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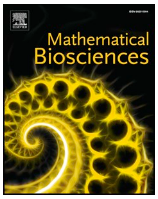

Coexistence and bistability of a competition model in open advective environments☆

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ABSTRACT

The community composition in open advective environments, where individuals are exposed to unidirectional flow, is formed by the complex interplays of hydrological and biological factors. We investigate the coexistence mechanism of species by a reaction-diffusion-advection competition model proposed by Lutscher et al. in [19]. It turns out that the locations of two critical curves, which separate the stable region of the semi-trivial solutions from the unstable one, determines whether coexistence or bistability happens. Furthermore, the analytical and numerical results suggest a tradeoff driven coexistence mechanism. More precisely, there is a tradeoff between the dispersal strategy and growth competence which allows the transition of competition outcomes, including competition exclusion, coexistence and bistability. This shifting may have an effect on the community composition in aquatic habitat.

1. Introduction

Many species, ranging from river-dwelling flora and fauna to gut-dwelling bacteria, live in environments with predominantly unidirectional flow, which induces a heavy bias in the dispersal of individuals such as algae, invertebrates and stream insects. The question of how populations resist washout and manage to maintain a foothold in such advective environments has been termed the "drift paradox" [6,24]. Inspired by the work of Speirs and Gurney [30], this question has received considerable attentions in the past few decades in theoretical spatial ecology (see [11,12,18,20–22,27,32]). One of the main insights from all these models is that there exists a threshold value for the flow speed separating population persistence from extinction (see e.g. [20,21,27,30]). An intuitive explanation for this result is that unbiased diffusive movements can balance biased advective movements and give rise to population persistence.

Another important question is how unidirectional flow influences the outcome of competition and community compositionin aquatic habitats, and specifically how it may mediate coexistence of two species (see [19,25,26,31,33,34]). This issue has been addressed by Lutscher et al. in [19], and a general two-species competition model for algal communities in rivers was developed there as follows:

$$\begin{cases} u_t = d_1 u_{xx} - \alpha u_x + u(r_1 - a_{11}u - a_{12}v), \\ v_t = d_2 v_{xx} - \beta v_x + v(r_2 - a_{21}u - a_{22}v) \end{cases} \tag{1.1}$$

for $x \in (0, L)$, $t > 0$, where $u(x, t)$ and $v(x, t)$ are the population densities of two competing species at time t and location x, respectively. d_i are the diffusion rates and α, β denote the effective advection rates caused by unidirectional flow. r_i account for the intrinsic growth rates, and a_{ij} measure the inter- and intra-specific competition, $i, j = 1, 2$. In this paper, $d_1, d_2, \alpha, \beta, r_1, r_2$ are constants.

Under the assumption that $d_1 = d_2$ and $\alpha = \beta$, which means that two species are adopting identical diffusive and advective movements, Lutscher et al. [19] demonstrated numerically that coexistence or competitive reversal induced by advection can be achieved via boundary effect or spatial heterogeneity. Imposing Danckwerts boundary conditions [1,33], Vasilyeva and Lutscher gave an analytical confirmation on these numerical results of [19] by using variational techniques as well as a spatially implicit approximation in [33]. They explored various tradeoffs between biological and hydrological

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parameters that allow species to invade and persist. Their results illustrate that transition between different competitive outcomes may occur with a change in flow speed, which implies the composition of river communities can change when flow speeds change. Moreover, competitive ability becomes less important as flow speed increases and intrinsic growth rate becomes more important in determining the competitive outcome. The effect of changes in flow speed on competition among multiple species has also been investigated in [31,34].

System (1.1) also serves as a model to study the biological invasion and evolution of dispersal in open advective environments. Starting with the work by Hastings [5], one robust prediction is that lower dispersal rate will be selected in temporally constant but spatially varying environments, provided that dispersal is unbiased [4]. In contrast, under the assumption that two species are identical except their diffusion rates, it is shown in [14] that unidirectional flow can put slow dispersers at a disadvantage and higher dispersal rate can evolve. It is also shown in [15] that slower advection wins ultimately if two species are identical except their advection rates. However, the combined effects of multiple factors, such as the combination of diffusion and advection [36,37], diffusion and boundary effect [17], advection and spatial heterogeneity [13,35], can result in complex dynamical behaviors and give rise to much richer phenomena including competition exclusion and coexistence. Although analytical results in [36,37] suggest that the strategy of faster diffusion combined with weaker advection is always favorable for species to win the competition, some intermediate diffusion rate may be selected as the loss at the downstream end increases [17] or as the result of spatial heterogeneity [13]. Furthermore, coexistence can happen in some scenarios, for instance, where faster diffusion goes along with strong advection [36], two species drift along opposite directions [37], or environmental heterogeneity is involved [35]. We refer to Lou and Coworkers [16,38,39] for more recent progress.

In the current paper we will focus on the joint influence of dispersal strategy and growth ability on the competition outcomes by investigating the following special model:

$$\begin{cases} u_t = d_1 u_{xx} - \alpha u_x + u(r_1 - u - v), \\ \qquad\qquad\qquad x \in (0,1),\ t > 0, \\ v_t = d_2 v_{xx} - \beta v_x + v(r_2 - u - v), \\ \qquad\qquad\qquad x \in (0,1),\ t > 0, \\ d_1 u_x(0,t) - \alpha u(0,t) = 0,\ t > 0, \\ u_x(1,t) = 0, \qquad t > 0, \\ d_2 v_x(0,t) - \beta v(0,t) = 0,\ t > 0, \\ v_x(1,t) = 0, \qquad t > 0, \\ u(x,0) = u_0(x) \geq , \neg \equiv 0,\ x \in (0,1), \\ v(x,0) = v_0(x) \geq , \neg \equiv 0,\ x \in (0,1). \end{cases} \tag{1.2}$$

Here we assume $L = 1$ for simplicity and neglect the impact of inter- and intra-specific competition between species due to the observation in [33] that competitive ability becomes less important than intrinsic growth rate in determining competitive outcome as flow speed increases. To this end, we first recall some existing results on the dynamics of the following single species models:

$$\begin{cases} u_t = d_1 u_{xx} - \alpha u_x + u(r_1 - u), \\ \qquad\qquad\qquad x \in (0,1),\ t > 0, \\ d_1 u_x(0,t) - \alpha u(0,t) = 0,\ t > 0, \\ u_x(1,t) = 0,\ t > 0, \\ u(x,0) = u_0(x) \geq , \neg \equiv 0,\ x \in (0,1), \end{cases} \tag{1.3}$$

and

$$\begin{cases} v_t = d_2 v_{xx} - \beta v_x + v(r_2 - v), \\ \qquad\qquad\qquad x \in (0,1),\ t > 0, \\ d_2 v_x(0,t) - \beta v(0,t) = 0,\ t > 0, \\ v_x(1,t) = 0, \quad t > 0, \\ v(x,0) = v_0(x) \geq , \neg \equiv 0, x \in (0,1). \end{cases} \tag{1.4}$$

Consider the linear eigenvalue problem

$$\begin{cases} d(\phi_1)_{xx} - \alpha(\phi_1)_x + r\phi_1 \\ \qquad = \lambda_1(d, r, \alpha)\phi_1,\ x \in (0,1), \\ d(\phi_1)_x(0) - \alpha\phi_1(0) = 0,\ (\phi_1)_x(1) = 0, \end{cases} \tag{1.5}$$

where d, r, α are constants with $d > 0$ and $\alpha \geq 0$. It is well known that (see, e.g., [3,10]) problem (1.5) admits a principal eigenvalue continuously depending on the parameters d, r, α, which is simple, and its corresponding eigenfunction, denoted by ϕ_1, can be chosen positive in $[0, 1]$. To emphasize the dependence of the principal eigenvalue on the parameters d, r, α, we denote it by $\lambda_1(d, r, \alpha)$. It follows from Lemma 2.2(b) of Lou and Zhou [17] that for $d_1, r_1 > 0$ fixed, there exists a unique critical value $\alpha_0 = \alpha_0(d_1, r_1) > 0$ such that

$$\begin{cases} \lambda_1(d_1, r_1, \alpha) > 0 \text{ if } 0 \leq \alpha < \alpha_0, \\ \lambda_1(d_1, r_1, \alpha) = 0 \text{ if } \alpha = \alpha_0, \\ \lambda_1(d_1, r_1, \alpha) < 0 \text{ if } \alpha > \alpha_0. \end{cases} \tag{1.6}$$

Similarly, for $d_2, r_2 > 0$ fixed, there exists a unique critical value $\beta_0 = \beta_0(d_2, r_2) > 0$ such that

$$\begin{cases} \lambda_1(d_2, r_2, \beta) > 0 \text{ if } 0 \leq \beta < \beta_0, \\ \lambda_1(d_2, r_2, \beta) = 0 \text{ if } \beta = \beta_0, \\ \lambda_1(d_2, r_2, \beta) < 0 \text{ if } \beta > \beta_0. \end{cases} \tag{1.7}$$

Here $\lambda_1(d_1, r_1, \alpha)$ and $\lambda_1(d_2, r_2, \beta)$ are the principal eigenvalues of the problem (1.5) with d, r, α replaced by d_1, r_1, α and d_2, r_2, β respectively.

Now we are ready to state the results on the single population models. It follows from Theorem 2.1(b) in [17] (see also Section 3.2.3 of the monograph of [2]) that the following results hold.

