motivated by the phenomenon "slower diffuser prevails" observed in the spatially heterogeneous but temporally constant environments [34, 48], Hutson et al. [61] considered a heterogeneous time-periodic environment as described below

$$\begin{cases} u_t = d_1 \triangle u + u[r(x,t) - u - v], & x \in \Omega,\ t > 0, \\ v_t = d_2 \triangle v + v[r(x,t) - u - v], & x \in \Omega,\ t > 0, \\ \dfrac{\partial u}{\partial \nu} = \dfrac{\partial v}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0, \\ u(x,0) = u_0(x) \geq, \not\equiv 0, & x \in \Omega, \\ v(x,0) = v_0(x) \geq, \not\equiv 0, & x \in \Omega, \end{cases} \tag{3.4}$$

where $r(x, t)$ is supposed to be a positive periodic function in time t. By employing a wide range of techniques and numerous computation efforts, the authors found very rich dynamics: (i) the slower diffusion rate may be favored; (ii) the higher diffusion rate may be favored; and (iii) there may be co-existence of phenotypes. Some latest advances on system (3.4) can be found in Bai, He and Ni [5].

For more discussions on the classical Lotka-Volterra competition models, we refer the interested readers to the monographs by Cantrell and Cosner [13], Ni [113], and Lam and Lou [78, Chapter 8]. See also Lou [93] for some challenging issues in this direction.

4. R-D-A systems

Recently, there is a growing interest in the population dynamics of competitive systems governed by reaction-diffusion-advection equations. In what follows, we mainly talk about three types of models. See subsection (4.1) for models with resource gradient, subsection (4.2) for models from river ecology and subsection (4.3) for general reaction-diffusion-advection models.

4.1. Models with resource gradient

One of the active research areas of studying reaction-diffusion-advection equations concerns the population dynamics where the individuals are supposed to be very smart so that they can sense and follow gradients in resource distribution. This was firstly raised by Belgacem and Cosner in [10] for a single species model and then by Cantrell, Cosner and Lou [14] for a two-species competition model.

We write below a general version of such a kind of models

$$\begin{cases} u_t = d_1 \triangle u - \alpha_1 \nabla \cdot [u \nabla r(x)] + u[r(x) - u - v], & x \in \Omega,\ t > 0, \\ v_t = d_2 \triangle v - \alpha_2 \nabla \cdot [v \nabla r(x)] + v[r(x) - u - v], & x \in \Omega,\ t > 0, \\ d_1 \dfrac{\partial u}{\partial \nu} - \alpha_1 u \dfrac{\partial r(x)}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0, \\ d_2 \dfrac{\partial v}{\partial \nu} - \alpha_2 v \dfrac{\partial r(x)}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0, \\ u(x,0) = u_0(x) \geq, \not\equiv 0, & x \in \Omega, \\ v(x,0) = v_0(x) \geq, \not\equiv 0, & x \in \Omega, \end{cases} \tag{4.1}$$

where, compared with the diffusive models in section 3, two populations are supposed to have directed movements along the resource gradient as described by the term $\nabla r(x)$ with advection rates denoted by $\alpha_1, \alpha_2 > 0$. The no-flux boundary conditions imposed here mean that no individuals would cross over the boundary of the habitat.

For the single species case (i.e., $v \equiv 0$), it has been shown in [10] that sufficiently rapid movement along the resource gradient (i.e., large α_1) is always beneficial for the single species to survive. But the story is different if hostile boundary condition or non-convex domain is considered [10, 25].

For the case $\alpha_1 > 0 = \alpha_2$ (one species taking a combination of diffusive and directed movements while the other one adopting pure random diffusion), Cantrell, Cosner and Lou [14] found that species u may have some competitive advantages even if it diffuses relatively faster (different from previous "slower diffuser prevails" [34, 48]). For the special case with $d_1 = d_2$, Cantrell, Cosner and Lou [15] proved that a small amount of directed movements (small α_1) is more favorable but interestingly, a large amount of such movements does not continue to maintain the advantages of species u and surprisingly two species would coexist instead. A possible explanation to this phenomenon is that the smarter species u occupies only the extremely favorable environments (local maxima of $r(x)$), leaving the remaining reasonably good locations for its competitor. Indeed, this was mathematically further pursued by investigating the limiting behaviors of positive steady states in the sense of $\alpha_1 \to \infty$, and some interesting concentration phenomena are revealed at the local maxima of $r(x)$, see, e.g., Chen et al. [20–22], Lam [72, 73] and Lam and Ni [81, 83]. Also, we mention here a work by Averill, Lam and Lou [2], where, via a bifurcation approach, the authors carefully examined the effect of advection (especially intermediate advection) on the population dynamics and obtained different types of bifurcation diagrams of positive steady states.

For the case with $\alpha_1, \alpha_2 > 0$ (both populations adopting a combination of diffusive and advective movements), much attention has been payed to the study of the existence of the so-called *Evolutionarily Stable Strategy* (ESS), which was initially introduced by Maynard Smith and Price [108]. Recall that a strategy is said to be an ESS if a population using it cannot be invaded by any small population taking a different strategy. On this topic, a fundamental tool to study it is the "selection gradient" defined in [33], which is closely related to the principal eigenvalue obtained by linearization. The discussion in this direction can be consulted in, e.g., [45,76,77], where one finds that the answer of evolution of conditional dispersal turns out to depend closely on the shape of environmental function $r(x)$.

System (4.1) with $\nabla r(x)$ replaced by $\nabla \ln r(x)$ is related to another biological topic *Ideal Free Distribution* (IFD) that was initially introduced by Fretwell and Lucas [36]. Some previous study on this issue can be seen in [3,16,40] and a further discussion about the connection between ESS and IFD can be found in [16].

We end this subsection by mentioning two review papers, by Cosner [24] and Lam, Liu and Lou [74] respectively, for more discussions on both biological and mathematical aspects concerning these models with resource gradient.

4.2. Models from river ecology

Advective environments like river/stream are usually featured by a constantly unidirectional water flow. Individuals living in such environments not only take random movements due to water turbulence or self-propelling, but also experience the passive movements caused by the downstream water flow. A fascinating question in river ecosystems is how aquatic species resist washout and persist over many generations. This biological phenomenon is also termed the "drift paradox" in the literature, see, e.g., [54,111].

Speirs and Gurney [122] proposed one of the first mathematical models to understand the influence of environmental variables on population persistence. Specifically, they formulated the following single species growth model

$$\begin{cases} u_t = du_{xx} - qu_x + u(r-u), & x \in (0,L),\ t>0, \\ du_x(0,t) - qu(0,t) = u(L,t) = 0, & t>0, \\ u(x,0) = u_0(x) \geq, \not\equiv 0, & x \in [0,L], \end{cases} \tag{4.2}$$

where the river/stream is abstracted by a one-dimensional interval $(0,L)$; $w(x,t)$ represents the population density of an aquatic species at location $x \in (0,L)$ and time $t>0$; $d>0$ denotes the rate of random movement and $q>0$ measures the effective advection speed incurred by the downstream flow; and $r>0$ stands for the intrinsic growth rate. At the upstream end $x=0$, no-flux condition is imposed so that no individuals would cross over this boundary, while at the downstream end $x=L$, the hostile condition is considered to model the situation "stream to ocean".

By some standard arguments, it is proved in [122] that the trivial solution $w=0$ of (4.2) is linearly unstable if and only if $q<2\sqrt{dr}$ and $L>L^*(d,q,r)$ with

$$L^*(d,q,r) := 2d\frac{\pi - \arctan(\frac{\sqrt{4rd-q^2}}{q})}{\sqrt{4rd-q^2}}, \tag{4.3}$$

which, biologically, suggests that weak advection (relative to diffusion) and a suitably long river are more beneficial for a single species to survive. Similar conclusions are obtained by Vasilyeva and Lutscher for problem (4.2) with "free-flow" condition at $x=L$ [127], but for more general boundary condition at $x=L$ involving a loss rate $b \geqslant 0$ (similar to b_d in (4.4) below), a transition phenomenon was observed at $b = \frac{1}{2}$ by Lou and Zhou [101], and later a critical value of $b = \frac{3}{2}$, governing the monotonicity of L^* (see (4.3)) with respect to d, was found by Hao, Lam and Lou [46].

Maybe of more interest is to understand how populations disperse in such advective environments could convey some competitive advantages. With this goal, one has to consider a two species competition system. We present below a very general version (see, e.g, [94, 102–104])

$$\begin{cases} u_t = d_1 u_{xx} - q_1 u_x + u(r_1 - u - v), & x \in (0, L),\ t > 0, \\ v_t = d_2 v_{xx} - q_2 v_x + v(r_2 - u - v), & x \in (0, L),\ t > 0, \\ d_1 u_x(0, t) - q_1 u(0, t) = b_u q_1 u(0, t), & t > 0, \\ d_1 u_x(L, t) - q_1 u(L, t) = -b_d q_1 u(L, t), & t > 0, \\ d_2 v_x(0, t) - q_2 v(0, t) = b_u q_2 u(L, t), & t > 0, \\ d_2 v_x(L, t) - q_2 v(L, t) = -b_d q_2 v(L, t), & t > 0, \\ u(x, 0) = u^0(x) \geq, \not\equiv 0,\ v(x, 0) = v^0(x) \geq, \not\equiv 0, & x \in [0, L], \end{cases} \tag{4.4}$$

where all parameters can be understood in a similar way to that in problem (4.2) except the parameters $b_u, b_d \in [0, \infty]$, which are used to measure the loss rate of individuals at the boundary relative to the flow rate (see [94, 102] for more detailed derivation and explanation). Note that b_u could also take some negative values, which biologically means that there is a flow of populations into the river at the upstream $x = 0$ (in other words, the upstream end is acting as a downstream end of another advective environment, e.g., a lake). Moreover, by $b_u = \infty$ or $b_d = \infty$, we mean that the hostile (Dirichlet) boundary condition holds. Different values of b_u and b_d could reflect different environmental situations. For example, $b_d = 0$, no-flux condition, models a closed environment [79, 99, 136]; $b_d = 1$, "free flow" condition, models an open environment "stream to lake" [94, 98, 127]; $b_d = \infty$, the Dirichlet condition, models a hostile environment "stream to ocean" [122, 132, 141].

