



# **Evolution of Dispersal in Advective Patchy Environments**

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# Abstract

We study a two-species competition model in a patchy advective environment, where the species are subject to both directional drift and undirectional random dispersal between patches and there are losses of individuals in the downstream end (e.g., due to the flow into a lake or ocean). The two competing species are assumed to have the same growth rates but different advection and random dispersal rates. We focus our studies on the properties of an associated eigenvalue problem which characterizes the extinction/persistence dynamics of the underlying patch population model. We also derive conditions on the advection and random dispersal rates under which a mutant species can or cannot invade the resident species.

Keywords Patch population model  $\cdot$  Advective environment  $\cdot$  Competition model  $\cdot$  Invasion analysis  $\cdot$  Evolution of dispersal

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# 1 Introduction

The organisms in streams are subject to both directional drift and undirectional random diffusion. Intuitively, the stream flow takes the organisms to the downstream locations which are often fatal to them, while random diffusion may drive them to favorable locations in the upstream. How the joint force of directed and undirectional movements affects the extinction and persistence of a biological species have attracted the attention of many researchers (Huang et al. 2016; Jin and Lewis 2011; Lou and Lutscher 2014; Lutscher et al. 2006, 2007, 2005; Speirs and Gurney 2001).

In the framework of discrete patch models, a population in a stream environment with logistic type growth can be described by the following system (Chen et al. 2022b; Cosner 1996; Li and Shuai 2010; Lu and Takeuchi 1993):

$$\begin{cases} \frac{du_i}{dt} = \sum_{j=1}^n L_{ij} u_j + u_i (r_i - u_i), & i = 1, \dots, n, \quad t > 0, \\ u(0) = u_0 \ge (\not\equiv) 0, \end{cases}$$
(1.1)

where  $n \ge 2$  is the number of patches;  $u = (u_1, \ldots, u_n)$ , and  $u_i$  denotes the population density in patch i;  $L_{ij}$  is the movement rate of individuals from patch j to patch i; and  $r_i$  is the intrinsic growth rate in patch i. The connection matrix  $L = (L_{ij})$  depends on the topology of the stream and the directional and undirectional movement rates of the species. In this paper, we only consider the population dynamics in a stream with free flow from upstream end (patch i = 1) to the downstream end (patch i = n). The following three ecological scenarios at the downstream end are typical (Lou and Lutscher 2014; Lutscher et al. 2006; Speirs and Gurney 2001):

- (i) Stream to lake. The lake environment is as favorable as the stream environment for the species, and individuals can return to the stream from the lake by diffusion. Moreover, the diffusive flux into and from the lake balances;
- (ii) **Stream to ocean**. The ocean environment is fatal to the species in the stream, and individuals cannot return to the stream from the ocean;
- (iii) Inland stream. Individuals cannot move in or out through the downstream end.

The above cases (i)–(iii) correspond to three types of movements at the downstream end, see (a)-(c) in Fig. 1.

The movement of the species among patches in Fig. 1 can be described by an  $n \times n$  matrix L = dD + qQ with d and q being the diffusion and advection rates, respectively, and  $D = (D_{ij})$  representing the diffusion pattern and  $Q = (q_{ij})$  describing the directed movement pattern of individuals. Then, the matrices D and Q satisfy one of the following three assumptions:



**Fig. 1** Advective and diffusive movement of the species among patches. Here, **a** stream to lake; **b** stream to ocean; and **c** inland stream. Here, d > 0 is the diffusion rate, and  $q \ge 0$  is the advection rate

**H**1. Case (a): stream to lake. The matrix  $D = (D_{ij})$  is given by

$$D_{ij} = \begin{cases} 1, & i = j - 1 \text{ or } i = j + 1, \\ -2, & i = j = 2, \dots, n - 1, \\ -1, & i = j = 1, n, \\ 0, & \text{otherwise}, \end{cases}$$
(1.2)

and  $Q = (Q_{ij})$  is given by

$$Q_{ij} = \begin{cases} 1, & i = j + 1, \\ -1, & i = j = 1, \dots, n, \\ 0, & \text{otherwise.} \end{cases}$$
(1.3)

H1\*. Case (b): stream to ocean. The same as H1 except that  $D_{nn} = -2$ . H1\*\*. Case (c): inland stream. The same as H1 except that  $Q_{nn} = 0$ .

We will consider the following two-species Lotka–Volterra competition model in a spatially homogeneous patchy stream environment:

$$\begin{cases} \frac{du_i}{dt} = \sum_{j=1}^n (d_1 D_{ij} + q_1 Q_{ij}) u_j + u_i (r - u_i - v_i), & i = 1, \dots, n, \quad t > 0, \\ \frac{dv_i}{dt} = \sum_{j=1}^n (d_2 D_{ij} + q_2 Q_{ij}) v_j + v_i (r - u_i - v_i), & i = 1, \dots, n, \quad t > 0, \\ u(0) = u_0 \ge (\neq) \mathbf{0}, \quad v(0) = v_0 \ge (\neq) \mathbf{0}. \end{cases}$$
(1.4)

Here, the growth rate r is assumed to be a positive constant for all patches, and the two species have the same interspecific and intraspecific competition coefficients (normalized to be 1 for simplicity). So the two competing species are identical except their diffusion and advection rates. The connection matrices are

$$L^{(k)} = \left(L_{ij}^{(k)}\right) = d_k D + q_k Q, \quad k = 1, 2,$$
(1.5)

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where  $(D_{ij})$  and  $(Q_{ij})$  are defined in (1.2) and (1.3) for case (a)–(c), respectively. For the purpose of brevity, we will restrict our attention to cases (a) and (b) where there are losses of individuals in the downstream end, and case (c) will be studied in a follow-up paper.