Lemma 1.1. *Suppose $d_1, d_2 > 0$ fixed. Let $\alpha_0(d_1, r_1), \beta_0(d_2, r_2)$ be uniquely determined by (1.6) and (1.7) respectively.*

- (i) *There exists a unique positive steady state of (1.3) (denoted by θ_α), which is globally asymptotically stable among all nonnegative and nontrivial initial conditions provided that $0 \leq \alpha < \alpha_0$, and $u = 0$ is globally asymptotically stable among all nonnegative and nontrivial initial conditions provided that $\alpha \geq \alpha_0$;*
- (ii) *There exists a unique positive steady state of (1.4) (denoted by ϑ_β), which is globally asymptotically stable among all nonnegative and nontrivial initial conditions provided that $0 \leq \beta < \beta_0$, and $v = 0$ is globally asymptotically stable among all nonnegative and nontrivial initial conditions provided that $\beta \geq \beta_0$.*

It follows from Lemma 1.1 that for $0 \leq \alpha < \alpha_0$ and $0 \leq \beta < \beta_0$, (1.2) has two semitrivial steady state solutions $(\theta_\alpha, 0)$ and $(0, \vartheta_\beta)$. As (1.2) can be cast into a strongly monotone dymical system (see [7–9,23,29]), its global dynamics is related to the semi-trivial equilibria and their stability. Indeed, the global dynamics of system (1.2) with $r_1 = r_2$ has been investigated by Zhou and Zhao in [36]. We recall their main results in the following theorem:

Theorem 1.1. *[36] Assume that $0 < d_1 < d_2$ and $r_1 = r_2 = r > 0$. Then*

- *$(0, 0)$ is globally asymptotically stable among all nonnegative and nontrivial initial conditions provided that $\alpha \geq \alpha_0, \beta \geq \beta_0$ (i.e. the white region in Fig. 1);*
- *$(\theta_\alpha, 0)$ is globally asymptotically stable among all nonnegative and nontrivial initial conditions provided that $\beta \geq \beta_0,\ 0 \leq \alpha < \alpha_0$ or $0 < \beta < \beta_0, 0 \leq \alpha \leq \frac{d_1}{d_2}\beta$ (i.e. the blue and red regions in Fig. 1);*
- *$(0, \vartheta_\beta)$ is globally asymptotically stable among all nonnegative and nontrivial initial conditions provided that $\alpha \geq \alpha_0,\ 0 \leq \beta < \beta_0$ or $0 < \alpha \leq \alpha_0, 0 \leq \beta \leq \alpha$ (i.e. the yellow and green regions in Fig. 1).*

When the advection rates α, β lie in the grey region of Fig. 1, the authors have also shown that for some $\alpha \in (\frac{d_1}{d_2}\beta, \beta)$, a positive steady state exists (see Lemma 6.2 of [36]). However, the stability of two

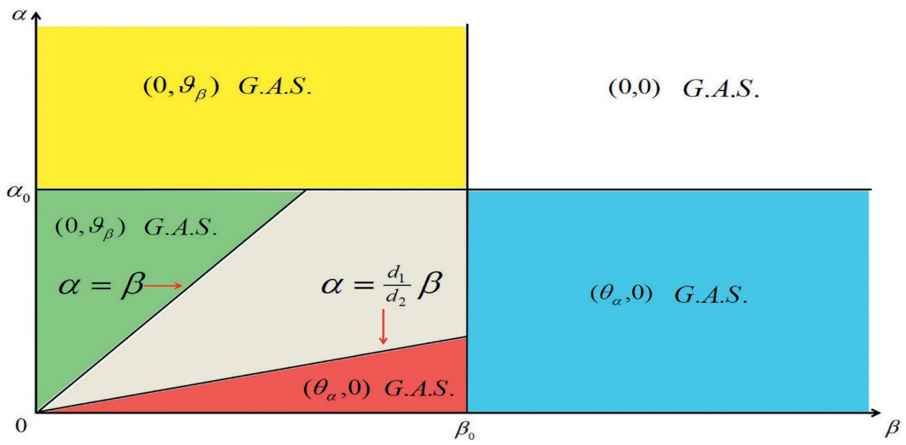


Fig. 1. The global dynamics of system (1.2) with $0 < d_1 < d_2$, $r_1 = r_2$ fixed in $\beta - \alpha$ plane. More precisely, (0, 0) is globally asymptotically stable in the white region; $(\theta_\alpha, 0)$ is globally asymptotically stable in the blue and red regions; $(0, \vartheta_\beta)$ is globally asymptotically stable in the yellow and green regions; there may be a positive steady state when the advection rates α, β lie in the grey region. Note that $0 < d_1 < d_2$, $r_1 = r_2$ implies $\frac{d_1}{d_2} < \frac{\alpha_0}{\beta_0} < 1$ by Lemma 5.3 below. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

semitrivial equilibria and the global dynamics of system (1.2) are still not quite clear, even if $r_1 = r_2$.

Biologically, the global stability of $(0, \vartheta_\beta)$ in the green region of Fig. 1 indicates that the movement strategy of faster diffusion together with weaker advection has more competitive advantages. That is, unidirectional flow can put the species with slower diffusion and faster advection at a disadvantage and the faster diffusion together with weaker advection rate can evolve. This interesting phenomenon has also been discovered in [14,37]. However, for the strategy of both faster diffusion and advection, lower ratio of advection and diffusion always wins as demonstrated in the red region (see [36,37]). These interesting outcomes illustrate that there is a tradeoff between diffusion and advection, which affects the competition between species in open advective environments.

As observed above, both the population persistence and competition outcomes depend on their diffusion rates, advection rates, as well as intrinsic growth rates. We further investigate the combined effects of diffusion, advection and intrinsic growth rates on the competition results of two aquatic species in open advective environments. It turns out that the interactions of these factors bring much richer dynamical phenomena, including competition exclusion, coexistence and, in addition, bistability (see Figs. 2 and 3).

Arguments similar to those used in [36] show that Theorem 1.1 still holds when $r_1 \neq r_2$ and α, β are located in the white, blue and yellow regions in Fig. 1 with minor modification of α_0, β_0. As mentioned before, α_0 and β_0 are dependent on the parameters d_1, r_1 and d_2, r_2 respectively. Hence, we only need to study the case of $0 \le \alpha < \alpha_0$, $0 \le \beta < \beta_0$. By symmetry, we always assume the species u has a slower diffusion rate throughout this paper, that is, $d_1 < d_2$. As described in Figs. 2 and 3, the results indicate that there exist two critical increasing curves in the $\beta - \alpha$ plane, which separate the stable regions of the semitrivial solutions $(\theta_\alpha, 0)$ and $(0, \vartheta_\beta)$ from the unstable regions. In what follows, the critical curves $\beta^*(\alpha)$, $\beta^{**}(\alpha)$ and $\alpha^*(\beta)$, $\alpha^{**}(\beta)$ are uniquely determined by Lemmas 2.4 and 2.5 and Lemmas 2.7 and 2.8, respectively.

Theorem 1.2. *Suppose* $0 < d_1 < d_2$ *and* $0 < r_1 \le r_2$ *fixed. Then for* $0 \le \alpha \le \alpha_0$, *there exist* $\beta^*(\alpha)$ *and* $\beta^{**}(\alpha)$ *satisfying* $\alpha \le \beta^*(\alpha)$, $\beta^{**}(\alpha) \le \beta_0$ *such that*

- (i) *if* $0 \le \beta < \min\{\beta^*(\alpha), \beta^{**}(\alpha)\}$, *then* $(\theta_\alpha, 0)$ *is unstable and* $(0, \vartheta_\beta)$ *is stable;*
- (ii) *if* $\max\{\beta^*(\alpha), \beta^{**}(\alpha)\} < \beta < \beta_0$, *then* $(\theta_\alpha, 0)$ *is stable and* $(0, \vartheta_\beta)$ *is unstable;*
- (iii) *if* $\beta^*(\alpha) < \beta < \beta^{**}(\alpha)$, *then both* $(\theta_\alpha, 0)$ *and* $(0, \vartheta_\beta)$ *are stable;*
- (iv) *if* $\beta^{**}(\alpha) < \beta < \beta^*(\alpha)$, *then* $(\theta_\alpha, 0)$ *and* $(0, \vartheta_\beta)$ *are unstable.*

Theorem 1.3. *Suppose* $0 < d_1 < d_2$ *and* $r_1 > r_2 > 0$ *fixed. Then for* $0 \le \beta \le \beta_0$, *there exist* $\alpha^*(\beta)$ *and* $\alpha^{**}(\beta)$ *satisfying* $0 < \alpha^*(\beta)$, $\alpha^{**}(\beta) \le \alpha_0$ *such that*

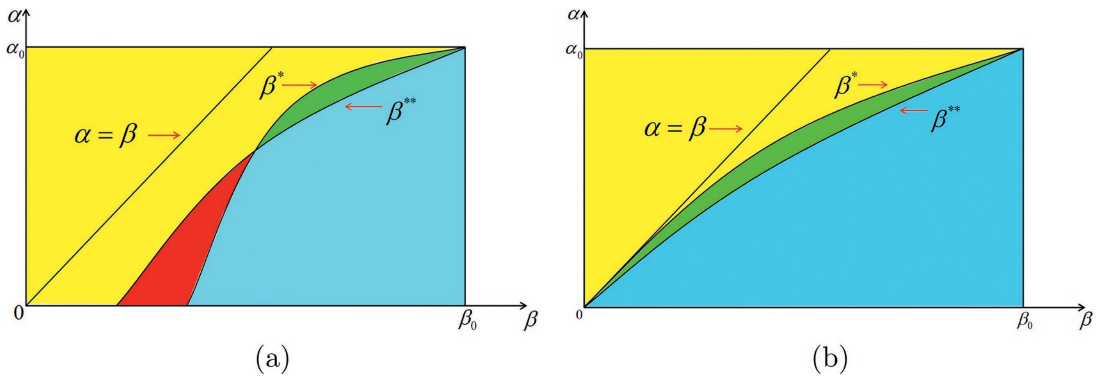
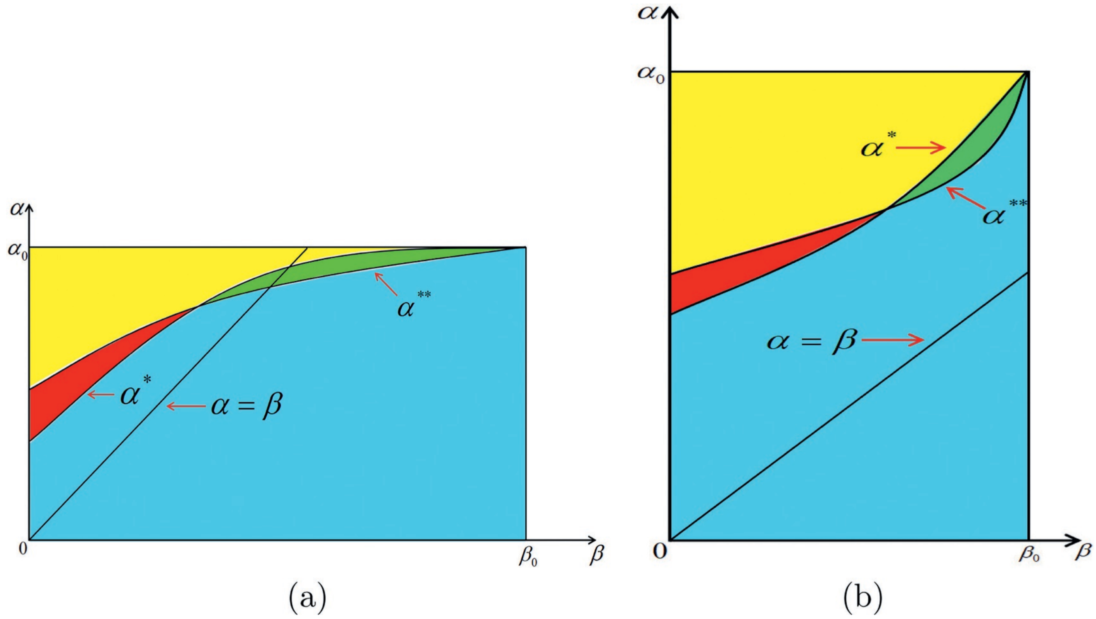