System (4.4) has been extensively studied in many different settings. We include below a summarization on recent developments.

- (•) *Evolution of diffusion*: $d_1 \neq d_2$, $q_1 = q_2$, $r_1 = r_2$. For $b_u = 0$ and $b_d = -1$, Lou and Lutscher [94] found that higher diffusion rate is selected for, in sharp contrast to the widely accepted result "slower diffuser prevails" in non-advective environments [34, 48]; this is later extended by Lou and Zhou [101] to a bit more wide class of boundary conditions $b_d \in [0, 1)$ by developing completely different argument; furthermore, Hao, Lam and Lou [46] performed a careful analysis for $b_d \in [0, \infty]$ and in particular, they found that $b_d = \frac{3}{2}$ is critical value for $d = \infty$ to be a global ESS and that there may appear multiple global ESS even when $b \in (1, \frac{3}{2})$. The story of $r_1 = r_2 := r_0(x)$ being non-constant is quite complicated and we refer to Lam, Lou and Lutscher [79] for discussions on the existence of ESS based on various types of $r_0(x)$. We mention here another interesting case with $b_u = -1$, for which Tang and Chen [124] observed that large diffusion is selected for if $b_d < 1$ and selected against if $b_d > 1$. See also [125] for an extension to $r_0(x)$ being a decreasing function.
- (•) *Evolution of advection*: $d_1 = d_2$, $q_1 \neq q_2$, $r_1 = r_2$. For $b_u = b_d = 0$, Lou, Xiao and Zhou [99] confirmed that weaker advection is more favorable for species

to win the competition and particularly the strategy $q = 0$ (no advection) is a global ESS. This is later generalized by Zhou and Zhao [141] to a more general setting with $b_d \in [0, \infty]$ and $r_1 = r_2 := r_0(x)$ being a non-increasing function. Furthermore, Xu and Gan [129] illustrated that such a result, when $b_d \in [\frac{1}{2}, \infty]$, does not depend on the shape of $r_0(x)$ by a more direct approach (monotonicity of principal eigenvalue).

- (•) *Evolution of diffusion and advection*: $d_1 \neq d_2$, $q_1 \neq q_2$, $r_1 = r_2$. For $b_u = b_d = 0$, among other things, Zhou [136] proved that (i) the strategy with larger diffusion but smaller advection is always more advantageous, which can be viewed as a mixture of the results in [99, 101]; and (ii) the strategy with both larger diffusion and advection may or may not be favorable depending on the ratio of diffusion and advection. This is extended by Zhou and Zhao [140] to $b_d \in (0, 1]$ and some different dynamics is shown for some $b_d > 1$. A special situation with $b_u = -1$ and $b_d = \infty$ is investigated by Ma and Tang [105], where some interesting argument is developed to exclude the positive steady states. The inhomogeneous case with $r_1 = r_2 := r_0(x)$ being non-constant is more difficult to deal with, and currently only some special cases (monotonic functions) are discussed in [100, 135], where some different phenomena from the homogeneous case are revealed.
- (•) *Joint action of movement and spatial variations*: $d_1 \neq d_2$, $q_1 \neq q_2$, $r_1 \neq r_2$. To understand the combined effect of movement and spatial variations, Tang and Zhou [126] studied a special case with $b_u = b_d = 0$, $\frac{q_1}{d_1} = \frac{q_2}{d_2}$, r_1 being a positive constant, and r_2 being a positive function with the same average as r_1, and found that the outcome of competition could be very different depending closely on the movement rates and resource shape. Different boundary conditions are further discussed in several works, see, e.g., Lou, Nie and Wang [98] for $b_u = 0$ and $b_d = 1$ and Yan, Nie and Zhou [132] for $b_u = 0$ and $b_d = \infty$, where the bistable phenomenon is observed numerically.

4.3. General models

As a further development of the diffusive competition models in section 3, one may formulate the following more general system by involving the advection terms

$$\begin{cases} u_t = \mathcal{L}u + u[r_1(x) - u - bv], & x \in \Omega,\ t > 0, \\ v_t = \mathcal{M}v + v[r_2(x) - cu - v], & x \in \Omega,\ t > 0, \\ \mathcal{B}_1 u = \mathcal{B}_2 v = 0, & x \in \partial\Omega,\ t > 0, \\ u(x,0) = u_0(x) \geq, \not\equiv 0, & x \in \Omega, \\ v(x,0) = v_0(x) \geq, \not\equiv 0, & x \in \Omega, \end{cases} \tag{4.5}$$

where the operators $\mathcal{L}$ and $\mathcal{M}$ are defined in the following divergence form

$$\mathcal{L}w := \operatorname{div}\Big(d_1 \nabla w - \alpha_1 w \nabla A_1(x)\Big), \tag{4.6}$$

and

$$\mathcal{M}w := \operatorname{div}\Big(d_2 \nabla w - \alpha_2 w \nabla A_2(x)\Big). \tag{4.7}$$

In comparison with system (3.2), the additional function $A_i(x) \in C^1(\overline{\Omega})$ is used to specify the direction of advection with advection speed measured by $\alpha_i \geqslant 0$,

$i = 1, 2$. The boundary operator $\mathcal{B}_i$ is defined by

$$\mathcal{B}_i w = d_i \frac{\partial w}{\partial \nu} - \alpha_i w \frac{\partial A_i}{\partial \nu} = 0, \quad i = 1, 2, \tag{4.8}$$

which, again, shows that there are no populations passing through the habitat boundary.

System (4.5)-(4.8) was firstly studied by Zhou and Xiao [139] in the following special setting

(C_1) $\frac{d_2}{d_1} = \frac{\alpha_2}{\alpha_1} := k > 0$ (or equivalently, $\frac{\alpha_1}{d_1} = \frac{\alpha_2}{d_2} := k' > 0$);

(C_2) $A_1(x) = A_2(x) := P(x)$;

(C_3) $(b, c) \in \Pi_1$;

where for any $\xi > 0$,

$$\Pi_\xi := \{(b, c) \in \mathbb{R}^+ \times \mathbb{R}^+ : bc \leqslant \xi\}.$$

Under the conditions of (C_1)-(C_3), the authors obtained a complete classification of all possible long time behaviors, which can be seen as an extension of that of [51] without advection. Moreover, for the case with identical growth rate $r_1(x) = r_2(x)$, a further determination on the global dynamics is presented for all $(b, c) \in (0, 1] \times (0, 1]$.

The above conditions (C_1) and (C_2) seem too strict on given parameters. In a later work by Zhou, Tang and Xiao [138], these conditions are removed but at the expense of restricting (C_3) in certain sense. Specifically, they make the following basic hypotheses

(H_1) $\frac{\alpha_2}{d_2} A_2(x) \leqslant \frac{\alpha_1}{d_1} A_1(x)$ in Ω and $\frac{\alpha_2}{d_2} A_2(x) - \frac{\alpha_1}{d_1} A_1(x) = 0$ somewhere in $\overline{\Omega}$;

(H_2) $(b, c) \in \Pi_{\kappa_0}$;

where

$$\kappa_0 := \min_{x \in \Omega} e^{\left(\frac{\alpha_2}{d_2} A_2(x) - \frac{\alpha_1}{d_1} A_1(x)\right)} \in (0, 1]. \tag{4.9}$$

Note that (H_1) is imposed without losing generality since one can always replace $A_1(x)$ by $A_1(x) + M$ for some appropriate constant M. In the special case (C_1) and (C_2), κ_0 defined in (4.9) becomes one, coinciding with (C_3). Also, when the effect of advection is ignored (i.e., $\alpha_1 = \alpha_2 = 0$), again, one has $\Pi_{\kappa_0} = \Pi_{\kappa_1}$, matching the condition in He and Ni [51]. But in general, κ_0 defined in (4.9) is strictly smaller than 1.

Under the hypotheses (H_1) and (H_2), the long time behaviors is completely classified for the R-D-A system (4.5)–(4.8) (including the R-D system (3.2)) in [138]. Moreover, by choosing the competition coefficients b and c as bifurcation parameters, two critical values b^* and c^*, sharply governing the local stability of the two semi-trivial steady states, are obtained, and the global dynamics is further determined in b-c plane (see [138, Theorems 4 and 5]). Interestingly, via b^* and c^*, the authors proposed a parallel way to that of the classical ODE system (2.1) to define the weak, strong-weak, and strong competition for infinite dimensional systems including both R-D-A system (4.5)–(4.8) and R-D system (3.2). Precisely, they defined

(i) weak competition case: $0 < b < b^*$ and $0 < c < c^*$;

(ii) strong-weak competition case:

$(ii.1)$ $0 < b < b^*$ and $c > c^*$ (u-strong and v-weak);

$(ii.2)$ $b > b^*$ and $0 < c < c^*$ (u-weak and v-strong);

(iii) strong competition case: $b > b^*$ and $c > c^*$.

Roughly speaking, (b^*, c^*) in the infinite dimensional case plays the same role as $(\frac{r_1}{r_2}, \frac{r_2}{r_1})$ in the finite dimensional system (2.1). We will discuss this definition further in the last section.