Our work is largely motivated by previous researches on population dynamics in streams in the framework of partial differential equation models (Cantrell and Cosner 2004; Lam et al. 2015, 2016; Lou and Lutscher 2014; Lou et al. 2016; Lou and Zhou 2015; Ma and Tang 2020; Vasilyeva and Lutscher 2012; Zhao and Zhou 2016; Zhou 2016). The reaction–diffusion–advection model analogous to (1.1) is

$$\begin{cases} u_t = \tilde{d}u_{xx} - \tilde{q}u_x + u[r(x) - u], & 0 < x < l, t > 0, \\ \tilde{d}u_x(0, t) - \tilde{q}u(0, t) = 0, & t > 0, \\ \tilde{d}u_x(l, t) - \tilde{q}u(l, t) = -\beta \tilde{q}u(l, t), t > 0, \\ u(x, 0) \ge (\not\equiv)0. \end{cases}$$
(1.6)

Here, the species u lives in a stream represented by  $0 \le x \le l$ ;  $\tilde{d}$  is the diffusion rate and  $\tilde{q}$  is the advection rate of the species; x = 0 is the upstream end and x = lis the downstream end. The no-flux boundary condition is imposed at the upstream end x = 0, which means that individuals cannot move in or out through the upstream boundary. A parameter  $\beta$  is introduced for the boundary condition at the downstream end x = l to measure the loss rate of individuals. The corresponding three cases in Fig. 1 are as follows: (1) free-flow boundary condition  $u_x(l, t) = 0$  for  $\beta = 1$ ; (2) hostile boundary condition u(l, t) = 0 for  $\beta \to \infty$ ; and (3) no-flux boundary condition  $\tilde{d}u_x(l, t) - \tilde{q}u(l, t) = 0$  for  $\beta = 0$ .

The reaction-diffusion-advection version of the two species competition model (1.4) over a stream with different boundary conditions in the downstream end has been studied by many authors (Lam et al. 2015; Lou and Lutscher 2014; Lou et al. 2016; Lou and Zhou 2015; Ma and Tang 2020; Vasilyeva and Lutscher 2012; Zhao and Zhou 2016; Zhou 2016). In the seminal work of Hastings (1983) and Dockery et al. (1998), it has been shown that a mutant species can invade if and only if it has a smaller diffusion rate when both species have no directional movement and are identical except for the diffusion rates. However, in a stream environment with free-flow boundary conditions (Lou and Lutscher 2014; Vasilyeva and Lutscher 2012; Zhou and Zhao 2018) or inland boundary conditions (Lam et al. 2015; Lou et al. 2018, 2016; Lou and Zhou 2015; Zhou 2016), the species with larger diffusion rate and/or smaller advection rate may be selected. The Dirichlet boundary condition case seems to be less studied, and the authors in Yan et al. (2022) showed that both coexistence and bi-stability are possible numerically.

Model (1.1) is a discrete version of (1.6). We divide the interval [0, l] into n + 1 sub-intervals with equal length  $\Delta x = l/(n + 1)$  and endpoints 0, 1, ..., n + 1. At endpoints i = 1, ..., n, we discretize  $u_{xx}$  and  $u_x$  to obtain the following equation:

$$\frac{du_i}{dt} = \tilde{d} \frac{u_{i+1} - 2u_i + u_{i-1}}{(\Delta x)^2} - \tilde{q} \frac{u_i - u_{i-1}}{\Delta x} + u_i(r_i - u_i), \quad i = 1, \dots, n, \quad (1.7)$$

where  $u_i(t)$  is the population density at endpoint *i*. Note that for  $i = 2, \dots, n-1$ , (1.7) is the same as (1.1) with  $d = \tilde{d}/(\Delta x)^2$  and  $q = \tilde{q}/\Delta x$ . At the upstream end x = 0, we discretize the no-flux boundary condition to obtain

$$\tilde{d}\frac{u_1 - u_0}{\Delta x} - \tilde{q}u_0 = 0.$$

Substituting it into (1.7) for i = 1, we obtain (1.1) for i = 1. If the downstream end x = l is imposed with the free-flow boundary condition, then the discrete version is

$$\tilde{d}\frac{u_{n+1}-u_n}{\Delta x}=0.$$

Substituting it into (1.7) for i = n, we obtain (1.1) for i = n. If the downstream end is associated with the hostile boundary condition, then we obtain  $u_{n+1} = 0$  at the endpoint of the stream. Again, we can substitute it into (1.7) for i = n to obtain the corresponding equation in (1.1). The no-flux boundary condition at x = l can be treated similarly.