Fig. 2. The stability of the semi-trivial equilibria $(\theta_\alpha, 0)$ and $(0, \vartheta_\beta)$ of (1.2) in $\beta - \alpha$ plane with $d_1 < d_2$, $r_1 < r_2$ in (a) and $d_1 < d_2$, $r_1 = r_2$ in (b) (see Theorem 1.2). More precisely, $(\theta_\alpha, 0)$ is stable and $(0, \vartheta_\beta)$ is unstable in the blue region; $(\theta_\alpha, 0)$ is unstable and $(0, \vartheta_\beta)$ is stable in the yellow region; $(\theta_\alpha, 0)$ and $(0, \vartheta_\beta)$ are bistable in the green region; both $(\theta_\alpha, 0)$ and $(0, \vartheta_\beta)$ are unstable in the red region. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



(a)

(b)

Fig. 3. Illustration of the stability of the semi-trivial equilibria $(\theta_\alpha, 0)$ and $(0, \vartheta_\beta)$ of (1.2) in $\beta-\alpha$ plane with $d_1 < d_2$, $r_1 > r_2$ (see Theorem 1.3). $\alpha_0 < \beta_0$ in (a), and $\alpha_0 > \beta_0$ in (b). As above, $(\theta_\alpha, 0)$ is stable and $(0, \vartheta_\beta)$ is unstable in the blue region; $(\theta_\alpha, 0)$ is unstable and $(0, \vartheta_\beta)$ is stable in the yellow region; $(\theta_\alpha, 0)$ and $(0, \vartheta_\beta)$ are both stable in the green region; both $(\theta_\alpha, 0)$ and $(0, \vartheta_\beta)$ are unstable in the red region. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(i) *if* $0 \le \alpha < \min\{\alpha^*(\beta), \alpha^{**}(\beta)\}$, *then* $(\theta_\alpha, 0)$ *is stable and* $(0, \vartheta_\beta)$ *is unstable;*

(ii) *if* $\max\{\alpha^*(\beta), \alpha^{**}(\beta)\} < \alpha < \alpha_0$, *then* $(\theta_\alpha, 0)$ *is unstable and* $(0, \vartheta_\beta)$ *is stable;*

(iii) *if* $\alpha^{**}(\beta) < \alpha < \alpha^*(\beta)$, *then* $(\theta_\alpha, 0)$ *and* $(0, \vartheta_\beta)$ *are stable;*

(iv) *if* $\alpha^*(\beta) < \alpha < \alpha^{**}(\beta)$, *then both* $(\theta_\alpha, 0)$ *and* $(0, \vartheta_\beta)$ *are unstable.*

Theorems 1.2and 1.3 provide a picture on the stability of the semitrivial steady states $(\theta_\alpha, 0)$ and $(0, \vartheta_\beta)$ in $\beta-\alpha$ plane when two species have different dispersal strategy and intrinsic growth rates (see Figs. 2 and 3). By the theory of the monotone dynamical system, we have the following results for coexistence and bistability of system (1.2):

Corollary 1.4. *Suppose* $0 < d_1 < d_2$ *and* $0 < r_1 \le r_2$ *fixed.*

(i) *If* $\beta^{**}(\alpha) < \beta < \beta^*(\alpha)$, *then the two semitrivial solutions* $(\theta_\alpha, 0)$ *and* $(0, \vartheta_\beta)$ *are unstable, and system (1.2) has a locally stable coexistence steady state;*

(ii) *If* $\beta^*(\alpha) < \beta < \beta^{**}(\alpha)$, *then* $(\theta_\alpha, 0)$ *and* $(0, \vartheta_\beta)$ *are both stable, and system (1.2) has at least one unstable positive steady state.*

Corollary 1.5. *Suppose* $0 < d_1 < d_2$ *and* $r_1 > r_2 > 0$ *fixed.*

(i) *If* $\alpha^*(\beta) < \alpha < \alpha^{**}(\beta)$, *then the two semitrivial solutions* $(\theta_\alpha, 0)$ *and* $(0, \vartheta_\beta)$ *are unstable, and system (1.2) has a locally stable coexistence steady state;*

(ii) *If* $\alpha^{**}(\beta) < \alpha < \alpha^*(\beta)$, *then* $(\theta_\alpha, 0)$ *and* $(0, \vartheta_\beta)$ *are both stable, and system (1.2) has at least one unstable positive steady state.*

The results above indicate that the sizes of two critical curves determines whether coexistence or bistability happens. Nevertheless, if $d_1 = d_2$, $r_1 = r_2$, it follows from the proof of Lemma 2.4 that both $\beta^*(\alpha)$ and $\beta^{**}(\alpha)$ coincide exactly with the curve $\alpha = \beta$ which implies only competition exclusion can occur for two almost identical species except their advection rates (see also [15]). Furthermore, the study in [15] indicates that the weaker advection may evolve in this case. Meanwhile, the results in [14] show that faster diffusion rate should be selected when two species are identical except their random diffusion rates. In view of (5.12) (see Appendix 5.2), similar arguments as in [14,15] suggest that the larger intrinsic growth rate is always beneficial for species to win the competition when two species are identical except their intrinsic growth rates. That is, both coexistence and bistability are impossible for species with only one different trait. A large number of numerical simulations in the subsequent section illustrate the tradeoff driven coexistence mechanism, which means that the tradeoff between different traits of species can drive coexistence of species (see Figs. 5–7).

The rest of this paper is organized as follows. The goal of Section 2 is to establish the stability of semi-trivial steady states and to deduce the main results. In Section 3, we calculate the locations of two critical curves numerically and determine when coexistence or bistability happens. The conclusions are discussed in Section 4. The proofs for the stability of semitrivial solutions are given in Appendix.

2. The stability of semi-trivial solutions

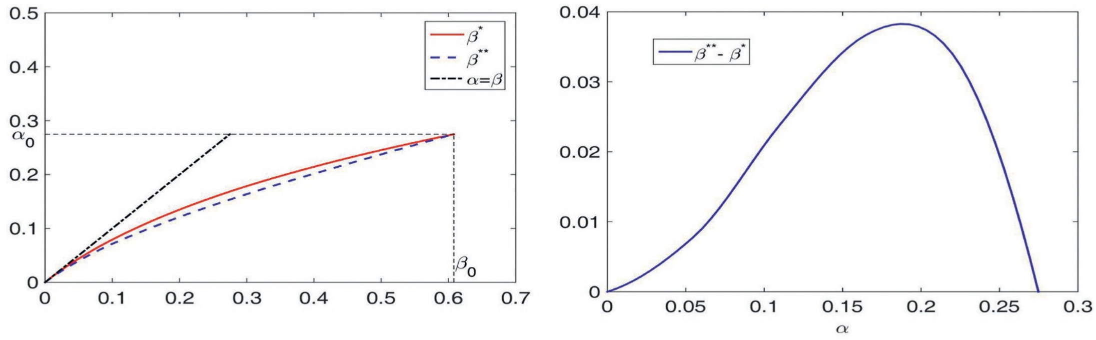
The goal of this section is to investigate the stability of the semi-trivial steady states $(\theta_\alpha, 0)$ and $(0, \vartheta_\beta)$, and to prove Theorems 1.2 and 1.3. To this end, we linearize the corresponding steady state system of (1.2) at $(\theta_\alpha, 0)$ and $(0, \vartheta_\beta)$ with respect to (u, v), and obtain the following two eigenvalue problems

$$\begin{cases} d_2\psi_{xx} - \beta\psi_x + (r_2 - \theta_\alpha)\psi = \mu\psi, \ x \in (0,1), \\ d_2\psi_x(0) - \beta\psi(0) = 0, \ \psi_x(1) = 0 \end{cases} \tag{2.1}$$

and

$$\begin{cases} d_1\varphi_{xx} - \alpha\varphi_x + (r_1 - \vartheta_\beta)\varphi = \sigma\varphi, \ x \in (0,1), \\ d_1\varphi_x(0) - \alpha\varphi(0) = 0, \ \varphi_x(1) = 0. \end{cases} \tag{2.2}$$

Denote by (μ_1, ψ_1) and (σ_1, φ_1) the first pair of eigenvalue-eigenfunction of problems (2.1) and (2.2), respectively. It follows from Lemma 5.1 (see Appendix 5.1) that both μ_1 and σ_1 are simple, and their corresponding eigenfunctions ψ_1 and φ_1 can be chosen strictly positive on [0, 1]. Moreover, the linear stability of $(\theta_\alpha, 0)$ and $(0, \vartheta_\beta)$ can be determined by the signs of μ_1 and σ_1 respectively. More precisely, $(\theta_\alpha, 0)$ is stable if $\mu_1 < 0$ and unstable if $\mu_1 > 0$, and $(0, \vartheta_\beta)$ is stable if $\sigma_1 < 0$ and unstable if $\sigma_1 > 0$. By virtue of Lemma 5.4 (see Appendix 5.1), one can



(a) (b)

Fig. 4. The diagrams of the critical curves $\beta^*(\alpha)$ and $\beta^{**}(\alpha)$ in $\beta-\alpha$ plane with $d_1 = 0.25$ m^2/s, $d_2 = 2$ m^2/s, $r_1 = r_2 = 1$ day^{-1}. By computation, $\alpha_0 = 0.2748$ km/day and $\beta_0 = 0.6081$ km/day. The difference between $\beta^*(\alpha)$ and $\beta^{**}(\alpha)$ is plotted in (b) versus the advection rate α.

conclude that the two principal eigevalues are continuously dependent on the advection coefficients α, β. To emphasize the dependence of the principal eigenvalues on the parameters α and β, we denote them by $\mu_1(\alpha, \beta)$ and $\sigma_1(\alpha, \beta)$.

We first study the properties of the principal eigenvalue $\mu_1(\alpha, \beta)$. The proofs of the following lemmas are given in Appendix 5.2.