It deserves mentioning here that in a recent work by Guo, He and Ni [44], through a *different* argument, the authors found a critical value

$$\kappa_1 := \frac{\min\limits_{x\in\Omega} e^{\left(\frac{\alpha_2}{d_2}A_2(x)-\frac{\alpha_1}{d_1}A_1(x)\right)}}{\max\limits_{x\in\Omega} e^{\left(\frac{\alpha_2}{d_2}A_2(x)-\frac{\alpha_1}{d_1}A_1(x)\right)}}$$

so that for $(b, c) \in \Pi_{\kappa_1}$, a similar classification result [44, Corollary 5.1] to [138, Theorem 2] is obtained. We point out that κ_1, in view of the assumption (H_1), is indeed the same as κ_0. So concerning system (4.5)-(4.8), two different arguments developed, respectively, in [44] and [138], give the same value to classify the long time dynamics. Such ideas, as shown in [44], are also feasible to treat more general nonlinear terms (symmetric) like

$$u[r_1(x) - b_1(x)u - c_1(x)v] \quad \text{and} \quad v[r_2(x) - b_2(x)u - c_2(x)v].$$

Moreover, we refer to [137] for the treatment of *asymmetric* nonlinear terms.

We emphasize here that the basic strategy in [138, 139] to understand system (4.5)-(4.8) is to regard competition coefficients b and c as bifurcation parameters (see also [38, 130] for the generalization to the one spatial dimensional river population models but with general boundary conditions). Nevertheless, in the above mentioned works [43, 44] and those mentioned in previous subsections 4.1 and 4.2, diffusion and/or advection rates are viewed as bifurcation parameters. These different strategies, mathematically, require us to understand the dependence of the principal eigenvalue on different parameters. See the next section.

5. Mathematical approaches

In this section, we aim to introduce several fundamental mathematical approaches in the study of two species competitive R-D and R-D-A systems.

We note here that the stability and asymptotic stability of steady states are defined in the standard dynamical system sense with the $C(\overline{\Omega}) \times C(\overline{\Omega})$ topology [121], and that a non-negative steady state $(u(x), v(x))$ is called trivial if both components are zero, semi-trivial if only one component is zero, and nontrivial if both components are not identically zero. Moreover, if one component is not identically zero, then by the strong maximum principle [118], it must be positive in $\overline{\Omega}$, and so the nontrivial $(u(x), v(x))$ is also called a positive (coexistence) steady state. Hereafter, we denote the two semi-trivial steady states by $(\tilde{u}, 0)$ and $(0, \tilde{v})$, respectively.

5.1. Monotone theory

Let $X = C(\overline{\Omega})$ be the set of all real-valued continuous functions defined on $\overline{\Omega}$, and let X^+ be the subset of X consisting of all non-negative functions. The usual cone in the study of competitive systems is denoted by $K := X^+ \times (-X^+)$ with nonempty interior given by $\mathrm{Int}K = \mathrm{Int}X^+ \times (-\mathrm{Int}X^+)$. The usual partial order relations generated by K, $K \setminus \{(0,0)\}$ and $\mathrm{Int}K$ are, respectively, denoted by $\leq_K$, $<_K$, $\ll_K$. Precisely, for $u_i, v_i \in X^+$ $(i = 1, 2)$,

$$\begin{aligned}
(u_1, v_1) \leq_K (u_2, v_2) \quad &\Longleftrightarrow \quad u_1 \leqslant u_2 \quad \text{and} \quad v_2 \leqslant v_1 \quad \text{in} \quad \overline{\Omega}, \\
(u_1, v_1) <_K (u_2, v_2) \quad &\Longleftrightarrow \quad (u_1, v_1) \leq_K (u_2, v_2) \quad \text{and} \quad (u_1, v_1) \neq (u_2, v_2) \quad \text{in} \quad \overline{\Omega}, \\
(u_1, v_1) \ll_K (u_2, v_2) \quad &\Longleftrightarrow \quad u_1 < u_2 \quad \text{and} \quad v_2 < v_1 \quad \text{in} \quad \overline{\Omega}.
\end{aligned}$$

As we know, the two species competitive R-D and R-D-A systems, according to the above cone, generate a strongly monotone dynamical system (see, e.g., [20, Lemma 5.4] and [16, Theorem 3]). Take system (4.5)-(4.8) as an example. It is strongly monotone in the sense that if $\big(u_0^1(x), v_0^1(x)\big) <_K \big(u_0^2(x), v_0^2(x)\big)$ and $u_0^i(x) \not\equiv 0$, $v_0^i(x) \not\equiv 0$, then

$$\big(u^1(x,t), v^1(x,t)\big) \ll_K \big(u^2(x,t), v^2(x,t)\big) \quad \text{for any} \quad t > 0,$$

where $\big(u_0^i(x), v_0^i(x)\big) \in X^+ \times X^+$ and $\big(u^i(x,t), v^i(x,t)\big)$ is the unique positive solution of system (4.5)–(4.8) with initial condition $\big(u_0^i(x), v_0^i(x)\big)$, $i = 1, 2$.

The basic theory of abstract competitive systems for two competing species has been made by Hess and Lazer [56] for discrete semi-dynamical systems, and later by Hess [55], Hsu et al. [58,59] and Lam et al. [80] for continuous-time versions. See also the monograph by Zhao [134].

In what follows, taking system (4.5)–(4.8) as an example, we apply the above abstract monotone theory to this model and present a more specific statement on the underlying long time dynamics (see Theorem 5.1 below). Note that Theorem 5.1 holds also for many other competitive models (e.g., those mentioned in previous sections).

Theorem 5.1. *The following statements on system* (4.5)–(4.8) *are true:*

(1) *Let* $(u, v) \in X^+ \times X^+$ *be any steady state of system* (4.5)–(4.8). *Then*

$$(0, \tilde{v}) \leq_K (u, v) \leq_K (\tilde{u}, 0).$$

(2) *If system* (4.5)–(4.8) *has no positive steady states and one of the two semi-trivial steady states is linearly unstable, then the other one is globally asymptotically stable [56], see also [58, 80];*

(3) *If both semi-trivial steady states are unstable, then system* (4.5)–(4.8) *has at least one stable positive steady state [26,106]; moreover, if every positive steady state is linearly stable, then there is a unique positive steady state which is globally asymptotically stable [55].*

Although great effort via a topological approach has been made for monotone dynamical systems, to achieve a clear understanding on the global dynamics of a specific competition model, as indicated in Theorem 5.1, one has to face the following several problems:

($\mathcal{P}_1$) How to get a clear understanding on the local dynamics around the two semi-trivial steady states? Basically, this issue is closely related to some eigenvalue problems obtained by linearization, and it may not be so easy as we imagine since the dependence of the principal eigenvalue on certain parameters may be very complicated. Indeed, in many situations, it is very hard to determine the local stability of the two semi-trivial steady states *simultaneously*, that is, to draw a clear picture on the local dynamics in the plane of bifurcation/varying parameters (see [132] for some detailed discussion on both R-D and R-D-A systems).

($\mathcal{P}_2$) How to realize the assumption that there are no positive steady states? For competitive parabolic systems, this is equivalent to verifying the non-existence of any positive solutions of the corresponding elliptic (stationary) system, which generally is highly nontrivial.

($\mathcal{P}_3$) How to discuss the stability and multiplicity of positive steady states if these solutions do exist? A feasible way, as mentioned in Theorem 5.1 (2), is to establish the a priori estimate on the linear stability of all positive steady states, which, again, is related to a linear eigenvalue problem (but a system governed by two equations). For this issue, some recent developments have been made in [44, 51, 137–139], but there is still room to make further improvement. We will return to this point in the last discussion section.

As indicated above, when investigating a particular competitive system, beside the obvious requirement on the basic theory of monotone dynamical systems [55, 58, 80], one also has to develop new ideas and techniques to overcome the difficulties as mentioned in ($\mathcal{P}_1$)–($\mathcal{P}_3$). See later subsections.

5.2. Principal eigenvalue theory: single equation

The principal eigenvalue theory for a single equation is usually helpful in the study of local stability of the two semi-trivial steady states, that is, problem $\mathcal{P}_1$ (sometimes it is also useful in the investigation of $\mathcal{P}_2$, see subsection 5.4).

We first talk about the following diffusion type operator (self-adjoint) with zero Neumann boundary condition

$$\begin{cases} d\triangle\varphi + m(x)\varphi + \lambda\varphi = 0, & x \in \Omega, \\ \dfrac{\partial \varphi}{\partial \nu} = 0, & x \in \partial\Omega, \end{cases} \tag{5.1}$$

where $d > 0$, $m(x) \in L^\infty(\Omega)$ and ν is the outward unit normal vector on $\partial\Omega$. It follows from the Krein-Rutman theorem [70] that problem (5.1) has a principal eigen-pair denoted by (λ_1, φ_1) with λ_1 being a real number and $\varphi_1 > 0$ in $\overline{\Omega}$. Moreover, by the variational approach,

$$\lambda_1 = \inf_{\zeta \in \Gamma} \frac{\int d|\nabla\zeta|^2 \mathrm{d}x - \int m(x)\zeta^2 \mathrm{d}x}{\int \zeta^2 \mathrm{d}x}, \quad \Gamma := H^1(\Omega) \setminus \{0\}.$$

The following properties of λ_1 are well known.

Proposition 5.1. *Assume that $m(x)$ is non-constant. Then*

(a) λ_1 *depends continuously and differentially on the parameter d;*

(b) λ_1 *is strictly increasing and concave in* $d \in (0, \infty)$*, and*

$$\lim_{d\to 0} \lambda_1 = -\max_{x\in\Omega} m(x), \quad \lim_{d\to\infty} \lambda_1 = -\frac{1}{|\Omega|}\int_\Omega m(x)\,dx;$$

(c) λ_1 *is strictly decreasing in the weight function* $m(x)$ *in the* L^∞ *sense, that is, if* $m_1(x) \leqslant, \not\equiv m_2(x)$ *in* Ω*, then* $\lambda_1(m_1) > \lambda_1(m_2)$.

The proof of Proposition 5.1 is standard, see, e.g., [13, 49, 96, 113].