The discrete patch model (1.1) and the two-species competition model (1.4) with the dispersal matrix D, Q defined as in (1.2)–(1.3) approximate the reaction–diffusion–advection model (1.6) and the corresponding two-species competition model as the number of patches gets large and the total length of the system remains fixed. Similar approach for spatial population dynamics has been used in DeAngelis et al. (2016), Keitt et al. (2001), Levin (1976), Owen and Lewis (2001), and comparison of continuous and discrete space models was also made in these work. While the two types of models often produce similar results, it is known that they can also have different outcomes when there is Allee effect in the system (Keitt et al. 2001; Owen and Lewis 2001).

We will investigate model (1.4) in the approach of adaptive dynamics framework (Dieckmann and Law 1996; Geritz et al. 1998), which is the method adopted in Lou and Lutscher (2014), Vasilyeva and Lutscher (2012). For this purpose, we will first impose conditions on  $d_1$  and  $q_1$  such that **u**-species is established as a semi-trivial equilibrium  $E_1 = (\boldsymbol{u}^*, \boldsymbol{0})$  (the *v*-only equilibrium will be denoted by  $E_2 = (\boldsymbol{0}, \boldsymbol{v}^*)$ ) when there is no v-species in the system. Then, we investigate the stability/instability of  $E_1$  when  $d_2$  and  $q_2$  varies. We show that there is a curve  $q = q^*_{r-u^*}(d)$  passing through  $(d_1, q_1)$  and dividing the d - q plane into two regions such that  $E_1$  is stable if  $(d_2, q_2)$  is above the curve while  $E_1$  is unstable if  $(d_2, q_2)$  is below it. When the downstream end is coupled with no-flux boundary conditions (case (a)), we show that the curve  $q = q_{r-u^*}^*(d)$  is strictly increasing, and v species can invade if it has larger diffusion or smaller advection rate. If the hostile boundary conditions (case (b)) are imposed at the downstream end, we show that smaller advection rate is selected. If  $q_2 = q_1$  and  $d_2$  is close to  $d_1, [q_{r-u^*}^*(d)]'|_{d=d_1} > (<)0$  means that species v can invade if and only if  $d_2 > (<)d_1$ . We show that  $\left[q_{r-u^*}^*(d)\right]'|_{d=d_1}$  changes sign in case (b) as  $(d_1, q_1)$  varies, which indicates whether smaller or larger diffusion rate is favored depends on  $(d_1, q_1)$ . For both cases, we find parameter ranges of  $d_2$  and  $q_2$  such that

competitive exclusion happens. We also give conditions under which coexistence or bi-stability of the two species occurs.

The global dynamics of the single species patch model (1.1) is well-known. In Cosner (1996), Li and Shuai (2010); Lu and Takeuchi (1993), it has been shown that either the trivial equilibrium of (1.1) is globally stable or the model has a globally asymptotically stable positive equilibrium. There are also many research works on the two-species competition model (1.4), especially when the number of patches n is small (n = 2 or 3). We refer interested readers to the works on two-patch models without directional dispersal (Cheng et al. 2019; Gourley and Kuang 2005; Lin et al. 2014) and the ones with directional dispersal (Hamida 2017; Jiang et al. 2020, 2021; Lou 2019; Noble 2015; Xiang and Fang 2019). More recently, the competition on a river network was considered for three-patch models (Jiang et al. 2020, 2021). When  $(d_1, q_1)$  is a multiple of  $(d_2, q_2)$ , complete global dynamics of (1.4) has been classified in our recent work (Chen et al. 2022a). We refer to Cantrell et al. (2007), Cantrell et al. (2012, 2017), Kirkland et al. (2006), Levin et al. (1984), McPeek and Holt (1992), Smith (1995) and the references therein for more works on competition models in patchy environment.

Our paper is organized as follows. In Sect. 2, we introduce the terminology and state some useful results; in Sect. 3, we study the properties of the principal eigenvalue of an associated eigenvalue problem which determines the existence/nonexistence of positive equilibrium of (1.1); and in Sect. 4, we perform invasion analysis for the two-species competition model (1.4). In Sect. 5, we present some numerical simulations and formulate some conjectures on coexistence and bi-stability about the solutions of the model.

# 2 Preliminaries

Let  $u = (u_1, ..., u_n)^T \in \mathbb{R}^n$  be a vector. We write  $u \gg 0$  ( $u \ge 0$ ) if  $u_i > 0$  ( $u_i \ge 0$ ) for all  $1 \le i \le n$ , and u > 0 if  $u \ge 0$  and  $u \ne 0$ . Let  $A = (a_{ij})_{n \times n}$  be a real-valued square matrix, and let  $\sigma(A)$  be the set of all eigenvalues of A. The *spectral bound* s(A) of A is defined as

$$s(A) = \max{\operatorname{Re}(\lambda) : \lambda \in \sigma(A)}.$$

The matrix *A* is *reducible* if we can partition  $\{1, 2, ..., n\}$  into two nonempty subsets *E* and *F* such that  $a_{ij} = 0$  for all  $i \in E$  and  $j \in F$ . Otherwise, *A* is *irreducible*. A real-valued square matrix *A* is called *essentially nonnegative* if all its off-diagonal entries are nonnegative. If *A* is an irreducible essentially nonnegative matrix, then by the Perron–Frobenius Theorem (Li and Schneider 2002), s(A) is an eigenvalue of *A* (called the principal eigenvalue), which is the unique eigenvalue corresponding with a positive eigenvector. It is easy to see that *D* and *L* defined in the Introduction are irreducible and essentially nonnegative. If *D* satisfies **H**1 or **H**1<sup>\*\*</sup>, then s(D) = 0 corresponding with a positive eigenvector (1/n, ..., 1/n); and if *D* satisfies **H**1<sup>\*</sup>, then s(D) < 0.