Lemma 2.1. *Suppose $d_1, d_2 > 0$ fixed, and $\alpha, \beta \geq 0$. Then*

(i) *$\mu_1(\alpha, \beta)$ is strictly increasing with respect to α in $[0, \alpha_0)$;*
(ii) *$\mu_1(\alpha, \beta)$ is strictly decreasing with respect to β in $[0, +\infty)$.*

Lemma 2.2. *Suppose $d_1, d_2 > 0$ fixed, and $\alpha, \beta \geq 0$. Then*

(i) *$\mu_1(0, 0) = r_2 - r_1$, $\mu_1(\alpha_0, \beta_0) = 0$, $\mu_1(\alpha_0, 0) = r_2$, $\mu_1(0, \beta_0) = -r_1$;*
(ii) *$\mu_1(\alpha_0, \beta) > 0$ for $0 \leq \beta < \beta_0$, and $\mu_1(\alpha, \beta_0) < 0$ for $0 \leq \alpha < \alpha_0$;*
(iii) *if $r_1 \leq r_2$, then $\mu_1(\alpha, 0) > 0$ for $0 < \alpha \leq \alpha_0$; if $r_1 > r_2$, then $\mu_1(0, \beta) < 0$ for $0 \leq \beta \leq \beta_0$.*

Lemma 2.3. *Suppose $d_1, d_2 > 0$ and $\alpha, \beta \geq 0$.*

(i) *If $d_1 < d_2$, $\alpha \geq \beta$, then $\mu_1(\alpha, \beta) \geq r_2 - r_1$, and if $d_1 \geq d_2$, $\alpha \leq \beta$, then $\mu_1(\alpha, \beta) \leq r_2 - r_1$;*
(ii) *If $0 < \alpha < \alpha_0$, then $\mu_1(\alpha, \alpha) > r_2 - r_1$ provided $d_1 < d_2$, $\mu_1(\alpha, \alpha) = r_2 - r_1$ provided $d_1 = d_2$, and $\mu_1(\alpha, \alpha) < r_2 - r_1$ provided $d_1 > d_2$.*

By Lemmas 2.1–2.3, we can prove the following two lemmas.

Lemma 2.4. *Suppose $0 < d_1 < d_2$ and $0 < r_1 \leq r_2$ fixed. Then for $0 \leq \alpha \leq \alpha_0$, there exists $\beta^*(\alpha)$ satisfying that $\alpha \leq \beta^*(\alpha) \leq \beta_0$, and*

(i) *$(\theta_\alpha, 0)$ is stable if $\beta > \beta^*(\alpha)$, and unstable if $0 \leq \beta < \beta^*(\alpha)$, where $\beta^*(\alpha)$ is uniquely determined by $\mu_1(\alpha, \beta^*(\alpha)) = 0$;*
(ii) *the function $\beta^*(\alpha)$ is strictly increasing with respect to α on $[0, \alpha_0]$ with $\beta^*(\alpha_0) = \beta_0$.*

Lemma 2.5. *Suppose $0 < d_1 < d_2$ and $r_1 > r_2 > 0$ fixed. Then for $0 \leq \beta \leq \beta_0$, there exists $\alpha^*(\beta) \in (0, \alpha_0]$ such that*

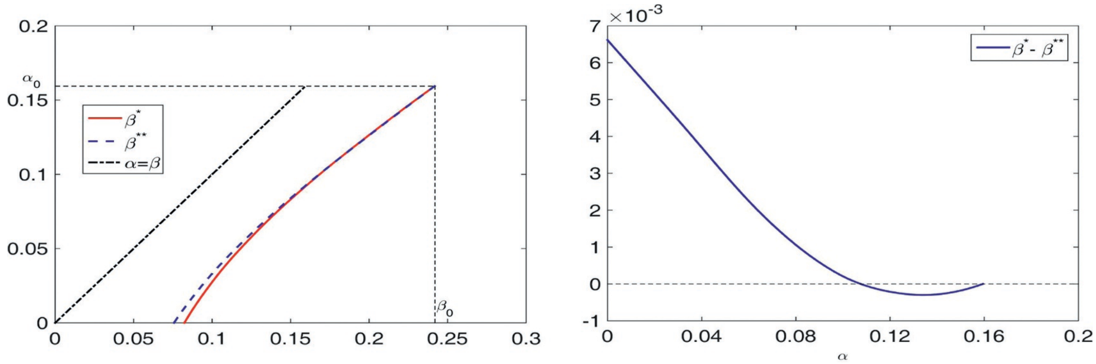
(i) *$(\theta_\alpha, 0)$ is stable if $0 \leq \alpha < \alpha^*(\beta)$, and unstable if $\alpha^*(\beta) < \alpha < \alpha_0$, where $\alpha^*(\beta)$ is uniquely determined by $\mu_1(\alpha^*(\beta), \beta) = 0$;*
(ii) *the function $\alpha^*(\beta)$ is strictly increasing with respect to β on $[0, \beta_0]$ with $\alpha^*(\beta_0) = \alpha_0$.*

Repeating the similar arguments as in Lemmas 2.1–2.3, we can find that the principal eigenvalue $\sigma_1(\alpha, \beta)$ has the following properties.

Lemma 2.6. *Suppose $d_1, d_2 > 0$ fixed, and $\alpha, \beta \geq 0$. Then*

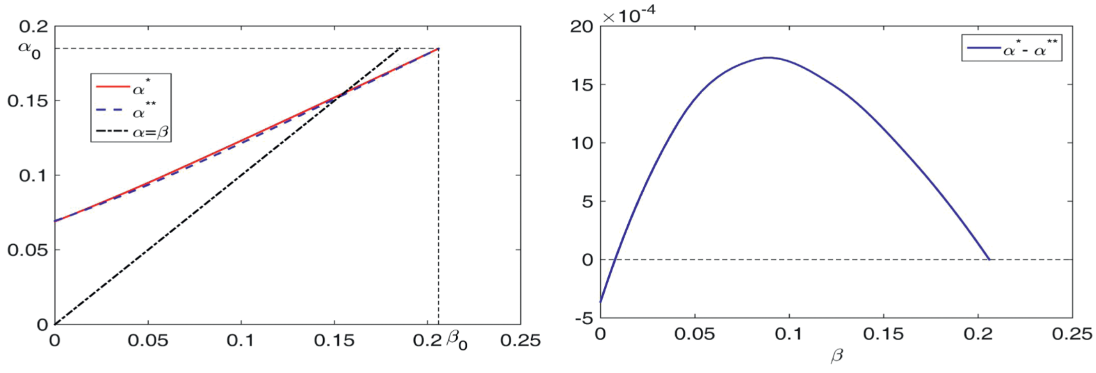
(i) *$\sigma_1(\alpha, \beta)$ is strictly decreasing with respect to α in $[0, +\infty)$;*
(ii) *$\sigma_1(\alpha, \beta)$ is strictly increasing with respect to β in $[0, \beta_0)$;*
(iii) *$\sigma_1(0, 0) = r_1 - r_2$, $\sigma_1(\alpha_0, \beta_0) = 0$, $\sigma_1(\alpha_0, 0) = -r_2$, $\sigma_1(0, \beta_0) = r_1$;*
(iv) *$\sigma_1(\alpha_0, \beta) < 0$ for $0 \leq \beta < \beta_0$, and $\sigma_1(\alpha, \beta_0) > 0$ for $0 \leq \alpha < \alpha_0$;*
(v) *if $r_1 \leq r_2$, then $\sigma_1(\alpha, 0) < 0$ for $0 < \alpha \leq \alpha_0$; if $r_1 > r_2$, then $\sigma_1(0, \beta) > 0$ for $0 \leq \beta \leq \beta_0$;*
(vi) *if $d_1 < d_2$, $\alpha \geq \beta$, then $\sigma_1(\alpha, \beta) \leq r_1 - r_2$, and if $d_1 \geq d_2$, $\alpha \leq \beta$, then $\sigma_1(\alpha, \beta) \geq r_1 - r_2$;*
(vii) *if $0 < \alpha < \alpha_0$, then $\sigma_1(\alpha, \alpha) < r_1 - r_2$ provided $d_1 < d_2$, $\sigma_1(\alpha, \alpha) = r_1 - r_2$ provided $d_1 = d_2$, and $\sigma_1(\alpha, \alpha) > r_1 - r_2$ provided $d_1 > d_2$.*

With the aid of Lemma 2.6, similar arguments as in Lemmas 2.4 and 2.5 indicate that there exists a strictly increasing curve in the plane



(a) (b)

Fig. 5. The diagrams of the critical curves $\beta^*(\alpha)$ and $\beta^{**}(\alpha)$ in $\beta-\alpha$ plane with $d_1 = 0.25$ m^2/s, $d_2 = 0.5$ m^2/s, $r_1 = 0.39$ day^{-1}, $r_2 = 0.5$ day^{-1}. By computation, $\alpha_0 = 0.1594$ km/day and $\beta_0 = 0.2419$ km/day. The difference between $\beta^*(\alpha)$ and $\beta^{**}(\alpha)$ is plotted in (b) versus the advection rate α.



(a) (b)

Fig. 6. The diagrams of the critical curves $\alpha^*(\beta)$ and $\alpha^{**}(\beta)$ in $\beta - \alpha$ plane with $d_1 = 0.25$ m^2/s, $d_2 = 0.5$ m^2/s, $r_1 = 0.5$ day^{-1}, $r_2 = 0.39$ day^{-1}. By computation, $\alpha_0 = 0.1850$ km/day and $\beta_0 = 0.2059$ km/day. The difference between $\alpha^*(\beta)$ and $\alpha^{**}(\beta)$ is plotted in (b) versus the advection rate β.

$\beta - \alpha$, which separates the stable region of the semi-trivial solution $(0, \vartheta_\beta)$ from the unstable one. The results are illustrated in the following two lemmas.

Lemma 2.7. *Suppose* $0 < d_1 < d_2$ *and* $0 < r_1 \le r_2$ *fixed. Then for* $0 \le \alpha \le \alpha_0$, *there exists* $\beta^{**}(\alpha)$ *such that* $\alpha \le \beta^{**}(\alpha) \le \beta_0$, *and*

(i) $(0, \vartheta_\beta)$ *is unstable if* $\beta^{**}(\alpha) < \beta < \beta_0$, *and stable if* $0 \le \beta < \beta^{**}(\alpha)$, *where* $\beta^{**}(\alpha)$ *is uniquely determined by* $\sigma_1(\alpha, \beta^{**}(\alpha)) = 0$.

(ii) *the function* $\beta^{**}(\alpha)$ *is strictly increasing with respect to* α *on* $[0, \alpha_0]$ *with* $\beta^{**}(\alpha_0) = \beta_0$.