Remark 5.1. The increasing property and limiting behaviors of λ_1 stated in Proposition 5.1 (b) play an extremely important role in the analysis of local stability of $(\tilde{u}, 0)$ and $(0, \tilde{v})$. Indeed, for the general R-D system (3.2), the linearly stable region Σ_u (resp. Σ_v) of $(\tilde{u}, 0)$ (resp. $(0, \tilde{v})$) can be described in certain "abstract" manner in terms of the diffusion rates d_1 and d_2 (see [51, Theorem 3.3]), but a clear picture on Σ_u and Σ_v in d_1-d_2 plane is far from being completely understood (since the description of Σ_u and Σ_v involves many parameters that are implicitly determined). For system (3.3) (a very special case of system (3.2)), Σ_u and Σ_v are exactly separated by the diagonal line $d_2 = d_1$ in d_1-d_2 plane, a complete understanding. For some other special cases of system (3.2), a relatively clear understanding on Σ_u and Σ_v was obtained by He and Ni [49, 50, 52, 53], but not completely. The issue to further examine the geometric behaviors of Σ_u and Σ_v in d_1-d_2 plane may deserve further consideration. In comparison, for both the competitive R-D system (3.2) and R-D-A system (4.5)-(4.8), by using the monotonicity in weight function as stated in Proposition 5.1 (c) (see also Proposition 5.2 (d) below), Zhou, Tang and Xiao [138] obtained a complete understanding on Σ_u and Σ_v in terms of the competition coefficients b and c (a different strategy), that is, a clear picture on Σ_u and Σ_v in b-c plane. This enables them to further determine the global dynamics in b-c plane.

We now discuss the diffusion-advection type operator with no-flux boundary condition

$$\begin{cases} d\triangle\varphi - \alpha \operatorname{div}(\varphi\nabla A(x)) + m(x)\varphi + \lambda\varphi = 0, & x \in \Omega, \\ d\dfrac{\partial\varphi}{\partial\nu} - \alpha\varphi\dfrac{\partial A}{\partial\nu} = 0, & x \in \partial\Omega, \end{cases} \tag{5.2}$$

where $\alpha > 0$, $A(x) \in C^1(\overline{\Omega})$ is a non-constant function, and the other parameters can be understood in a similar way to that in problem (5.1). Again, by using the Krein-Rutman theorem [70], problem (5.2) has a real principal eigenvalue $\bar{\lambda}_1$ with a positive eigenfunction $\bar{\varphi}_1$ in $\overline{\Omega}$. Moreover, $\bar{\lambda}_1$ has the following variational characterization

$$\bar{\lambda}_1 = \inf_{\zeta\in\Gamma} \frac{\int d e^{\frac{\alpha}{d}A(x)} |\nabla\big(e^{-\frac{\alpha}{d}A(x)}\zeta\big)|^2 \mathrm{d}x - \int m(x) e^{-\frac{\alpha}{d}A(x)}\zeta^2 \mathrm{d}x}{\int e^{-\frac{\alpha}{d}A(x)}\zeta^2 \mathrm{d}x}.$$

We include below several properties of $\bar{\lambda}_1$.

Proposition 5.2. *Assume that* $m(x)$ *is non-constant. Then we have*

(a) $\bar{\lambda}_1$ *depends continuously and differentiably on the parameters* $d > 0$ *and* $\alpha > 0$*;*

(b) *Assume that all critical points of* $A(x)$ *are non-degenerate and let* $\mathcal{A}$ *be the set of all local maximum points of* $A(x)$*. Then*

$$\lim_{\alpha\to\infty} \lambda_1 = \min_{x\in\mathcal{A}} \big(-m(x)\big);$$

(c) *Assume that* $|\nabla A(x)| \neq 0$ *on* $\partial\Omega$. *For any given* $\alpha > 0$, *one has*

$$\lim_{d\to 0} \lambda_1 = \min_{x\in\Gamma_1\cup\Gamma_2} \Big\{ -m(x) + \alpha\Sigma_{i=1}^N(\kappa_i(x) + |\kappa_i(x)|)\Big\},$$

where

$$\Gamma_1 := \{x \in \overline{\Omega} : |\nabla A(x)| = 0\},$$
$$\Gamma_2 := \{x \in \partial\Omega : |\nabla A(x)| = \nabla A(x) \cdot \nu > 0\},$$

and $\kappa_i(x)$, $(i = 1, ..., N)$, *are eigenvalues of* $D^2A(x)$;

(d) $\bar{\lambda}_1$ *is strictly decreasing in the weight function* $m(x)$ *in the* L^∞ *sense, that is, if* $m_1(x) \leqslant, \not\equiv m_2(x)$ *in* Ω, *then* $\bar{\lambda}_1(m_1) > \bar{\lambda}_1(m_2)$.

The proof of the above statements (a) and (d) are standard, see, e.g., [13]. Statement (b) is proved in [22, Theorem 1.1] and statement (c) is proved in [23, Theorem 1.2].

Remark 5.2. We make some comments on $\bar{\lambda}_1$ and Proposition 5.2.

(1) For the diffusion-advection type operator as given in problem (5.2), its principal eigenvalue has quite different properties from that of the diffusion type (i.e., $\alpha = 0$) in (5.1). For instance, $\bar{\lambda}_1$, in general, is no longer a monotonic function in the parameter d; see [23, inquality (1.12)] for some detailed explanation. Moreover, $\bar{\lambda}_1$, as a function of two variables d and α, is not continuous at the point $(0, 0)$, and it has very rich and complex behaviors when both d and α are small. We refer the interested readers to [23] for more details.

(2) Concerning the question whether $\bar{\lambda}_1$ is monotonic in the parameter α, Berestycki et al. [11], Godoy et al. [41], and Liu and Lou [88] considered a more general situation where $\nabla A(x)$ above is replaced by a general vector field $\mathbf{V}$, and found that a positive answer to this question requires

$$\mathrm{div}\mathbf{V} = 0 \text{ in } \Omega \text{ (divergence free)} \quad \text{and} \quad \mathbf{V} \cdot \nu = 0 \text{ on } \partial\Omega, \tag{5.3}$$

which, in the context of gradient flow $\mathbf{V} = \nabla A(x)$, implies $A(x) \equiv$ const. Hence, these results do not work for the gradient flow as given in problem (5.2). We will return to this point by discussing a one space dimension case; see Proposition 5.3 (d) and Proposition 5.4 below.

(3) A fundamental issue in the study of operator theory is to understand the limiting behaviors of principal eigenvalues as various parameters approach zero or infinity, see the pioneering works by Devinatz et al. [32] and Friedman [37] for small diffusion with divergence free vector field and Dirichlet boundary condition, and Berestycki et al. [11] for large advection with divergence free vector field and Dirichlet, Robin and Neumann boundary conditions. In the context of gradient flow (see (5.2)), Chen and Lou [22, 23] made important contributions by establishing Proposition 5.2 (b) and (c), which, as an application, can be applied to analyze the local stability of semi-trivial steady states of certain competitive models in the sense of large advection or small diffusion, see, e.g., [12, 15, 20, 22, 23].

Next, we consider a one-dimensional case of problem (5.2) but with differing boundary conditions (which is useful to study the river population models in subsection 4.2)

$$\begin{cases} d\varphi_{xx} - \alpha\varphi_x + m(x)\varphi + \lambda\varphi = 0, & x \in (0, L), \\ d\varphi_x(0) - \alpha\varphi(0) = b_1\alpha\varphi(0), \\ d\varphi_x(L) - \alpha\varphi(L) = -b_2\alpha\varphi(L), \end{cases} \tag{5.4}$$

where $d, \alpha, L > 0$, and the parameters b_i $(i = 1, 2)$ may vary in $[0, \infty]$ (note that $b_i = \infty$ means the Dirichlet boundary condition). Problem (5.4), in view of the Krein-Rutman theorem [70], also has a principal eigen-pair denoted by $(\tilde{\lambda}_1, \tilde{\varphi}_1)$, where $\tilde{\lambda}_1$ is real and $\tilde{\varphi}_1 > 0$ in $(0, L)$. Moreover, $\tilde{\lambda}_1$ can be characterized by

$$\tilde{\lambda}_1 = \inf_{\zeta\in\tilde{\Gamma}} \frac{b_2\alpha e^{-\frac{\alpha}{d}L}\zeta^2(L) + b_1\alpha\zeta^2(0) + \int de^{-\frac{\alpha}{d}x}\zeta_x^2 \mathrm{d}x - \int m(x)e^{-\frac{\alpha}{d}x}\zeta^2 \mathrm{d}x}{\int e^{-\frac{\alpha}{d}x}\zeta^2 \mathrm{d}x}, \tag{5.5}$$

where $\tilde{\Gamma} = H^1(0, L) \setminus \{0\}$ if $b_1, b_2 \neq \infty$. For b_1 and/or b_2 equals infinity, the numerator in (5.5) can be further simplified (e.g., $\zeta(L) = 0$ if $b_2 = \infty$), and $H^1(0, L)$ needs to be replaced by $H_0^1(0, L)$.

We present below a series of properties of $\tilde{\lambda}_1$ and $\tilde{\varphi}_1$.