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Denote by  $\lambda_1(d, q, \mathbf{r})$  the principal eigenvalue of the matrix  $dD + qQ + diag(r_i)$ , where  $\mathbf{r} = (r_1, \dots, r_n)$  is a real-valued vector, so  $\lambda_1(d, q, \mathbf{r})$  satisfies the following eigenvalue problem:

$$\sum_{j=1}^{n} (dD_{ij} + qQ_{ij})\phi_j + r_i\phi_i = \lambda\phi_i. \ i = 1, \dots, n,$$
(2.1)

The global dynamics of the single species model (1.1) is determined by the sign of  $\lambda_1(d, q, r)$  (see Cosner 1996; Li and Shuai 2010; Lu and Takeuchi 1993 for the proof):

**Lemma 2.1** Suppose that H1,  $H1^*$  or  $H1^{**}$  holds. Let  $\lambda_1(d, q, r)$  be the principal eigenvalue of (2.1). If  $\lambda_1(d, q, r) \leq 0$ , then the trivial equilibrium **0** of (1.1) is globally asymptotically stable; and if  $\lambda_1(d, q, r) > 0$ , then model (1.1) admits a unique positive equilibrium  $\mathbf{u}^* \gg \mathbf{0}$ , which is globally asymptotically stable.

For further applications, we need the following result about the monotonicity of the spectral bound/principal eigenvalue (Altenberg 2012; Chen et al. 2022b).

**Lemma 2.2** Let  $A = (a_{ij})_{n \times n}$  be an irreducible essentially nonnegative matrix and  $R = diag(r_i)$  be a real diagonal matrix. Then, the following results hold:

(i) *If* s(A) < 0, *then* 

$$\frac{\mathrm{d}}{\mathrm{d}\mu}s(\mu A + R) < 0$$

for  $\mu \in (0, \infty)$ ; Moreover,

$$\lim_{\mu \to 0} s(\mu A + R) = \max_{1 \le i \le n} \{r_i\} \text{ and } \lim_{\mu \to \infty} s(\mu A + R) = -\infty;$$

(ii) If s(A) = 0, then

$$\frac{\mathrm{d}}{\mathrm{d}\mu}s(\mu A + R) \le 0$$

for  $\mu \in (0, \infty)$  and the equality holds if and only  $r_1 = \cdots = r_n$ ; Moreover,

$$\lim_{\mu \to 0} s(\mu A + R) = \max_{1 \le i \le n} r_i \quad and \quad \lim_{\mu \to \infty} s(\mu A + R) = \sum_{i=1}^n \theta_i r_i,$$

where  $\theta_i \in (0, 1), 1 \le i \le n$ , is determined by A and  $\sum_{i=1}^{n} \theta_1 = 1$  (if A has each column sum equaling zero, then  $\boldsymbol{\theta} = (\theta_1, \dots, \theta_n)^T$  is a positive eigenvector of A corresponding to eigenvalue 0).

We will use the monotone dynamical system theory (Hess 1991; Hsu et al. 1996; Lam and Munther 2016; Smith 1995) to investigate the global dynamics of the Lotka– Volterra competition system (1.4). Let  $X = (\mathbb{R}^n_+ \times \mathbb{R}^n_+, \leq_K)$  be an ordered Banach space with the order  $\leq_K$  generated by the cone  $K = \mathbb{R}^n_+ \times (-\mathbb{R}^n_+)$ . That is, for x = $(u_1, v_1), y = (u_2, v_2) \in X$ , we say  $x \leq_K y$  if  $u_1 \leq u_2$  and  $v_1 \geq v_2$ ;  $x <_K y$  if  $x \leq_K y$ and  $x \neq y$ . The solutions of (1.4) induce a strictly monotone dynamical system in X: for two initial data  $(u_{1,0}, v_{1,0}) <_K (u_{2,0}, v_{2,0})$ , the corresponding solutions of (1.4) satisfy  $(u_1(t), v_1(t)) <_K (u_2(t), v_2(t))$  for all  $t \geq 0$ . By the strictly monotone dynamical system theory, the global dynamics of (1.4) is largely determined by the local/linearized stability of the semi-trivial equilibria  $E_1$  and  $E_2$ :

- 1. if  $E_2$  is unstable and (1.4) has no positive equilibrium, then  $E_1$  is globally asymptotically stable; if  $E_1$  is unstable and (1.4) has no positive equilibrium, then  $E_2$  is globally asymptotically stable;
- 2. if  $E_1$  and  $E_2$  are both unstable, then (1.4) has at least one stable positive equilibrium, which is globally asymptotically stable if it is unique;
- 3. if  $E_1$  and  $E_2$  are both locally asymptotically stable, then (1.4) has at least one unstable positive equilibrium.