Lemma 2.8. *Suppose* $0 < d_1 < d_2$ *and* $r_1 > r_2 > 0$ *fixed. Then for* $0 \le \beta \le \beta_0$, *there exists* $\alpha^{**}(\beta)$ *such that* $0 < \alpha^{**}(\beta) \le \alpha_0$, *and*

(i) $(0, \vartheta_\beta)$ *is unstable if* $0 \le \alpha < \alpha^{**}(\beta)$, *and stable if* $\alpha^{**}(\beta) < \alpha < \alpha_0$, *where* $\alpha^{**}(\beta)$ *is uniquely determined by* $\mu_1(\alpha^{**}(\beta), \beta) = 0$.

(ii) *the function* $\alpha^{**}(\beta)$ *is strictly increasing with respect to* β *on* $[0, \beta_0]$ *with* $\alpha^{**}(\beta_0) = \alpha_0$.

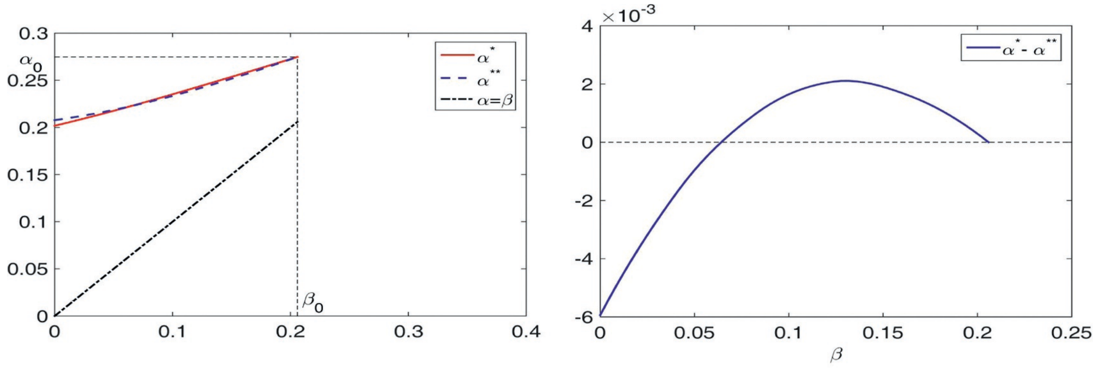
Remark 2.1. It is easy to see that Theorems 1.2 and 1.3 can be derived directly by Lemmas 2.4–2.5 and 2.7–2.8 repectively. As shown in Figs. 2–3, Theorems 1.2 and 1.3 provide us a clear picture on the stability of the semitrivial steady states $(\theta_\alpha, 0)$ and $(0, \vartheta_\beta)$. Moreover, coexistence of two species happens when $\beta^{**}(\alpha) < \beta^*(\alpha)$ or $\alpha^*(\beta) < \alpha^{**}(\beta)$, and bistability occurs when $\beta^*(\alpha) < \beta^{**}(\alpha)$ or $\alpha^{**}(\beta) < \alpha^*(\beta)$. However, we only determine the signs of $\beta^*(\alpha) - \beta^{**}(\alpha)$ and $\alpha^*(\beta) - \alpha^{**}(\beta)$ mathematically in some special cases (see Proposition 2.9). In fact, our numerical simulations demonstrate that both $\beta^*(\alpha) - \beta^{**}(\alpha)$ and $\alpha^*(\beta) - \alpha^{**}(\beta)$ could change sign when two species have different dispersal strategy and intrinsic growth rates. These numerical simulation results indicate that both coexistence and bistability can occur in advective environments.

Proposition 2.9. *Suppose* $0 < r_1 < r_2$ *fixed. There exist positive constants* M *large and* δ *small such that* $\beta^*(\alpha) < \beta^{**}(\alpha)$ *for* $0 < d_1 < \delta$, $d_2 > M$ *and* $0 < \alpha < \delta$.

Remark 2.2. We suspect that $\beta^*(0) < \beta^{**}(0)$ holds as long as $r_1 < r_2$. By symmetry, similar arguments as in Proposition 2.9 yield that for $0 < r_1 < r_2$ fixed, there exist positive constants M_1 large and δ_1 small such that $\alpha^{**}(\beta) < \alpha^*(\beta)$ provided that $0 < d_2 < \delta_1$, $d_1 > M$ and $0 < \beta < \delta_1$.

3. Numerical simulations

As shown before, the locations of two critical curves determine whether coexistence or bistability happens. However, it is generally difficult to compare them mathematically since they are determined by some spatially dependent eigenvalue problems. The purpose of this section is to calculate the two critical curves numerically. Throughout this section, we fix the length of stream or river $L = 1$ km, and vary the parameter values of d_1, d_2, r_1, r_2 to observe the various possible locations of the two critical curves. The data used here are taken from Speirs and Gurney [30]. With the assigned values, we have observed that both $\beta^*(\alpha) - \beta^{**}(\alpha)$ and $\alpha^*(\beta) - \alpha^{**}(\beta)$ could change sign, which indicates that coexistence or bistability can happen in open advective environments, depending on tradeoffs between species in their movement strategy and growth requirement.



(a) (b)

Fig. 7. The diagrams of the critical curves $\alpha^*(\beta)$ and $\alpha^{**}(\beta)$ in $\beta - \alpha$ plane with $d_1 = 0.25$ m^2/s, $d_2 = 0.5$ m^2/s, $r_1 = 1$ day^{-1}, $r_2 = 0.39$ day^{-1}. By computation, $\alpha_0 = 0.2748$ km/day and $\beta_0 = 0.2059$ km/day. The difference between $\alpha^*(\beta)$ and $\alpha^{**}(\beta)$ is plotted in (b) versus the advection rate β.

At first, assuming that two species have identical intrinsic growth rates and different movement strategy, i.e. $r_1 = r_2$, $d_1 \neq d_2$, we always observe that $\beta^*(\alpha) < \beta^{**}(\alpha)$ for $\alpha \in (0, \alpha_0)$ (see Fig. 4). Hence, competitive exclusion that depends on initial data (i.e. bistability) may occur when two species with identical growth rates take different movement strategy.

Secondly, assuming that $d_1 < d_2$ and the species u has smaller growth rate than the species v, i.e. $r_1 < r_2$, we conclude that $\alpha_0 < \beta_0$ by Lemma 5.3 (see Appendix 5.1). Numerical results demonstrate that $\beta^*(\alpha) - \beta^{**}(\alpha)$ may change sign from positive to negative with the increasing advection rates α of the first species, see Fig. 5(b). System (1.2) displays outcomes of competitive exclusion independent of initial conditions (see Fig. 1), competitive exclusion that depends on initial conditions (bistability), and coexistence, depending on tradeoffs between species in their movement strategy and growth competence (see Fig. 5). In biological terms, if the inferior competitor in growth (i.e. species u due to $r_1 < r_2$) takes a slower advection rate, it can coexist with, or even out-compete its superior opponent as the speed of directed movement of its superior opponent increases. In reverse, if the inferior competitor takes a strategy of faster advection rates, then, at most, bistability can be observed. Moreover, it is easier to be excluded by its superior counterpart.

Finally, if the species u possesses higher growth rate than the species v, i.e. $r_1 > r_2$, then there are two possibilities: (i) $\alpha_0 \leq \beta_0$ or (ii) $\alpha_0 > \beta_0$ due to the assumption $d_1 < d_2$. The numerical simulations illustrate that $\alpha^*(\beta) - \alpha^{**}(\beta)$ may change sign from negative to positive with the increasing advection rates β of the second species, see Figs. 6(b) and 7(b). As above, system (1.2) displays the similar transition between different competitive outcomes no matter the sizes of α_0 and β_0, see Figs. 6 and 7. In summary, the numerical simulations indicate that certain tradeoffs between growth competence and movement strategy allow coexistence or bistability to become apparent.

4. Conclusion

It is shown in [14] that unidirectional flow can put slow dispersers at a disadvantage and higher dispersal rate can evolve under the assumption that two species are identical except their diffusion rates. Coincidentally, the results in [15] show that slower advection should be selected when two species are identical except their advection rates. Noting that (5.12) (see Appendix 5.2), similar arguments as in [14,15] suggest that the larger intrinsic growth rate is always beneficial for species to win the competition when two species are identical except their intrinsic growth rates. These observations strongly suggest that both coexistence and bistability are impossible for aquatic species which differ only by a single trait. The question how aquatic species, exposed to unidirectional flow, can coexist has received much attention including ecologists and bio-mathematicians. It turns out that the combined effects of multiple factors, such as the combination of diffusion and advection [36,37], diffusion and boundary effect [17], advection and spatial heterogeneity[13,35], will result in complex dynamical behaviors and give rise to much richer phenomena including competition exclusion and coexistence. For instance, coexistence can happen in some scenarios, where faster diffusion goes along with strong advection [36], two species drift along opposite directions [37], or environmental heterogeneity is involved [35]. We mainly focus on the combined influence of the dispersal strategy and growth ability on the competition outcomes of two aquatic species in open advective environments. It turns out that two critical curves determine whether species can invade successfully or not. Due to the strict monotonicity of competition system, mutual invasibility implies stable coexistence. Hence the locations of the two critical curves determine whether coexistence or bistability happens.

Theorem 1.1shows that the curve $\alpha = k\frac{d_1}{d_2}\beta$ with $0 < k \leq 1$ belongs to the globally asymptotically stable region of $(\theta_\alpha, 0)$ (see Fig. 1). That is, the invasion of the species with faster diffusion and advection is impossible when two species have identical growth rates and adopt the dispersal strategy satisfying $\frac{\alpha}{\beta} \leq \frac{d_1}{d_2} < 1$.

Theorem 1.2indicates that for the case of $d_1 < d_2$, $r_1 < r_2$, the two critical curves $\beta^*(\alpha)$ and $\beta^{**}(\alpha)$, which separate the stable region of the semi-trivial solutions from the unstable one, lie on the right-hand side of the curve $\alpha = \beta$ in the $\beta - \alpha$ plane (see Fig. 2, or the numerical Fig. 5). Hence the curve $\alpha = k\frac{d_1}{d_2}\beta$ with $0 < k < \min\{1, \frac{\alpha_0}{\beta_0}/\frac{d_1}{d_2}\}$ passes through the yellow, red and blue regions or the yellow, green and blue regions in Fig. 2(a). In biological terms, the superior competitor with larger growth rate (i.e. species v due to $r_2 > r_1$) can invade the single species equilibrium of the inferior competitor as the speed of its directed movement decreases. In reverse, by adopting a dispersal strategy of slower diffusion and advection, the inferior competitor with smaller growth rate (i.e. species u due to $r_1 < r_2$) can coexist with, or even out-compete the superior competitor as the speed of directed movement of the superior competitor increases.