Proposition 5.3. *Assume that $m(x)$ is non-constant if $b_1 = b_2 = 0$. Then*

(a) *$\tilde{\lambda}_1$ depends continuously and differentiably on the parameters $d > 0$ and $\alpha > 0$;*

(b) *If $b_1 = b_2 = \infty$, then $\lim_{d\to 0} \tilde{\lambda}_1 = \infty$;*

If $b_1 = 0$ or ∞, and $b_2 = 0$, then $\lim_{d\to 0} \tilde{\lambda}_1 = -m(L)$;

If $b_1 = 0$ or ∞, and $b_2 = \infty$, then $\lim_{\alpha\to\infty} \tilde{\lambda}_1 = \infty$;

If $b_1 = 0$ or ∞, and $b_2 = 0$, then $\lim_{\alpha\to\infty} \tilde{\lambda}_1 = -m(L)$;

(c) *$\tilde{\lambda}_1$ is strictly decreasing in the weight function $m(x)$ in the L^∞ sense, that is, if $m_1(x) \leqslant, \not\equiv m_2(x)$ in Ω, then $\tilde{\lambda}_1(m_1) > \tilde{\lambda}_1(m_2)$;*

(d) *If $b_1 = 0$, $b_2 = -1$ and $m(x) \equiv const$, then $\tilde{\lambda}_1'(d) < 0$;*

(e) *If $b_1 \in [0, \infty]$ and $b_2 \in [\frac{1}{2}, \infty]$, then $\tilde{\lambda}_1'(\alpha) > 0$;*

(f) *If $b_1 = 0$ and $m'(x) \le 0$ in $(0, L)$, then $\frac{(\tilde{\varphi}_1)_x}{\tilde{\varphi}_1} < \frac{\alpha}{d}$ in $(0, L)$;*

(g) *Let $b_1 = 0$. For any $d_i > 0$, $\alpha_i > 0$ and $b_2^i \in [0, \infty]$, denote*

$$(\tilde{\lambda}_1^i,\ \tilde{\varphi}_1^i) = \Big(\tilde{\lambda}_1(d_i, \alpha_i, b_2^i),\ \tilde{\varphi}_1(d_i, \alpha_i, b_2^i)\Big), \quad i = 1, 2.$$

Then the following difference formula holds

$$\begin{aligned} &[\tilde{\lambda}_1^2 - \tilde{\lambda}_1^1] \int_0^L e^{-\frac{\alpha_2}{d_2}x} \cdot \tilde{\varphi}_1^1 \cdot \tilde{\varphi}_1^2 dx \\ &= \int_0^L \left[(d_2 - d_1)(\tilde{\varphi}_1^1)_x - (\alpha_2 - \alpha_1)\tilde{\varphi}_1^1\right] \cdot \left[e^{-\frac{\alpha_2}{d_2}x}\tilde{\varphi}_1^2\right]_x dx \\ &\quad + (b_2^2\alpha_2 - b_2^1\alpha_1)e^{-\frac{\alpha_2}{d_2}L}\tilde{\varphi}_1^1(L)\tilde{\varphi}_1^2(L). \end{aligned} \tag{5.6}$$

(h) *Let $b_1 = 0$ and $b_2 = -1$. Suppose that $m(x) > 0$ in $[0, L]$. If $\tilde{\lambda}_1(d^*) = 0$ for some $d^* > 0$, then $\tilde{\lambda}_1'(d^*) < 0$, which implies that $\tilde{\lambda}_1$, as a function of d, has "at most one positive root" (called "AMOPR" property for brevity and for later use).*

(i) *Let* $b_1 = -1$ *and* $b_2 = \infty$*. If* $m'(x) \leqslant 0$ *in* $(0, L)$*, then* $\tilde{\lambda}_1'(d) > 0$ *and* $\tilde{\lambda}_1'(\alpha) < 0$*; if* $m(0) > 0$ *and* $m'(x) \geqslant 0$ *in* $(0, L)$*, then* $\tilde{\lambda}_1$ *has the "AMOPR" property in* d*, and also in* α*.*

(j) *Let* $b_1 = -1$ *and* $b_2 > 1$*. Suppose that* $m(x) > 0$ *in* $[0, L]$ *and* $m'(x) > 0$ *in* $(0, L)$*. If* $\tilde{\lambda}_1(d^*) = 0$ *for some* $d^* > 0$*, then* $\tilde{\lambda}_1'(d^*) > 0$*, and so the "AMOPR" property in* d *holds.*
Let $b_1 = -1$ *and* $b_2 \in [0, 1)$*. Suppose that* $m(x) < 0$ *in* $[0, L]$ *and* $m'(x) < 0$ *in* $(0, L)$*. If* $\tilde{\lambda}_1(d^*) = 0$ *for some* $d^* > 0$*, then* $\tilde{\lambda}_1'(d^*) < 0$*, and so the "AMOPR" property in* d *holds.*

Statements (a) and (c) are direct consequences of the counterpart of Proposition 5.2. Statement (b) follows from the systematic works [115, 116]. Statement (d) is proved in [9, Proposition 2.1] and statement (e) holds due to [94, Remark 4.10]. Statements (f) and (g) are proved in [140, Lemmas 3.1 and 3.2]. See [94, Lemma 6.2] for statement (h), [105, Lemma 2.1] for statement (i), and [124, Lemma 2.3] for statement (j).

Remark 5.3. We make some comments on $\tilde{\lambda}_1$ and Proposition 5.3.

(1) Problem (5.4) with *standard* Dirichlet and Robin boundary conditions has been studied by Peng et al. [115, 116], where various limiting behaviors of the principal eigenvalue in the sense of small/large diffusion or large advection have been carefully examined. But these results, in general, cannot be directly applied to problem (5.4), since the boundary conditions in (5.4) also involve d and α. See also Liu et al. [90, 91] for some latest advances in the non-autonomous situation (time periodic).

(2) The limiting behaviors stated in Propositions 5.2 and 5.3, as mentioned before, are useful in the analysis of local stability of semi-trivial steady states, but mostly working only for the particular situation such as large advection or small diffusion. For general situation especially intermediate advection or diffusion, statements (f), (g), (h), (i) and (j) are shown to be quite helpful in the study of local dynamics of various cases of system (4.4), see [99, 101, 105, 124, 136, 140].

(3) The monotonicity result in Proposition 5.3 (e) can be seen as a further development of those works [11, 41, 88] mentioned in Remark 5.2 (2), since the setting $A(x) \equiv x$ in (5.4) does not satisfy the condition (5.3) required in [11, 41, 88]. In fact, such a monotonicity can be generalized to a much more wide setting. See Proposition 5.4 below. We also mention here a recent work by Liu and Lou [89] treating the periodic-in-space situation.

(4) Some new property of $\tilde{\lambda}_1$ was observed by Jiang, Lam and Lou [63, Proposition 2.1 (c) and (d)], which is useful to analyze the global dynamics of some phytoplankton competition models.

We end this subsection by including a recent monotonicity result obtained by Shao, Wang and Zhou [119]. See the following Proposition 5.4.

Consider

$$\begin{cases} d(\alpha)\left[D(x)\varphi_x\right]_x - \alpha\left[B(x)\varphi\right]_x + c(x)\varphi + \lambda\varphi = 0, & x \in (0, L), \\ d(\alpha)D(x)\varphi_x - \alpha B(x)\varphi = b_1\alpha B(x)\varphi, & x = 0, \\ d(\alpha)D(x)\varphi_x - \alpha B(x)\varphi = -b_2\alpha B(x)\varphi, & x = L, \end{cases} \tag{5.7}$$

where $D(x) > 0$ in $[0, L]$, $B(x) \in C^1([0, L])$, $\alpha, L > 0$, $d(\alpha)$ is a positive function of $\alpha > 0$, and $b_1, b_2 \in [0, \infty]$.

Proposition 5.4. *Assume that*

(A_1) $d'(\alpha) \geqslant 0$ *and* $\left[\frac{d(\alpha)}{\alpha^2}\right]'(\alpha) \leqslant 0$ *for* $\alpha > 0$;

(A_2) $B(x) \not\equiv 0$, $B(0) \geqslant 0$ *and* $B'(x) \geqslant 0$ *in* $[0, L]$;

(A_3) $b_1 \in [0, \infty]$ *and* $b_2 \in [\frac{1}{2}, \infty]$.

Then the principal eigenvalue of problem (5.7), *still denoted by* $\tilde{\lambda}_1$, *satisfies* $\tilde{\lambda}_1'(\alpha) > 0$.

Remark 5.4. We make some notes on the above conditions (A_1) and (A_2).

(1) Clearly, the condition (A_1) includes the standard case $d(\alpha) \equiv d$ (a positive constant). More importantly, such a condition, when applied to study the structure of positive steady states of competitive systems, would make some improvements; see Example 1.3 in subsection 5.4 later.

(2) The general vector field $\mathbf{V}$ in [11, 41, 88], in the setting of problem (5.7), becomes "$-B(x)$". By an easy inspection, one finds from (A_2) that the original condition (5.3) especially the divergence free condition is relaxed a lot.

5.3. Principal eigenvalue theory: system

The principal eigenvalue theory of systems is less understood than that of the single equation. In the sequel, we first discuss how to analyze the (linear) stability of positive steady states of competitive R-D and R-D-A systems, that is, problem $\mathcal{P}_3$. This is equivalent to studying a linear eigenvalue problem governed by a system of two equations (see (5.8) below). Then we introduce a convergence result of the principal eigenvalue of general linear cooperative elliptic systems given by Lam and Lou [75]. See Proposition 5.6 below.

Let us consider the R-D-A system (4.5)–(4.8) with $\alpha_1, \alpha_2 \geqslant 0$, which not only includes the R-D system (3.2) but also the situation where one equation has advection while the other one has no advection. Some notes are included in Remark 5.6 for other models.