# **3 Persistence of a Single Species**

In this section, we consider the mutual effects of the diffusion and advection rates on the dynamics of the single species model (1.1). By Lemma 2.1, the global dynamics of the model is determined by the sign of  $\lambda_1(d, q, r)$ . In this section, we study the properties of  $\lambda_1(d, q, r)$  with respect to *d* and *q* in cases (a)–(b).

# 3.1 Monotonicity of $\lambda_1(d, q, r)$ in q

In this subsection, we study the monotonicity of  $\lambda_1(d, q, r)$  with respect to the advection rate q.

**Lemma 3.1** Suppose that H1 or  $H1^*$  holds. Let  $\lambda_1(d, q, r)$  be the principal eigenvalue of (2.1). Then, for fixed d > 0,  $\lambda_1(d, q, r)$  is strictly decreasing with respect to q in  $[0, \infty)$ . Moreover,

$$\lim_{q \to 0} \lambda_1(d, q, \mathbf{r}) = \lambda_1(d, 0, \mathbf{r}) \text{ and } \lim_{q \to \infty} \lambda_1(d, q, \mathbf{r}) = -\infty.$$
(3.1)

**Proof** Let  $\boldsymbol{\phi} = (\phi_1, \phi_2, \dots, \phi_n)^T \gg \mathbf{0}$  be the eigenvector corresponding to the principal eigenvalue  $\lambda_1(d, q, r)$  with

$$\sum_{i=1}^{n} \phi_i = 1, \quad q \in [0, \infty).$$
(3.2)

Differentiating (2.1) with respect to q yields

$$\frac{\partial \lambda_1}{\partial q}\phi_i + \lambda_1 \frac{\partial \phi_i}{\partial q} = \sum_{j=1}^n \left( dD_{ij} + qQ_{ij} \right) \frac{\partial \phi_j}{\partial q} + \sum_{j=1}^n Q_{ij}\phi_j + r_i \frac{\partial \phi_i}{\partial q}.$$
 (3.3)

Then, multiplying (3.3) by  $\phi_i$  and (2.1) by  $\frac{\partial \phi_i}{\partial q}$  and taking the difference, we have

$$\frac{\partial\lambda_1}{\partial q}\phi_i^2 = \sum_{j\neq i} \left( dD_{ij} + qQ_{ij} \right) \left( \frac{\partial\phi_j}{\partial q}\phi_i - \frac{\partial\phi_i}{\partial q}\phi_j \right) + \sum_{j=1}^n Q_{ij}\phi_i\phi_j.$$
(3.4)

Let

$$(\beta_1, \beta_2, \beta_3, \dots, \beta_n) = \left(1, \frac{d}{d+q}, \left(\frac{d}{d+q}\right)^2, \dots, \left(\frac{d}{d+q}\right)^{n-1}\right)$$

Multiplying (3.4) by  $\beta_i$  and summing them over *i*, we obtain

$$\frac{\partial\lambda_1}{\partial q}\sum_{i=1}^n\beta_i\phi_i^2 = \sum_{i=1}^n\sum_{j\neq i}\beta_i\left(dD_{ij} + qQ_{ij}\right)\left(\frac{\partial\phi_j}{\partial q}\phi_i - \frac{\partial\phi_i}{\partial q}\phi_j\right) + \sum_{i=1}^n\sum_{j=1}^n\beta_iQ_{ij}\phi_i\phi_j.$$
(3.5)

A direct computation yields

$$\sum_{i=1}^{n} \sum_{j \neq i} \beta_i \left( dD_{ij} + q Q_{ij} \right) \left( \frac{\partial \phi_j}{\partial q} \phi_i - \frac{\partial \phi_i}{\partial q} \phi_j \right)$$
  
= 
$$\sum_{i=1}^{n-1} \left[ \beta_i d \left( \frac{\partial \phi_{i+1}}{\partial q} \phi_i - \frac{\partial \phi_i}{\partial q} \phi_{i+1} \right) + \beta_{i+1} (d+q) \left( \frac{\partial \phi_i}{\partial q} \phi_{i+1} - \frac{\partial \phi_{i+1}}{\partial q} \phi_i \right) \right]$$
  
= 
$$\sum_{i=1}^{n-1} \left[ (\beta_i d - \beta_{i+1} (d+q)) \left( \frac{\partial \phi_{i+1}}{\partial q} \phi_i - \frac{\partial \phi_i}{\partial q} \phi_{i+1} \right) \right] = 0,$$
  