Theorem 1.3illustrates that for the case of $d_1 < d_2$, $r_1 > r_2$, the two critical curves $\alpha^*(\beta)$ and $\alpha^{**}(\beta)$ locate above the curve $\alpha = \frac{\alpha_0}{\beta_0}\beta$ or $\alpha = \beta$ in the $\beta - \alpha$ plane (see Fig. 3, or the numerical Figs. 6 and 7). Hence the curve $\alpha = k\beta$ with $0 < k < \min\{1, \frac{\alpha_0}{\beta_0}\}$ lies in the stable region of $(\theta_\alpha, 0)$ completely, which suggests the invasion of species with lower growth rate is impossible.

In summary, the analytical results and numerical simulations suggest a tradeoff driven coexistence mechanism. More precisely, there is a tradeoff between the dispersal strategy and growth competence which allows the transition of competition outcomes, including competition exclusion, coexistence and bistability. This shifting may have an effect on the community composition in aquatic habitat. Moreover, the results show that the growth competence is crucial in determining the outcomes of competition.

5. Appendix

In this appendix, we will finish the proofs of Lemmas 2.1–2.5, and Proposition 2.9.

5.1. Preliminaries for proofs

In this subsection we present some useful lemmas in regard to the linear eigenvalue problem as well as some existing results concerning the steady state of single-species model as preliminaries. With this in mind, we consider the linear eigenvalue problem

$$\begin{cases} -d\varphi_{xx} + \alpha\varphi_x + q(x)\varphi = \eta\varphi, & 0 < x < 1, \\ d\varphi_x(0) - \alpha\varphi(0) = 0, & \varphi_x(1) = 0, \end{cases} \tag{5.1}$$

where d, α are nonnegative constants with $d > 0$, and $q(x)$ is a continuous function in $[0, 1]$.

Lemma 5.1. [3, 10] *Suppose $\alpha \geq 0$. Then all eigenvalues of* (5.1) *are real, and the smallest eigenvalue $\eta_1(q(x), \alpha)$ can be characterized as*

$$\eta_1(q(x), \alpha) = \inf_{\varphi \neq 0, \varphi \in H^1(0,1)} \frac{\int_0^1 e^{-\frac{\alpha}{d}x}(d\varphi_x^2 + q(x)\varphi^2)\mathrm{d}x + \alpha\varphi^2(0)}{\int_0^1 e^{-\frac{\alpha}{d}x}\varphi^2\mathrm{d}x},$$

which corresponds to a positive eigenfunction φ_1, and $\eta_1(q(x), \alpha)$ is the only eigenvalue whose corresponding eigenfunction does not change sign. Moreover,

(i) *$q_1(x) \geq q_2(x)$ implies $\eta_1(q_1(x), \alpha) \geq \eta_1(q_2(x), \alpha)$, and the equality holds only if $q_1(x) \equiv q_2(x)$;*
(ii) *$q_n(x) \to q(x)$ in $C([0, 1])$ implies $\eta_1(q_n(x), \alpha) \to \eta_1(q(x), \alpha)$.*

Remark 5.1. By Lemma 5.1, it is easy to see that if $q(x) \equiv q_0$ (a constant), then $\eta_1(q_0, \alpha) = \eta_1(0, \alpha) + q_0$.

Lemma 5.2. *Suppose d, r, α are constants with $d > 0$ and $\alpha \geq 0$. Let $\lambda_1(d, r, \alpha)$ be the principal eigenvalue of the eigenvalue problem (1.5) with the corresponding positive eigenfunction ϕ_1 normalized by $\max_{x\in[0,1]} \phi_1 = 1$. Then*

(i) *the positive eigenfunction ϕ_1 has the following properties:*

$$0 < (\phi_1)_x < \frac{\alpha}{d}\phi_1 \text{ if } \alpha > 0, \quad \text{and } \phi_1 \equiv 1 \text{ if } \alpha = 0;$$

(ii) *$\lambda_1(d, r, \alpha)$ is strictly decreasing with respect to α in $[0, +\infty)$ with $\lambda_1(d, r, 0) = r$ and $\lim_{\alpha\to+\infty} \lambda_1(d, r, \alpha) = -\infty$;*
(iii) *$\lambda_1(d, r, \alpha)$ is strictly increasing with respect to d in $(0, +\infty)$ with $\lim_{d\to0+} \lambda_1(d, r, \alpha) = -\infty$, and $\lim_{d\to+\infty} \lambda_1(d, r, \alpha) = r - \alpha$;*
(iv) *$\lambda_1(d, r, \alpha)$ is strictly increasing with respect to r in $(-\infty, +\infty)$.*

Proof. The proof of (ii) can refer to Lemmas 4.8 and 4.9 of [14] and Proposition 2.1 of [17]. In addition, (iv) is a direct result of Lemma 5.1. It remains to show (i) and (iii).

Set $P = \frac{(\phi_1)_x}{\phi_1}$. Then

$$\begin{cases} dP_{xx} + (2dP - \alpha)P_x = 0, & x \in (0, 1), \\ P(0) = \frac{\alpha}{d} > 0, & P(1) = 0. \end{cases}$$

By the strong maximum principle [28],

$$0 < P < \frac{\alpha}{d} \textit{ in } (0, 1),$$

which concludes the result (i).

Note that $\lambda_1(d, r, \alpha) = r - \lambda^*(d, \alpha)$, where $\lambda^*(d, \alpha)$ is the principal eigenvalue of the following eigenvalue problem

$$\begin{cases} d\omega_{xx} - \alpha\omega_x + \lambda^*(d, \alpha)\omega = 0, & x \in (0, 1), \\ d\omega_x(0) - \alpha\omega(0) = 0, & \omega_x(1) = 0. \end{cases} \tag{5.2}$$

Similar arguments as in Proposition 2.1 in [1] show that (iii) holds. ☐

As mentioned by (1.6) and (1.7), the critical advection rates α_0, β_0 are dependent on the diffusion rate and the growth rate of the species. Next, we investigate the combined effect of the diffusion rate and the growth rate on the critical advection rate. It turns out that faster diffusion along with higher growth is favorable for the persistence of species.

Lemma 5.3. *Suppose $0 < d_1 \leq d_2$ and $0 < r_1 \leq r_2$ fixed. Let $\alpha_0(d_1, r_1)$, $\beta_0(d_2, r_2)$ be uniquely determined by $\lambda_1(d_1, r_1, \alpha_0) = 0$ and $\lambda_1(d_2, r_2, \beta_0) = 0$ respectively. Then $\alpha_0(d_1, r_1)$, $\beta_0(d_2, r_2)$ are strictly increasing with respect to d_1, r_1 and d_2, r_2 respectively. Moreover,*

(i) *$\alpha_0 \leq \beta_0$, and $\alpha_0 = \beta_0$ if and only if $d_1 = d_2$, $r_1 = r_2$;*
(ii) *$\frac{d_1}{d_2}\beta_0 < \alpha_0 < \beta_0$ if $d_1 < d_2$ and $r_1 = r_2$;*
(iii) *$\lim_{d_1\to\infty} \alpha_0(d_1, r_1) = r_1$ and $\lim_{d_2\to\infty} \beta_0(d_2, r_2) = r_2$.*

Proof. By Lemma 5.2 and the implicit function theorem, one can easily conclude that $\alpha_0(d_1, r_1)$ is strictly increasing with respect to d_1 and r_1, and $\beta_0(d_2, r_2)$ is strictly increasing with respect to d_2 and r_2 respectively.

Next, we compare the values of $\alpha_0(d_1, r_1)$ and $\beta_0(d_2, r_2)$. To this end, we recall that

$$\begin{cases} d_1(\phi_1)_{xx} - \alpha_0(\phi_1)_x + r_1\phi_1 = 0, & x \in (0, 1), \\ d_1(\phi_1)_x(0) - \alpha_0\phi_1(0) = 0, & (\phi_1)_x(1) = 0, \end{cases} \tag{5.3}$$

$$\begin{cases} d_2(\phi_2)_{xx} - \beta_0(\phi_2)_x + r_2\phi_2 = 0, & x \in (0, 1), \\ d_2(\phi_2)_x(0) - \beta_0\phi_2(0) = 0, & (\phi_2)_x(1) = 0, \end{cases} \tag{5.4}$$

where ϕ_1 and ϕ_2 are the corresponding positive eigenfunctions. It follows from Lemma 5.2 that $0 < (\phi_1)_x < \frac{\alpha_0}{d_1}\phi_1$ and $0 < (\phi_2)_x < \frac{\beta_0}{d_2}\phi_2$. Rewrite (5.4) as

$$\begin{cases} d_1(\phi_2)_{xx} - \alpha_0(\phi_2)_x + r_2\phi_2 = (d_1 - d_2)(\phi_2)_{xx} \\ \qquad + (\beta_0 - \alpha_0)(\phi_2)_x, \quad x \in (0, 1), \\ d_2(\phi_2)_x(0) - \beta_0\phi_2(0) = 0, \quad (\phi_2)_x(1) = 0. \end{cases} \tag{5.5}$$

Multiplying (5.3) by $e^{-\frac{\alpha_0}{d_1}x}\phi_2$ and (5.5) by $e^{-\frac{\alpha_0}{d_1}x}\phi_1$, integrating over (0, 1) by parts, we get

$$\begin{aligned} &(d_1 - d_2) \int_0^1 (e^{-\frac{\alpha_0}{d_1}x}\phi_1)_x(\phi_2)_x \mathrm{d}x \\ &+ (r_2 - r_1) \int_0^1 e^{-\frac{\alpha_0}{d_1}x}\phi_1\phi_2 \mathrm{d}x \\ &= (\beta_0 - \alpha_0)[\int_0^1 e^{-\frac{\alpha_0}{d_1}x}\phi_1(\phi_2)_x \mathrm{d}x + \phi_1(0)\phi_2(0)]. \end{aligned} \tag{5.6}$$

In view of $d_1 \leq d_2$ and $r_1 \leq r_2$, one can easily conclude that (i) holds.

If $d_1 < d_2$, $r_1 = r_2$, then $\alpha_0 < \beta_0$ and (5.6) becomes

$$\begin{aligned} &(\beta_0 - \tfrac{d_2}{d_1}\alpha_0) \int_0^1 e^{-\frac{\alpha_0}{d_1}x}\phi_1(\phi_2)_x \mathrm{d}x \\ &= (d_1 - d_2) \int_0^1 e^{-\frac{\alpha_0}{d_1}x}(\phi_1)_x(\phi_2)_x \mathrm{d}x \\ &\quad + (\alpha_0 - \beta_0)\phi_1(0)\phi_2(0) < 0 \end{aligned}$$

since $(\phi_1)_x, (\phi_2)_x > 0$ on [0, 1]. This implies that $\frac{d_1}{d_2}\beta_0 < \alpha_0 < \beta_0$.