Let $(u(x), v(x))$ be any positive steady state of system (4.5)–(4.8), i.e.,

$$\begin{cases} 0 = \mathcal{L}u + u\Big[r_1(x) - u - bv\Big], & x \in \Omega, \\ 0 = \mathcal{M}v + v\Big[r_2(x) - cu - v\Big], & x \in \Omega, \\ \mathcal{B}_1 u = \mathcal{B}_2 v = 0, & x \in \partial\Omega, \\ u(x) > 0,\ v(x) > 0, & x \in \overline{\Omega}. \end{cases}$$

By linearization at $(u(x), v(x))$, one sees

$$\begin{cases} \mathcal{L}\varphi + \Big[r_1(x) - u - bv\Big]\varphi - u\Big[\varphi + b\psi\Big] + \tau\varphi = 0, & x \in \Omega, \\ \mathcal{M}\psi + \Big[r_2(x) - cu - v\Big]\psi - v\Big[c\varphi + \psi\Big] + \tau\psi = 0, & x \in \Omega, \\ \mathcal{B}_1\varphi = \mathcal{B}_2\psi = 0, & x \in \partial\Omega. \end{cases} \tag{5.8}$$

By the Krein-Rutman theorem [70], problem (5.8) admits a principal eigenvalue denoted τ_1, with the corresponding eigenfunction (φ, ψ) satisfying $\varphi > 0 > \psi$ in $\overline{\Omega}$; see [139, Page 366–367] or [121] for detailed explanation.

Remark 5.5. If $(u(x), v(x))$ above is replaced by the semi-trivial steady state $(\tilde{u}, 0)$ or $(0, \tilde{v})$, then the two equations of φ and ψ in (5.8) will be decoupled, and so the linear stability of $(\tilde{u}, 0)$ or $(0, \tilde{v})$ is, in fact, determined by an eigenvalue problem of a single equation. See [82, Corollary 2.10] for more explanations.

Recall the conditions (H_1) and (H_2) defined in subsection 4.3. The following result is due to Zhou, Tang and Xiao [138].

Proposition 5.5. *Assume that (H_1) and (H_2) hold. Then for any positive steady state of system (4.5)–(4.8) with $\alpha_1, \alpha_2 \geqslant 0$, one has $\tau_1 \geqslant 0$, with equality holding only if both semi-trivial steady states are neutrally stable (the principal eigenvalue of the operator linearized at semi-trivial steady states is zero).*

Basically speaking, Proposition 5.5 says that under certain conditions, all positive steady states of system (4.5)–(4.8) are linearly stable (non-degenerate). This, together with Theorem 5.1, implies that if there is a locally stable positive steady state, then it must be unique and globally asymptotically stable.

Remark 5.6. We make some further comments on Proposition 5.5. The condition (H_2) suggests that the linear stability of all positive steady states holds for competitive R-D systems provided $bc \leqslant 1$ (consistent with [51]), and for competitive R-D-A systems provided $bc \leqslant \kappa_0$, where κ_0 is defined in (4.9) and is usually less than 1. Similar results (but by different argument) are obtained by Guo, He and Ni [44] for more general nonlinear terms (symmetric)

$$u[r_1(x) - b_1(x)u - c_1(x)v] \quad \text{and} \quad v[r_2(x) - b_2(x)u - c_2(x)v].$$

Recently, Zhou and Huang [137] further developed the argument to handle *non-symmetric* reaction terms like

$$u[r - mu - nv] \qquad \text{and} \qquad h(x) - puv - qv, \quad r, h, m, n, p, q > 0.$$

Based on these works [44, 51, 137, 138], we point out that one can develop such arguments to deal with very general nonlinear terms like

$$f(x, u, v) \qquad \text{and} \qquad g(x, u, v),$$

which behave essentially in a competition way (i.e., $f_v, g_u < 0$), but the upper bound of bc should be different depending on situations.

We next recall a convergence result of general linear cooperative elliptic systems due to Lam and Lou [75]. Consider

$$\begin{cases} D\mathbb{L}\phi + M\phi + \mu\phi = 0, & x \in \Omega, \\ \mathbb{B}\phi = 0, & x \in \partial\Omega, \end{cases} \tag{5.9}$$

where $D = \operatorname{diag}(d_1, \ldots, d_n)$ and $\mathbb{L} = \operatorname{diag}(L_1, \ldots, L_n)$ with d_i being a positive constant and L_i being a general second order elliptic operator, $i = 1, 2, \ldots, n$;

$M = \big(m_{ij}\big) \in \big(C(\overline{\Omega})\big)^{n\times n}$ is a matrix satisfying $m_{i,j} \geqslant 0$ in $\overline{\Omega}$ for $i \neq j$. The boundary operators $\mathbb{B} = (B_1, B_2, \ldots, B_n)$ satisfy for each i, either

$$B_i\phi_i = \frac{\partial \phi}{\partial \nu} + h_i(x)\phi \quad \text{on} \quad \partial\Omega \qquad \text{(Robin type)},$$

or

$$B_i\phi_i = \phi \quad \text{on} \quad \partial\Omega \qquad \text{(Dirichlet type)},$$

where $h_i(x) \geqslant 0$ and ν is the outward unit normal vector on $\partial\Omega$.

The existence of the principal eigenvalue (denoted by μ_1) of problem (5.9) can be found in [123]. See also [30] by using the maximum principle and [112] by using the semi-group theory. Moreover, by the Krein-Rutman theorem [70], the corresponding eigenfunction $\phi = (\phi_1, \ldots, \phi_n)$ can be chosen to satisfy $\phi_i \geqslant 0$ for all i. If, in addition, we assume $m_{ij} > 0$ in Ω for all $i \neq j$, then μ_1 is simple and is the unique eigenvalue having a strictly positive eigenfunction, namely, $\phi_i > 0$ in Ω for all i.

The following result is proved by Lam and Lou [75, Theorem 1.4].

Proposition 5.6. *Let $d_0 := \max_{1\leqslant i\leqslant n} d_i$. Then*

$$\lim_{d_0\to 0} \mu_1 = -\max_{x\in\overline{\Omega}} \bar{\mu}(M),$$

where $\bar{\mu}(M)$ denotes the eigenvalue of the matrix M with the greatest real part (guaranteed by Perron-Frobenius theorem [39]).

Proposition 5.6 improves a previous result given by Dancer [27], where all d_i $(i = 1, \ldots, n)$ tend to zero at the same rate.

Remark 5.7. From the side of application, Proposition 5.6 indicates that sometimes the dynamics of a two species competitive parabolic system with small diffusion can be determined by the corresponding kinetic system. For example, if an ODE system has a unique equilibrium which is globally asymptotically stable, then the same result holds for the corresponding parabolic system with small diffusion, see, e.g., [60, 75]. Relevant study on the non-autonomous version (time-periodic) of problem (5.9) can be found, e.g., in [4, 133].

5.4. Analytical approaches

In this subsection, we primarily introduce several arguments (see $\mathcal{M}_1$-$\mathcal{M}_3$ below) to prove the non-existence of any positive steady states for competitive R-D or R-D-A systems, that is, problem $\mathcal{P}_2$. Note that once having this in hand, in view of Theorem 5.1, very possibly the principle of competitive exclusion holds (but note that usually one also needs to confirm the linear instability of a semi-trivial steady state due to the counterexample given in [58]).

$\mathcal{M}_1$: monotonicity of the principal eigenvalue. We include below three examples to show this method.

Example 1.1. By using the increasing property of the principal eigenvalue in diffusion rate (see Proposition 5.1 (b)), Dockery et al. [34] proved that the following elliptic problem (with $r(x)$ non-constant)

$$\begin{cases} 0 = d_1 \triangle u + u[r(x) - u - v], & x \in \Omega, \\ 0 = d_2 \triangle v + v[r(x) - u - v], & x \in \Omega, \\ \dfrac{\partial u}{\partial \nu} = \dfrac{\partial v}{\partial \nu} = 0, & x \in \partial\Omega, \end{cases} \tag{5.10}$$

has no positive solutions, and obtained the conclusion "slower diffuser prevails" for the corresponding parabolic system.

Example 1.2. Using the monotonicity of the principal eigenvalue in advection rate (see Proposition 5.3 (e)), Xu and Gan [129] showed that for any $d, q_1, q_2 > 0$, $b \in [\frac{1}{2}, \infty]$ and bounded function $r(x)$, the following boundary value problem

$$\begin{cases} 0 = du_{xx} - q_1 u_x + u[r(x) - u - v], & x \in (0, L), \\ 0 = dv_{xx} - q_2 v_x + v[r(x) - u - v], & x \in (0, L), \\ du_x(t) - q_1 u(0) = dv_x(0) - q_2 v(0) = 0, \\ du_x(L) - q_1 u(L) = -bq_1 u(L), \\ dv_x(L) - q_2 v(L) = -bq_2 v(L), \end{cases} \tag{5.11}$$

has no positive solutions, and concluded "weak advection prevails" for the corresponding parabolic system.

Example 1.3. In fact, the argument in Example 1.2 can be extended to deal with a bit more general situation: For any $d_2 > d_1 > 0$ and $q_1, q_2 > 0$ with $q_2 \geqslant \frac{d_2}{d_1} q_1$, $b \in [\frac{1}{2}, \infty]$ and bounded function $r(x)$, the following problem

$$\begin{cases} 0 = d_1 u_{xx} - q_1 u_x + u[r(x) - u - v], & x \in (0, L), \\ 0 = d_2 v_{xx} - q_2 v_x + v[r(x) - u - v], & x \in (0, L), \\ d_1 u_x(t) - q_1 u(0) = d_2 v_x(0) - q_2 v(0) = 0, \\ d_1 u_x(L) - q_1 u(L) = -bq_1 u(L), \\ d_2 v_x(L) - q_2 v(L) = -bq_2 v(L), \end{cases} \tag{5.12}$$

has no positive solutions (note that here one needs to consider, first, the special case with (d_1, q_1) and $(d_2, \frac{d_2}{d_1} q_1)$ by using the concavity of the principal eigenvalue in the ratio $\frac{d_2}{d_1}$). As a further development, we exhibit below a more general result by applying the monotonicity result in Proposition 5.4. Consider

$$\begin{cases} 0 = d_1 \left[D(x) u_x\right]_x - \alpha_1 \left[B(x) u\right]_x + u\big[r(x) - u - v\big], & x \in (0, L), \\ 0 = d_2 \left[D(x) v_x\right]_x - \alpha_2 \left[B(x) v\right]_x + v\big[r(x) - u - v\big], & x \in (0, L), \\ d_1 D(x) u_x(x) - \alpha_1 B(x) u(x) = b_1 \alpha_1 B(x) u(x), & x = 0, \\ d_1 D(x) u_x(x) - \alpha_1 B(x) u(x) = -b_2 \alpha_1 B(x) u(x), & x = L, \\ d_2 D(x) v_x(x) - \alpha_2 B(x) v(x) = b_1 \alpha_2 B(x) v(x), & x = 0, \\ d_2 D(x) v_x(x) - \alpha_2 B(x) v(x) = -b_2 \alpha_2 B(x) v(x), & x = L. \end{cases} \tag{5.13}$$

Assume that (A_2) and (A_3) in Proposition 5.4 hold. Then for

$$d_2 > d_1 > 0, \ \alpha_2 \geqslant \sqrt{\frac{d_2}{d_1}} \alpha_1, \ (d_2 - d_1)^2 + (\alpha_2 - \sqrt{\frac{d_2}{d_1}} \alpha_1)^2 \neq 0,$$

Shao, Wang and Zhou [119] recently apply Proposition 5.4 to establish the non-existence of positive solutions of system (5.13). This result improves previous ones due to $\sqrt{\frac{d_2}{d_1}} < \frac{d_2}{d_1}$.