(3.6)

where we have used  $\beta_i d - \beta_{i+1}(d+q) = 0$  for all i = 1, 2, ..., n-1. This, combined with (3.5), implies that

$$\frac{\partial \lambda_1}{\partial q} \sum_{i=1}^n \beta_i \phi_i^2 = \sum_{i=1}^n \sum_{j=1}^n \beta_i Q_{ij} \phi_i \phi_j$$

$$= -\sum_{i=1}^n \beta_i \phi_i^2 + \sum_{i=1}^{n-1} \beta_{i+1} \phi_i \phi_{i+1}$$

$$= -\frac{\beta_1}{2} \phi_1^2 - \frac{\beta_n}{2} \phi_n^2 - \sum_{i=1}^{n-1} \left( \frac{\beta_i}{2} \phi_i^2 - \beta_{i+1} \phi_i \phi_{i+1} + \frac{\beta_{i+1}}{2} \phi_{i+1}^2 \right) < 0,$$
(3.7)

where we have used the fact that

$$\frac{\beta_i}{2}\phi_i^2 - \beta_{i+1}\phi_i\phi_{i+1} + \frac{\beta_{i+1}}{2}\phi_{i+1}^2 \ge \frac{\beta_{i+1}}{2}(\phi_i - \phi_{i+1})^2 \ge 0$$

as  $\beta_i \ge \beta_{i+1}$  for i = 1, ..., n-1. This implies that  $\lambda_1(d, q, r)$  is strictly decreasing with respect to q in  $[0, \infty)$ .

Clearly,  $\lim_{q\to 0} \lambda_1(d, q, r) = \lambda_1(d, 0, r)$ . It remains to show  $\lim_{q\to\infty} \lambda_1(d, q, r) = -\infty$ . Since  $\lambda_1(d, q, r)$  is decreasing in q, the limit  $\lim_{q\to\infty} \lambda_1(d, q, r)$  exists in  $[-\infty, \infty)$ . Suppose to the contrary that  $\lim_{q\to\infty} \lambda_1(d, q, r) \in (-\infty, \infty)$ . By (3.2), up to a subsequence, we have  $\lim_{q\to\infty} \phi = \phi^*$ , where  $\phi^* = (\phi_1^*, \dots, \phi_n^*)^T \ge \mathbf{0}$  and  $\sum_{i=1}^n \phi_i^* = 1$ . Dividing both sides of (2.1) by q and taking  $q \to \infty$ , we have

$$\sum_{j=1}^{n} Q_{ij} \phi_j^* = \mathbf{0}, \ i = 1, \dots, n.$$

This implies that  $\phi^* = 0$ , which is a contradiction. Therefore, we have  $\lim_{q \to \infty} \lambda_1(d, q, \mathbf{r}) = -\infty$ .

From Lemmas 2.1–2.2 and 3.1, we obtain the following results about the impact of d and q on the dynamics of model (1.1) for case (a).

**Proposition 3.2** Suppose that H1 holds. Then, the following statements hold:

- (i) If  $\sum_{i=1}^{n} r_i > 0$ , then for any d > 0 there exists  $q_r^*(d) > 0$  such that  $\lambda_1(d, q_r^*(d), \mathbf{r}) = 0$ ,  $\lambda_1(d, q, \mathbf{r}) < 0$  for  $q > q_r^*(d)$ , and  $\lambda_1(d, q, \mathbf{r}) > 0$  for  $q < q_r^*(d)$ . Moreover, we have the following results:
  - (i1) If  $q \ge q_r^*(d)$ , then the trivial equilibrium **0** of model (1.1) is globally asymptotically stable;
  - (i2) If  $q < q_r^*(d)$ , model (1.1) admits a unique positive equilibrium, which is globally asymptotically stable;
- (ii) If  $\sum_{i=1}^{n} r_i < 0 < \max_{1 \le i \le n} r_i$ , then there exists  $d^* > 0$  such that  $\lambda_1(d^*, 0, \mathbf{r}) = 0$ ,  $\lambda_1(d, 0, \mathbf{r}) < 0$  for  $d > d^*$ , and  $\lambda_1(d, 0, \mathbf{r}) > 0$  for  $d < d^*$ ; Moreover, we have the following results:
- (ii) If  $d \in (0, d^*)$ , then there exists  $q_r^*(d) > 0$  such that (i<sub>1</sub>)–(i<sub>2</sub>) hold;
- (ii<sub>2</sub>) If  $d \ge d^*$ , then for any q > 0, the trivial equilibrium **0** of model (1.1) is globally asymptotically stable;
- (iii) If  $\max_{1 \le i \le n} r_i \le 0$ , then the trivial equilibrium **0** of model (1.1) is globally asymptotically stable for any d > 0 and  $q \ge 0$ .

**Proof** Note that D is an irreducible essentially nonnegative matrix with s(D) = 0 corresponding with a positive eigenvector (1/n, ..., 1/n). It follows from Lemma 2.2 that

$$\frac{\partial\lambda_1(d,0,\boldsymbol{r})}{\partial d} \leq 0,$$

where the equality holds if and only  $r_1 = \cdots = r_n$ . Moreover,

$$\lim_{d\to 0} \lambda_1(d,0,\boldsymbol{r}) = \max_{1\leq i\leq n} r_i \text{ and } \lim_{d\to\infty} \lambda_1(d,0,\boldsymbol{r}) = \frac{\sum_{i=1}^n r_i}{n}.$$

This, combined with Lemmas 2.1 and 3.1, implies (i)–(iii).

A similar result holds for case (b).