(iii) Integrating the first equation of (5.3) on [0, x], we have

$$d_1(\phi_1)_x - \alpha\phi_1 + r_1 \int_0^x \phi_1 \mathrm{d}x = 0.$$

Assume $\max_{[0,1]}\phi_1(x) = 1$. One can conclude that $(\phi_1)_x$ is uniformly bounded, and then from (5.3) $(\phi_1)_{xx}$ is uniformly bounded. Passing to a subsequence if necessary, we can deduce that $\phi_1 \to 1$ as $d_1 \to \infty$ uniformly on [0, 1]. Integrating the first equation of (5.3) on [0, 1], we have $-\alpha_0\phi_1(1) + r_1\int_0^1 \phi_1(x)\mathrm{d}x = 0$, which implies that $\lim_{d_1\to\infty} \alpha_0(d_1, r_1) = r_1$. Similar arguments yield $\lim_{d_2\to\infty} \beta_0(d_2, r_2) = r_2$. ☐

The unique positive steady state θ_α for single population model (1.3) has the following properties. Similar properties hold for ϑ_β.

Lemma 5.4. *Suppose$0 \leq \alpha < \alpha_0$. Then*

(i) *$0 < \theta_\alpha < r_1$ on [0, 1], and $0 < (\theta_\alpha)_x < \frac{\alpha}{d_1}\theta_\alpha$ in (0,1) if $0 < \alpha < \alpha_0$;*
(ii) *θ_α is continuously differentiable for $\alpha \in [0, \alpha_0)$, and it is decreasing pointwisely on [0,1] when α increases;*
(iii) *$\lim_{d_1\to+\infty} \theta_\alpha = r_1 - \alpha$ uniformly on [0, 1].*

Proof. (i) By the strong maximum principle, it is easy to see that $0 < \theta_\alpha < r_1$ on [0, 1]. The proof for the conclusion $0 < (\theta_\alpha)_x < \frac{\alpha}{d_1}\theta_\alpha$ in (0,1) follows from Lemma 2.1 in [36].

(ii) Define G: $(0, \alpha_0) \times C_B^2([0, 1]) \to C([0, 1])$ by

$$G(\alpha, u) = d_1u_{xx} - \alpha u_x + u(r - u),$$

where $C_B^2([0, 1]) = \{u \in C^2([0, 1]): -d_1u_x(0) + \alpha u(0) = 0, u_x(1) = 0\}$. Clearly, G is a C^1 functional. For any given $\alpha \in (0, \alpha_0)$, it is easy to see that $G(\alpha, \theta_\alpha) = 0$ and the Fréchet derivative $D_uG(\alpha, \theta_\alpha) = d_1\frac{\partial^2}{\partial x^2} - \alpha\frac{\partial}{\partial x} + r - 2\theta_\alpha$. Noting that $\lambda_1(d_1\frac{\partial^2}{\partial x^2} - \alpha\frac{\partial}{\partial x} + r - \theta_\alpha) = 0$, one can assert that all eigenvalues of $D_uG(\alpha, \theta_\alpha)$ are strictly negative, which implies that $D_uG(\alpha, \theta_\alpha)$ is a non-degenerate and negative operator. It follows from the implicit function theorem and compactness arguments that there exists a C^1 function $u(s)$: $(0, \alpha_0) \to C_B^2([0, 1])$ such that $u(s)|_{s=\alpha} = \theta_\alpha$ and $G(s, u(s)) = 0$. From the uniqueness of the solution $(s, u(s))$ close to (α, θ_α), one can assert that $u(s) = \theta_\alpha$ if $s = \alpha$ and that θ_α is continuously differentiable with respect to α in $(0, \alpha_0)$.

Differentiating the equation of θ_α with respect to α, we obtain

$$\begin{cases} -d_1(\dot{\theta}_\alpha)_{xx} + \alpha(\dot{\theta}_\alpha)_x - (r - 2\theta_\alpha)\dot{\theta}_\alpha \\ \qquad = -(\theta_\alpha)_x < 0, \quad x \in (0, 1), \\ -d_1(\dot{\theta}_\alpha)_x(0) + \alpha\dot{\theta}_\alpha(0) = -\theta_\alpha(0) < 0, \\ (\dot{\theta}_\alpha)_x(1) = 0. \end{cases}$$

By the strong maximum principle, we have $\dot{\theta}_\alpha < 0$, that is, θ_α is decreasing pointwisely on [0,1] when α increases.

(iii) Integrating the equation for θ_α on $[0, x]$, we have

$$d_1(\theta_\alpha)_x - \alpha\theta_\alpha + \int_0^x (r_1 - \theta_\alpha)\theta_\alpha \mathrm{d}x = 0.$$

In view of $0 < \theta_\alpha < r_1$, one can conclude that $(\theta_\alpha)_x$ is uniformly bounded, and then $(\theta_\alpha)_{xx}$ is uniformly bounded. Passing to a subsequence if necessary, we can deduce that θ_α converges to some positive constant uniformly on [0, 1] when $d_1 \to \infty$. Integrating the equation for θ_α on [0, 1], we have

$$\int_0^1 (r_1 - \theta_\alpha)\theta_\alpha \mathrm{d}x = \alpha\theta_\alpha(1),$$

which implies that $\lim\limits_{d_1 \to +\infty} \theta_\alpha = r_1 - \alpha$ uniformly on [0, 1]. ☐

Remark 5.2. It is easy to see that $\theta_\alpha \equiv r_1$ on [0,1] if $\alpha = 0$.

5.2. *Some mathematical proofs*

Now, we are ready to establish Lemmas 2.1–2.5, and Proposition 2.9.

The proof of Lemma 2.1: (i) Recall that

$$\begin{cases} d_2(\psi_1)_{xx} - \beta(\psi_1)_x + (r_2 - \theta_\alpha)\psi_1 \\ \qquad\qquad = \mu_1(\alpha, \beta)\psi_1, \ x \in (0, 1), \\ d_2(\psi_1)_x(0) - \beta\psi_1(0) = 0, \ (\psi_1)_x(1) = 0. \end{cases} \tag{5.7}$$

Differentiating (5.7) with respect to α, we obtain

$$\begin{cases} d_2(\dot{\psi}_1)_{xx} - \beta(\dot{\psi}_1)_x + (r_2 - \theta_\alpha)\dot{\psi}_1 - \dot{\theta}_\alpha\psi_1 \\ \quad = \dot{\mu}_1(\alpha, \beta)\psi_1 + \mu_1(\alpha, \beta)\dot{\psi}_1, \ x \in (0, 1), \\ d_2(\dot{\psi}_1)_x(0) - \beta\dot{\psi}_1(0) = 0, \ (\dot{\psi}_1)_x(1) = 0, \end{cases} \tag{5.8}$$

where $\dot{\psi}_1$, $\dot{\mu}_1(\alpha, \beta)$, $\dot{\theta}_\alpha$ are the derivatives of ψ_1, $\mu_1(\alpha, \beta)$, θ_α with respect to α respectively. Multiplying (5.8) by $e^{-\frac{\beta}{d_2}x}\psi_1$ and (5.7) by $e^{-\frac{\beta}{d_2}x}\dot{\psi}_1$, and integrating over (0, 1) by parts, we get

$$\dot{\mu}_1(\alpha, \beta) \int_0^1 e^{-\frac{\beta}{d_2}x}\psi_1^2 \mathrm{d}x = -\int_0^1 e^{-\frac{\beta}{d_2}x}\psi_1^2\dot{\theta}_\alpha \mathrm{d}x > 0$$

by Lemma 5.4(ii). Hence, $\mu_1(\alpha, \beta)$ is strictly increasing with respect to α in $[0, \alpha_0)$.

(ii) Let $\psi_1 = e^{\frac{\beta}{d_2}x}\Psi$, where ψ_1 is the positive eigenfunction corresponding to the eigenvalue $\mu_1(\alpha, \beta)$. Then

$$\begin{cases} d_2\Psi_{xx} + \beta\Psi_x + (r_2 - \theta_\alpha)\Psi \\ \qquad\qquad = \mu_1(\alpha, \beta)\Psi, \ x \in (0, 1), \\ \Psi_x(0) = 0, \ d_2\Psi_x(1) + \beta\Psi(1) = 0. \end{cases} \tag{5.9}$$

Differentiating (5.9) with respect to β, we obtain

$$\begin{cases} d_2\Psi'_{xx} + \beta\Psi'_x + (r_2 - \theta_\alpha)\Psi' + \Psi_x \\ \quad = \mu_1'(\alpha,\beta)\Psi + \mu_1(\alpha,\beta)\Psi', \ x \in (0, 1), \\ \Psi'_x(0) = 0, \\ d_2\Psi'_x(1) + \beta\Psi'(1) + \Psi(1) = 0, \end{cases} \tag{5.10}$$

where Ψ', $\mu_1'(\alpha, \beta)$ are the derivatives of Ψ, $\mu_1(\alpha, \beta)$ with respect to β respectively. Multiplying (5.10) by $e^{\frac{\beta}{d_2}x}\Psi$ and (5.9) by $e^{\frac{\beta}{d_2}x}\Psi'$, and integrating over (0, 1) by parts, we get

$$\begin{aligned} & \mu_1'(\alpha, \beta) \int_0^1 e^{\frac{\beta}{d_2}x}\Psi^2 \mathrm{d}x \\ = \ & -e^{\frac{\beta}{d_2}}\Psi^2(1) + \int_0^1 e^{\frac{\beta}{d_2}x}\Psi\Psi_x \mathrm{d}x \\ = \ & -\frac{1}{2}[\Psi^2(0) + e^{\frac{\beta}{d_2}}\Psi^2(1) + \frac{\beta}{d_2}\int_0^1 e^{\frac{\beta}{d_2}x}\Psi^2 \mathrm{d}x] \\ < \ & 0, \end{aligned}$$

which implies that $\mu_1(\alpha, \beta)$ is strictly decreasing with respect to β in $[0, +\infty)$.

The proof of Lemma 2.2: (i) It follows from Remark 5.2 that if $\alpha = 0$, then $\theta_\alpha \equiv r_1$ on [0, 1]. Hence, it is easy to check that $\mu_1(0, 0) = r_2 - r_1$. In view of $\lambda_1(d_2, r_2, \beta_0) = 0$, it follows that $\mu_1(0, \beta_0) = -r_1$.