$\mathcal{M}_2$**: "AMOPR" property of the principal eigenvalue**. We present below two examples to show this method.

Example 2.1. By using the "AMOPR" property described in Proposition 5.3 (h), Lou and Lutscher [94] verified that for $d_1, d_2 > 0$ with $d_1 \neq d_2$ and $r_0 > 0$ (a constant), the following boundary value problem

$$\begin{cases} 0 = d_1 u_{xx} - q u_x + u[r_0 - u - v], \quad x \in (0, L), \\ 0 = d_2 v_{xx} - q v_x + v[r_0 - u - v], \quad x \in (0, L), \\ d_1 u_x(t) - q u(0) = d_2 v_x(0) - q v(0) = 0, \\ u_x(L) = v_x(L) = 0, \end{cases} \tag{5.14}$$

has no positive solutions, and found the phenomenon "faster diffuser prevails" for the corresponding parabolic system. Note that in this process, one also needs to make the a priori estimate $r_0 - u - v > 0$ for any possible positive solution (u, v) so that Proposition 5.3 (h) is available.

Example 2.2. The "AMOPR" properties described in Proposition 5.3 (i) and (j) have also been used to exclude the positive solutions of certain special cases of the stationary problem of system (4.4). We omit the details here and refer the interested readers to [85, 105, 124]. Again, in these proofs, one has to make some a priori estimates on the positive solution (u, v).

$\mathcal{M}_3$**: Technical argument**. We mainly take the following elliptic problem as an example

$$\begin{cases} d_1 u_{xx} - \alpha_1 u_x + u[r - u - v] = 0, \quad 0 < x < L, \\ d_2 v_{xx} - \alpha_2 v_x + v[r - u - v] = 0, \quad 0 < x < L, \\ d_1 u_x(0) - \alpha_1 u(0) = d_1 u_x(L) - \alpha_1 u(L) = 0, \\ d_2 v_x(0) - \alpha_2 v(0) = d_2 v_x(L) - \alpha_2 v(L) = 0. \end{cases} \tag{5.15}$$

If $r \equiv r_0$, a positive constant, system (5.15) has been systematically studied in [99, 101, 136], where the non-existence of positive solutions is established in different settings of d_i, α_i $(i = 1, 2)$. If $r = r(x)$ with $r'(x) \leqslant, \not\equiv 0$ in $[0, L]$, the same issue is addressed in [100, 135]. In these works, among other things, two fundamental observations turn to be extremely important and are frequently utilized in the proofs. See below.

The first one refers to two identities.

Lemma 5.1. *Assume that $d_1, d_2 > 0$, $\alpha_1, \alpha_2 \in \mathbb{R}$, and that (u, v) is a positive solution of system* (5.15). *Then for any two points $0 \leq y_1 \leq y_2 \leq L$, one has*

$$\begin{aligned} &\frac{1}{d_1} \int_{y_1}^{y_2} [d_1 - d_2] \cdot [v_x - \frac{\alpha_1 - \alpha_2}{d_1 - d_2} v] \cdot [d_1 u_x - \alpha_1 u] \cdot e^{-\frac{\alpha_1}{d_1} x} dx \\ =& \big\{ [d_1 u_x - \alpha_1 u] \cdot e^{-\frac{\alpha_1}{d_1} x} \cdot v \big\}\big|_{y_1}^{y_2} - \big\{ [d_2 v_x - \alpha_2 v] \cdot e^{-\frac{\alpha_1}{d_1} x} \cdot u \big\}\big|_{y_1}^{y_2}; \end{aligned}$$

and

$$\begin{aligned}&\frac{1}{d_2}\int_{y_1}^{y_2}[d_2-d_1]\cdot[u_x-\frac{\alpha_2-\alpha_1}{d_2-d_1}u]\cdot[d_2v_x-\alpha_2 v]\cdot e^{-\frac{\alpha_2}{d_2}x}dx\\ =&\big\{[d_2v_x-\alpha_2 v]\cdot e^{-\frac{\alpha_2}{d_2}x}\cdot u\big\}|_{y_1}^{y_2}-\big\{[d_1u_x-\alpha_1 u]\cdot e^{-\frac{\alpha_2}{d_2}x}\cdot v\big\}|_{y_1}^{y_2}.\end{aligned}$$

The second one is a maximum principle type result. Define

$$T:=\frac{u_x}{u}\quad\text{and}\quad S:=\frac{v_x}{v}.$$

Then one finds

$$\begin{cases}-d_1T_{xx}+[\alpha_1-2d_1T]T_x+uT+vS=r'(x), & 0<x<L,\\ -d_2S_{xx}+[\alpha_2-2d_2S]S_x+uT+vS=r'(x), & 0<x<L,\\ T(0)=T(L)=\dfrac{\alpha_1}{d_1}>0,\\ S(0)=S(L)=\dfrac{\alpha_2}{d_2}>0.\end{cases}$$

Lemma 5.2. *The following situations about T and S cannot occur*

(1) *T (resp. S) achieves a positive local maximum in (y_1,y_2) and $S\geq 0$ (resp. $T\geq 0$) in $[y_1,y_2]$;*

(2) *T (resp. S) achieves a negative local minimum in (y_1,y_2) and $S\leq 0$ (resp. $T\leq 0$) in $[y_1,y_2]$.*

where $[y_1,y_2]$ is any interval in $[0,L]$.

We remark here that the proof of each non-existence result in the above mentioned works [99–101,135,136] is technical, as it involves a lot of analysis. It should be pointed out that between the constant and non-constant case of r, there is big difference, e.g., for the non-constant case, the Cauchy-Kowalevski theory [68] cannot be used to guarantee the analyticity of solutions. We also mention here a series of works by Tang et al. [105,124,125] considering system (5.15) but with different boundary conditions, where, beside the use of Lemmas 5.1 and 5.2, the authors also introduced new ingredients in the argument, e.g., the "AMOPR" property of the principal eigenvalue mentioned in $\mathcal{M}_2$.

Remark 5.8. We make some comments on the above three different approaches.

(1) The monotonicity, in $\mathcal{M}_1$, is very rare. For diffusion-advection type operator, generally there is no such monotonicity result in the diffusion rate (see Remark 5.2). But once having such a monotonicity result (e.g., in the advection rate) in hand, it, when applied to certain competitive models, seems very powerful as, it not only determines the local stability of semi-trivial steady states, but also implies the non-existence of positive steady states.

(2) The "AMOPR" property in $\mathcal{M}_2$, to some extent, can be viewed as a weaker version of monotonicity in $\mathcal{M}_1$. It was firstly found by Lou and Lutscher [94] to be quite useful in the qualitative analysis of both semi-trivial and positive steady states.

(3) The argument in $\mathcal{M}_3$ is technical. The basic idea of Lemmas 5.1 and 5.2 originates from Lou and Zhou [101], and is later further developed by Zhou [136], where the proof of the non-existence results takes about 12 pages.

(4) We finally point out an interesting fact: the boundary loss rate b at $x = L$, in all examples in $\mathcal{M}_1$ and $\mathcal{M}_2$ (see problems (5.11), (5.12), (5.13) and (5.14)), satisfies $b \geqslant \frac{1}{2}$, and, as a complement, method $\mathcal{M}_3$ handles the homogeneous case with $b = 0$ in [99, 101, 136] and $b \in (0, 1]$ in [140], and the heterogeneous case with $b \in [0, \infty)$ in [100, 135].

6. Discussion

In this paper, we mainly give a review on the dynamics of competitive ODE, R-D and R-D-A systems, and for the latter two kinds of systems, we discuss in detail the main strategies and approaches to deal with such systems.

In the sequel, focusing on competitive R-D and R-D-A systems, we make some comments and propose several problems that may deserve future investigation.

(•) Generally speaking, for competitive R-D and R-D-A systems, there are two basic strategies to understand the population dynamics, namely, $\mathcal{S}_1$: the effect of movements (diffusion and/or advection); and $\mathcal{S}_2$: the effect of competition intensities (weak, strong-weak, and strong). Mathematically, $\mathcal{S}_1$ requires one to understand the dependence of the principal eigenvalue on diffusion and/or advection rates, while for $\mathcal{S}_2$, one needs to get a well understanding on the dependence of the principal eigenvalue on competition coefficients (usually included in the weight function).