**Proposition 3.3** Suppose that **H**1<sup>\*</sup> holds. Then, we the following results:

- (i) If  $\max_{1 \le i \le n} r_i > 0$ , then there exists  $d^* > 0$  such that  $\lambda_1(d^*, 0, \mathbf{r}) = 0$ ,  $\lambda_1(d, 0, \mathbf{r}) < 0$  for  $d > d^*$ , and  $\lambda_1(d, 0, \mathbf{r}) > 0$  for  $d < d^*$ ; Moreover, we have:
  - (i1) If  $d \in (0, d^*)$ , then there exists  $q_r^*(d) > 0$  such that (i1)–(i2) in Proposition 3.2 hold;
  - (i2) If  $d \ge d^*$ , then for any q > 0, the trivial equilibrium **0** of model (1.1) is globally asymptotically stable;
- (ii) If  $\max_{1 \le i \le n} r_i \le 0$ , then the trivial equilibrium **0** of model (1.1) is globally asymptotically stable for any d > 0 and  $q \ge 0$ .

**Proof** Since s(D) < 0, by Lemma 2.2, we have

$$\frac{\partial\lambda_1(d,0,\boldsymbol{r})}{\partial d} < 0,$$

and

$$\lim_{d\to 0} \lambda_1(d, 0, \boldsymbol{r}) = \max_{1 \le i \le n} r_i \text{ and } \lim_{d\to \infty} \lambda_1(d, 0, \boldsymbol{r}) = -\infty.$$

This, combined with Lemmas 2.1 and 3.1, implies (i)–(ii).

#### **3.2 Dependence of** $\lambda_1(d, q, r)$ on *d*

In this section, we study the dependence of  $\lambda_1(d, q, r)$  on d for cases (a)–(b). When the directed movement rate q = 0, we know that  $\lambda_1(d, 0, r)$  is decreasing in  $d \in (0, \infty)$ . However, this may no longer be true when q > 0.

We first compute the limits of  $\lambda_1$  as  $d \to 0$  or  $\infty$  in case (a).

**Lemma 3.4** Suppose that H1 holds. Let  $\lambda_1(d, q, r)$  be the principal eigenvalue of (2.1). Then, we have the following:

$$\lim_{d\to 0} \lambda_1(d, q, \mathbf{r}) = \max_{1 \le i \le n} r_i - q, \text{ and } \lim_{d\to \infty} \lambda_1(d, q, \mathbf{r}) = \frac{\sum_{i=1}^n r_i - q}{n}.$$

**Proof** Firstly, it is easy to see that  $\lim_{d\to 0} \lambda_1(d, q, \mathbf{r}) = \lambda_1(0, q, \mathbf{r}) = \max_{1 \le i \le n} r_i - q$ . Then, we compute the limit of  $\lambda_1(d, q, \mathbf{r})$  as  $q \to \infty$ . Let  $\boldsymbol{\phi} = (\phi_1, \phi_2, \dots, \phi_n)^T \gg$ 

**0** be the eigenvector corresponding to the principal eigenvalue  $\lambda_1(d, q, r)$  with  $\sum_{i=1}^{n} \phi_i = 1$ . Summing all the equations in (2.1), we have

$$\sum_{i=1}^{n} \sum_{j=1}^{n} (dD_{ij} + qQ_{ij})\phi_j + \sum_{i=1}^{n} r_i\phi_i = \lambda_1(d, q, \mathbf{r}) \sum_{i=1}^{n} \phi_i.$$
(3.8)

It follows from H1 that

$$\sum_{i=1}^{n} \sum_{j=1}^{n} D_{ij}\phi_j = 0 \text{ and } \sum_{i=1}^{n} \sum_{j=1}^{n} Q_{ij}\phi_j = -\phi_n.$$

Therefore, by (3.8), we have

$$-q\phi_n + \sum_{i=1}^n r_i\phi_i = \lambda_1(d, q, r) \sum_{i=1}^n \phi_i.$$
 (3.9)

This gives a bound for  $\lambda_1(d, q, r)$ :

$$\min_{1\leq i\leq n}r_i-q\leq \lambda_1(d,q,\mathbf{r})\leq \max_{1\leq i\leq n}r_i,$$

which implies that

$$\lim_{d \to \infty} \lambda_1(d, q, \mathbf{r}) \in (-\infty, \max_{1 \le i \le n} r_i].$$
(3.10)

Up to a subsequence, we may assume  $\lim_{d\to\infty} \lambda_1(d, q, \mathbf{r}) = a$  and  $\lim_{d\to\infty} \boldsymbol{\phi} = \bar{\boldsymbol{\phi}}$ , where  $\bar{\boldsymbol{\phi}} = (\bar{\phi}_1, \dots, \bar{\phi}_n)^T \ge \mathbf{0}$  and  $\sum_{i=1}^n \bar{\phi}_i = 1$ . Dividing both sides of (2.1) by dand taking  $d \to \infty$ , we have  $D\bar{\boldsymbol{\phi}} = \mathbf{0}$ , which implies that

$$\bar{\boldsymbol{\phi}} = (\bar{\phi}_1, \dots, \bar{\phi}_n)^T = \left(\frac{1}{n}, \dots, \frac{1}{n}\right)^T.$$
(3.11)

Taking  $d \to \infty$  in (3.9), we have

$$-q\bar{\phi}_n + \sum_{i=1}^n r_i\bar{\phi}_i = a\sum_{i=1}^n \bar{\phi}_i.$$

This gives

$$\lim_{d\to\infty}\lambda_1(d,q,\mathbf{r})=a=\frac{\sum_{i=1}^nr_i-q}{n}.$$

For  $\hat{\mathbf{r}} \gg \mathbf{0}$ , the principal eigenvalue  $\lambda_1(d, q, \hat{\mathbf{r}})$  satisfies the following property for case (*a*), which will be useful later.