Noting that $\theta_{\alpha_0} = 0$ on [0, 1] and $\lambda_1(d_2, r_2, \beta_0) = 0$, one can easily find that $\mu_1(\alpha_0, \beta_0) = \lambda_1(d_2, r_2, \beta_0) = 0$, and $\mu_1(\alpha_0, 0) = r_2$.

(ii) By virtue of $\mu_1(\alpha_0, \beta_0) = 0$ and $\mu_1(\alpha_0, 0) = r_2$, it follows from the strict monotonicity of $\mu_1(\alpha, \beta)$ with respect to β that $\mu_1(\alpha_0, \beta) > 0$ for $0 \le \beta < \beta_0$. In view of $\mu_1(\alpha_0, \beta_0) = 0$ and $\mu_1(0, \beta_0) = -r_1$, one can conclude that $\mu_1(\alpha, \beta_0) < 0$ for $0 \le \alpha < \alpha_0$ since $\mu_1(\alpha, \beta)$ is strictly increasing with respect to α in $[0, \alpha_0)$.

(iii) If $r_1 \le r_2$, then $\mu_1(0, 0) = r_2 - r_1 \ge 0$. Hence we deduce that $\mu_1(\alpha, 0) > 0$ for $0 < \alpha \le \alpha_0$ by Lemma 2.1(i). In reverse, if $r_1 > r_2$, then $\mu_1(0, 0) = r_2 - r_1 < 0$, which indicates that $\mu_1(0, \beta) < 0$ for $0 \le \beta \le \beta_0$ by Lemma 2.1(ii).

The proof of Lemma 2.3: Let ψ_1 be the corresponding positive eigenfunction of $\mu_1(\alpha, \beta)$ and set $P = \frac{(\psi_1)_x}{\psi_1}$. Then

$$\begin{cases} d_2P_{xx} + (2d_2P - \beta)P_x = (\theta_\alpha)_x \ge 0, \ x \in (0, 1), \\ P(0) = \frac{\beta}{d_2} > 0, \ P(1) = 0. \end{cases}$$

By the strong maximum principle, P cannot attain a nonnegative maximum in (0, 1). Hence $P < \frac{\beta}{d_2}$ in (0, 1), which implies $(\psi_1)_x - \frac{\beta}{d_2}\psi_1 < 0$ in (0, 1).

Note that

$$\begin{cases} d_2(\theta_\alpha)_{xx} - \beta(\theta_\alpha)_x + (r_1 - \theta_\alpha)\theta_\alpha \\ \quad = (d_2 - d_1)(\theta_\alpha)_{xx} + (\alpha - \beta)(\theta_\alpha)_x, \\ d_1(\theta_\alpha)_x(0) - \alpha\theta_\alpha(0) = 0, \ (\theta_\alpha)_x(1) = 0. \end{cases} \tag{5.11}$$

Multiplying (5.7) by $e^{-\frac{\beta}{d_2}x}\theta_\alpha$ and (5.11) by $e^{-\frac{\beta}{d_2}x}\psi_1$, integrating over (0, 1) by parts, we get

$$\begin{aligned} & (\mu_1(\alpha, \beta) + r_1 - r_2) \int_0^1 e^{-\frac{\beta}{d_2}x}\psi_1\theta_\alpha \mathrm{d}x \\ = & (d_1 - d_2) \int_0^1 (e^{-\frac{\beta}{d_2}x}\psi_1)_x(\theta_\alpha)_x \mathrm{d}x \\ & + (\alpha - \beta)[\int_0^1 e^{-\frac{\beta}{d_2}x}\psi_1(\theta_\alpha)_x \mathrm{d}x + \psi_1(0)\theta_\alpha(0)]. \end{aligned} \tag{5.12}$$

The conclusions (i) and (ii) can be deduced directly from the equation (5.12) by means of $(\theta_\alpha)_x > 0$ in (0, 1) for $0 < \alpha < \alpha_0$ and $(\psi_1)_x - \frac{\beta}{d_2}\psi_1 < 0$ in (0, 1).

The proof of Lemma 2.4: Clearly, we have $\alpha_0 \le \beta_0$ by Lemma 5.3. If $d_1 = d_2$, $r_1 = r_2$, it follows from Lemma 2.3(i) that $\mu_1(\alpha, \alpha) = 0$, which implies $\beta^*(\alpha) = \alpha$ when $0 \le \alpha \le \alpha_0$. Otherwise, we can conclude $\mu_1(\alpha, \alpha) > 0$ when $0 < \alpha < \alpha_0$. Note that $\mu_1(0, 0) = r_2 - r_1 \ge 0$ and $\mu_1(\alpha, \beta_0) < 0$ when $0 \le \alpha < \alpha_0$. By continuity and the strict monotonicity of the eigenvalue $\mu_1(\alpha, \beta)$ with respect to β, we can conclude that for $0 \le \alpha \le \alpha_0$, there exists a unique $\beta^*(\alpha)$ such that $\alpha \le \beta^*(\alpha) \le \beta_0$ and

$$\begin{cases} \mu_1(\alpha, \beta) < 0 \ \text{ if } \beta > \beta^*(\alpha), \\ \mu_1(\alpha, \beta) = 0 \ \text{ if } \beta = \beta^*(\alpha), \\ \mu_1(\alpha, \beta) > 0 \ \text{ if } 0 \le \beta < \beta^*(\alpha). \end{cases}$$

That is, (i) holds. By Lemma 2.1 and the implicit function theorem, we can conclude that the function $\beta^*(\alpha)$ is strictly increasing with respect to α in $[0, \alpha_0]$. Moreover, it is easy to see that $\beta^*(\alpha_0) = \beta_0$ by means of $\mu_1(\alpha_0, \beta_0) = 0$.

The proof of Lemma 2.5: By Lemma 2.2, we have $\mu_1(\alpha_0, \beta) > 0$ for $0 \le \beta < \beta_0$, and $\mu_1(0, \beta) < 0$ for $0 \le \beta \le \beta_0$ based on $r_1 > r_2$. By continuity and the strict monotonicity of the eigenvalue $\mu_1(\alpha, \beta)$ with respect to α, we can conclude that for $0 \le \beta \le \beta_0$, there exists a unique $\alpha^*(\beta)$ such that $0 < \alpha^*(\beta) \le \alpha_0$ and

$$\begin{cases} \mu_1(\alpha,\beta) < 0 \ \text{ if } \ 0 \le \alpha < \alpha^*(\beta), \\ \mu_1(\alpha,\beta) = 0 \ \text{ if } \ \alpha = \alpha^*(\beta), \\ \mu_1(\alpha,\beta) > 0 \ \text{ if } \ \alpha^*(\beta) < \alpha < \alpha_0. \end{cases}$$

That is, (i) holds. By Lemma 2.1 and the implicit function theorem, we can conclude that the function $\alpha^*(\beta)$ is strictly increasing with respect to β on $[0, \beta_0]$. Moreover, it is easy to see that $\alpha^*(\beta_0) = \alpha_0$ by means of $\mu_1(\alpha_0, \beta_0) = 0$.

The proof of Proposition 2.9: Suppose $d_{2,n} \to +\infty$ as $n \to \infty$. It follows from Lemma 5.4 that $\vartheta_{\beta,n} \to r_2 - \beta$ as $n \to \infty$, where $\vartheta_{\beta,\ n}$ is the unique positive steady state of the single population model (1.4) with $d_2 = d_{2,n}$. Let $\sigma_{1,\ n}(\alpha, \beta)$ be the principal eigenvalue of (2.2) with ϑ_β replaced by $\vartheta_{\beta,\ n}$. Then

$$\begin{aligned} \sigma_{1,n}(\alpha,\beta) &\to \lambda_1(d_1, \alpha, r_1 - r_2 + \beta) \\ &= \lambda_1(d_1, \alpha, 0) + r_1 - r_2 + \beta \end{aligned}$$

as $n \to \infty$, which implies

$$\beta_n^{**}(\alpha) \to (r_2 - r_1) - \lambda_1(d_1, \alpha, 0) \tag{5.13}$$

as $n \to \infty$. Here $\beta_n^{**}(\alpha)$ is uniquely determined by $\sigma_{1,n}(\alpha, \beta_n^{**}(\alpha)) = 0$. By Lemma 5.2, $\lambda_1(d_1, \alpha, 0)$ is strictly increasing with respect to d_1 in $(0, +\infty)$ with $\lim\limits_{d_1 \to 0+} \lambda_1(d_1, \alpha, 0) = -\infty$. Hence, $(r_2 - r_1) - \lambda_1(d_1, \alpha, 0) \to +\infty$ as $d_1 \to 0+$.

On the other hand, let $(\mu_{1,\ n}(\alpha, \beta), \psi_n(x))$ be the pair of principal eigenvalue-eigenfunction of problem (2.1) with $d_2 = d_{2,n}$. Hence, $\beta_n^*(\alpha)$ satisfies that

$$\begin{cases} d_{2,n}(\psi_n^*)_{xx} - \beta(\psi_n^*)_x \\ \quad + (r_2 - \theta_\alpha)\psi_n^* = 0, \ \ x \in (0,1), \\ d_2(\psi_n^*)_x(0) {-} \beta(\psi_n^*)(0) {=} 0, \ \ (\psi_n^*)_x(1) {=} 0. \end{cases} \tag{5.14}$$

Similar arguments as in Lemma 5.3(iii) yield that $\psi_n^* \to 1$ as $n \to \infty$ due to the assumption of $\max\limits_{[0,1]} \psi_n^*(x) = 1$. Integrating the first equation of (5.14) on [0, 1], we easily deduce that

$$\beta_n^*(\alpha) \to \int_0^1 (r_2 - \theta_\alpha) \mathrm{d}x \ \text{ as } \ n \to \infty. \tag{5.15}$$

Recalling that $\theta_\alpha \to r_1$ as $\alpha \to 0+$ and $(r_2 - r_1) - \lambda_1(d_1, \alpha, 0) \to +\infty$ as $d_1 \to 0+$, one can deduce that there exists some constant $\delta > 0$ small such that for $0 < d_1 \le \delta$ and $0 < \alpha \le \delta$, we have $\frac{r_1}{2} < \theta_\alpha < r_1$ on [0, 1] and $(r_2 - r_1) - \lambda_1(d_1, \alpha, 0) > (r_2 - \frac{r_1}{2})$.

Combining (5.13) and (5.15), we can conclude that there exist positive constants M large and δ small such that for $d_2 \ge M$, $0 < d_1 \le \delta$, and $0 < \alpha \le \delta$, we have $\beta^{**}(\alpha) > (r_2 - \frac{r_1}{2}) > \beta^*(\alpha)$. The proof is finished.

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