(•) The strategy $\mathcal{S}_1$ has been successfully used in competitive R-D systems, which, to a large extent, is due to the monotonic property and limiting behaviors of the principal eigenvalue described in Proposition 5.1 (b). A good example to this point is that the general R-D system (3.2) has been understood in a deep way by He and Ni [51], where not only the local dynamics around $(\tilde{u}, 0)$ and $(0, \tilde{v})$ is described in certain abstract way in terms of d_1 and d_2, but also the global dynamics is completely classified according to the local dynamics. An interesting problem, as stated in Remark 5.1 (1), is to make further efforts to reveal the geometric property of the stable regions Σ_u and Σ_v so that one can see more clearly the global dynamics in d_1-d_2 plane. For this problem, following the ideas in [52, 53], one may consider some special cases of system (3.2) first.

In contrast, the strategy $\mathcal{S}_1$, if applied to competitive R-D-A systems, is not that successful, at least for the general R-D-A system (4.5)–(4.8). The main reason, from the viewpoint of operator theory, is that the diffusion-advection type operator is no longer self-adjoint and the dependence of the principal eigenvalue on diffusion or advection rate is not as clear as that of the self-adjoint case; see Remark 5.2 (1). For the general situation in (5.2), as seen from Proposition 5.2 (b) and (c), the limiting behaviors of the principal eigenvalue in the sense of small diffusion or large advection are clear, and hence, in application, the dynamics in the limiting sense (i.e., small diffusion or large advection) is possible to figure out; a typical example is the R-D-A model

(4.1), for which, in subsection 4.1, we have introduced many works focusing on the situation with strong advection as well as some others discussing "ESS" (which is also based on sort of limiting arguments, see, e.g., [76, 77]). For the special one dimensional situation in (5.4) (see also (5.7)), much richer qualitative behaviors of the principal eigenvalue are observed (see Propositions 5.3 and 5.4), and so, in application, it is more likely to reveal the population dynamics in a much bigger region of parameters including intermediate diffusion or advection; a good example is the river population model (4.4) given in subsection 4.2, where a lot of existing results are introduced. In a word, the strategy $\mathcal{S}_1$ has achieved more success in the one dimensional R-D-A models than those in the higher space dimension.

(•) Different from $\mathcal{S}_1$, the strategy $\mathcal{S}_2$ is efficient for both competitive R-D and R-D-A systems, since the monotonicity of the principal eigenvalue in the weight function always holds no matter whether there is advection term (see Proposition 5.1 (c) and Proposition 5.2 (d)). Indeed, as we saw in subsection 4.3, this monotonicity has been utilized by Zhou, Tang and Xiao [138] to treat both the general R-D system (3.2) and R-D-A system (4.5)–(4.8), and a completely clear understanding on the local dynamics of $(\tilde{u}, 0)$ and $(0, \tilde{v})$ in terms of competition coefficients b and c is obtained. Furthermore, the global dynamics is also determined in a big parameter region in b-c plane (see [138, Theorems 4 and 5]). In summary, the strategy $\mathcal{S}_2$, if compared with $\mathcal{S}_1$, can treat more general competitive systems, and also, the dynamics obtained by the strategy $\mathcal{S}_2$ is more clear in the plane of bifurcation parameters (note that Σ_u and Σ_v are completely clear in b-c plane, different from the counterpart in d_1-d_2 plane).

(•) We make some discussion on the definition of strong, weak, and strong-weak competition proposed in [138] (see also subsection 4.3). Denote by (p_1, p_2) the critical point distinguishing the weak, strong-weak, and strong competition. For the classical ODE system (2.1),

$$(p_1, p_2) = (\frac{r_1}{r_2}, \frac{r_2}{r_1}).$$

Following this manner, for the following parameterized ODE system

$$\begin{cases} u_t = u[r(x) - u - bv], & t > 0, \\ v_t = v[r(x) - cu - v], & t > 0, \\ u(0) = u_0 > 0, \ v(0) = v_0 > 0, \end{cases} \tag{6.1}$$

one has

$$(p_1, p_2) = (1, 1) = (\frac{r(x)}{r(x)}, \frac{r(x)}{r(x)}) \qquad (\text{note} \quad r_1 = r_2 = r(x)).$$

Consider further the following R-D system

$$\begin{cases} u_t = d_1 \triangle u + u[r(x) - u - bv], & x \in \Omega, \ t > 0, \\ v_t = d_2 \triangle v + v[r(x) - cu - v], & x \in \Omega, \ t > 0, \\ \dfrac{\partial u}{\partial \nu} = \dfrac{\partial v}{\partial \nu} = 0, & x \in \partial\Omega, \ t > 0, \\ u(x, 0) = u_0(x) \geq, \not\equiv 0, & x \in \Omega, \\ v(x, 0) = v_0(x) \geq, \not\equiv 0, & x \in \Omega. \end{cases} \tag{6.2}$$

What is (p_1,p_2) for system (6.2)? Is it still $(1,1)$ through a simply formal extension from system (6.1) to (6.2)? We think that one needs to think deeply how the numbers $\frac{r_1}{r_2}$ and $\frac{r_2}{r_1}$ are obtained or what roles these two numbers are playing for the ODE system (2.1). Indeed, one can check that $\frac{r_1}{r_2}$ and $\frac{r_2}{r_1}$ are the critical numbers which sharply govern the local stability of the two boundary equilibria $(0,r_2)$ and $(r_1,0)$, respectively. So a reasonable way is to explore such numbers for system (6.2). Without the loss of generality, one may assume $d_1>d_2>0$. Then by some simple analysis (see, e.g., [138, Proposition 1]), one can obtain two critical numbers denoted by b_1^* and c_1^* for system (6.2) (playing the same role as $\frac{r_1}{r_2}$ and $\frac{r_2}{r_1}$ for the ODE system (2.1)) but with

$$c_1^*>1>b_1^*>0 \quad \text{and} \quad b_1^*c_1^*>1. \tag{6.3}$$

Hence, for system (6.2),

$$(p_1,p_2)=(b_1^*,c_1^*), \qquad \text{not simply} \quad (1,1).$$

In a similar way, one can consider the following R-D-A system

$$\begin{cases} 0=d_1\Big(\triangle u-\alpha\mathrm{div}\big(u\nabla P(x)\big)\Big)+u[r(x)-u-bv], & x\in\Omega,\\ 0=d_2\Big(\triangle v-\alpha\mathrm{div}\big(v\nabla P(x)\big)\Big)+v[r(x)-cu-v], & x\in\Omega,\\ \dfrac{\partial u}{\partial\nu}-\alpha u\dfrac{\partial P(x)}{\partial\nu}=0, & x\in\partial\Omega,\\ \dfrac{\partial v}{\partial\nu}-\alpha v\dfrac{\partial P(x)}{\partial\nu}=0, & x\in\partial\Omega,\end{cases}$$

and establish a pair (b_2^*,c_2^*) playing the same role as $(\frac{r_1}{r_2},\frac{r_2}{r_1})$ and satisfying the property (6.3).

(•) If the above definition makes sense, there are several interesting problems that deserve further consideration: (i) In the weak competition case, there is always a unique positive equilibrium that is globally asymptotically stable for the ODE system (2.1), but in the same competition case, this is *partially* confirmed for both the R-D system (3.2) and R-D-A system (4.5)–(4.8), and there is still a parameter region (see $\mathcal{R}_8$ in [138, Figure 2]) for which the uniqueness of positive steady states is unsolved; and (ii) In the strong-weak competition case, the competitive exclusion always holds for the ODE system (2.1), but for the PDE systems (3.2) and (4.5)–(4.8), this is true for most parameters in the same competition case, with a bounded parameter region (see $\mathcal{R}_5^2$ and $\mathcal{R}_7^2$ in [138, Figure 2]) left as open. We suspect that there may appear quite different dynamics in $\mathcal{R}_5^2\cup\mathcal{R}_7^2$, e.g., multiple positive steady states or even the bistable phenomenon. If this were proved, it is a good example to show the striking differences between finite and infinite dimensional competition systems.

(•) For the general competitive R-D system (3.2), the estimate on the linear stability of positive steady states is established by He and Ni [51] under the condition $bc\leqslant 1$, while for the competitive R-D-A system (4.5)–(4.8), a sufficient condition $bc\leqslant\kappa_0$ with $\kappa_0\in(0,1]$ is given by Zhou, Tang and Xiao [138] (see a similar condition given by Guo, He and Ni [44]). In particular, $\kappa_0=1$ if advection is ignored. A natural question, as proposed in [44,138], is how to get an *optimal* criteria for such an estimate. This issue generally is challenging. We note here that for competitive R-D-A systems, the optimal number (if it exits) would not be greater than one (see an example given in [138]). Moreover, for competitive R-D-A systems, *numerically* it has been observed the bistable phenomenon for $b = c = 1$ [98,132] (see also [128,131] for general competition coefficients), and an interesting problem concerns whether one can construct a specific example to show the bistable structure.

We end this section by mentioning some works (but a few) on other types of competitive models: (i) competitive patch models (a system of ODEs) recently received considerable attention, see, e.g., Slavik [120] for symmetric connection matrix, Chen et al. [18] for general connection matrix (including the asymmetric case), and Jiang et al. [65,66] for the study in river networks (a discrete version of those models mentioned in subsection 4.2); (ii) competitive models with nonlocal dispersal (an integral operator) have been systematically studied in [6–8,84], and in particular, Bai and Li [7] considered a complex situation including both local and non-local operators and gave a sufficient condition for the classification of dynamics of such systems; (iii) diffusive competition systems involving time delay have been studied by Chen and Shi [19] where the effect of time delay on the global dynamics is examined; (iv) competitive phytoplankton models with integral reaction terms have been extensively studied in, e.g., [35,63,64,109], and in particular, an interesting cone is found in [64] to guarantee the monotonic property of such systems; (v) N-species competition models ($N \geqslant 3$) have not been studied extensively and the global dynamics of such systems is a highly challenging issue, see, e.g., [28,29,71,95] and some latest advances in [17]; (vi) we finally mention the recent works [86,114] in which the Lyapunov functional method is developed to treat the competition-diffusion models.

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