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**Lemma 3.5** Suppose that H1 holds. Let  $\lambda_1(d, q, \hat{r})$  be the principal eigenvalue of (2.1) with  $\hat{r} \gg 0$ . If  $\lambda_1(d^*, q, \hat{r}) = 0$  for some  $d^* > 0$ , then

$$\frac{\partial}{\partial d}\lambda_1(d,q,\hat{\boldsymbol{r}})\Big|_{d=d^*} > 0.$$
(3.12)

**Proof** Let  $\boldsymbol{\phi} = (\phi_1, \phi_2, \dots, \phi_n)^T \gg \mathbf{0}$  be the positive eigenvector corresponding to the eigenvalue  $\lambda_1(d, q, \hat{\boldsymbol{r}})$  with  $\sum_{i=1}^n \phi_i = 1$ . By similar arguments as in the proof of Lemma 3.1, we obtain

$$\frac{\partial \lambda_1}{\partial d} \sum_{i=1}^n \beta_i \phi_i^2 = \sum_{i=1}^n \sum_{j=1}^n \beta_i D_{ij} \phi_i \phi_j,$$

where  $\beta_i$  is defined in (3.1). A direct computation implies that

$$\frac{\partial \lambda_1}{\partial d} \sum_{i=1}^n \beta_i \phi_i^2 = \sum_{i=1}^{n-1} \beta_i \left( \phi_{i+1} - \phi_i \right) \left[ \phi_i - \left( \frac{d}{d+q} \right) \phi_{i+1} \right].$$
(3.13)

If  $\lambda_1(d^*, q, \hat{r}) = 0$ , then we see from (2.1) that

$$(d^* + q)(\phi_{n-1} - \phi_n) = -\hat{r}_n \phi_n, (d^* + q)(\phi_{i-1} - \phi_i) = -\hat{r}_i \phi_i + d^*(\phi_i - \phi_{i+1}), \quad i = 2, \dots, n-1.$$
(3.14)

Since  $\hat{r} \gg 0$ , we have

$$\phi_1 < \phi_2 < \dots < \phi_n. \tag{3.15}$$

Summing the first k equations in (2.1), where  $1 \le k \le n - 1$ , we find

$$d^*\phi_{k+1} - (d^* + q)\phi_k = -\sum_{i=1}^k \hat{r}_i\phi_i < 0.$$

This, combined with (3.13) and (3.15), implies (3.12).

We also have the limits of  $\lambda_1$  as  $d \to 0$  or  $\infty$  in case (b).

**Lemma 3.6** Suppose that  $H1^*$  holds. Let  $\lambda_1(d, q, r)$  be the principal eigenvalue of (2.1). Then, we have the following:

$$\lim_{d\to 0} \lambda_1(d, q, \mathbf{r}) = \max_{1 \le i \le n} r_i - q, \text{ and } \lim_{d\to \infty} \lambda_1(d, q, \mathbf{r}) = -\infty.$$

**Proof** The proof is similar to that of Lemma 3.4, and the difference is that (3.9) is replaced by the following equation:

$$-(d+q)\phi_n + \sum_{i=1}^n r_i\phi_i = \lambda_1(d,q,r) \sum_{i=1}^n \phi_i.$$
 (3.16)

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This gives a bound for  $\lambda_1(d, q, \mathbf{r})$ :

$$\min_{1\leq i\leq n}r_i-(d+q)\leq \lambda_1(d,q,r)\leq \max_{1\leq i\leq n}r_i.$$

Assume to the contrary that  $\lim_{d\to\infty} \lambda_1(d, q, r) \neq -\infty$ . Up to a subsequence, we may assume  $\lim_{d\to\infty} \lambda_1(d, q, r) = a \in (-\infty, \max_{1 \le i \le n} r_i]$  and  $\lim_{d\to\infty} \phi = \overline{\phi}$ , where  $\overline{\phi} = (\overline{\phi}_1, \ldots, \overline{\phi}_n) \ge 0$  and  $\sum_{i=1}^n \overline{\phi}_i = 1$ . Dividing both sides of (2.1) by *d* and taking  $d \to \infty$ , we have  $D\overline{\phi} = 0$ . So  $\overline{\phi}$  is a nonnegative eigenvector corresponding with eigenvalue 0 of *D*. This contradicts with s(D) < 0. Therefore,  $\lim_{d\to\infty} \lambda_1(d, q, r) = -\infty$ .

#### 3.3 Some Properties on $q_r^*(d)$

In this subsection, we give some properties on function  $q_r^*(d)$  obtained in Propositions 3.2 and 3.3, which will be used in the next section.

We first consider case (a).

**Lemma 3.7** Suppose that H1 holds and  $r \gg 0$ , and let  $q_r^*(d)$  be defined in Proposition 3.2. Then, the following statements about  $q_r^*(d)$  hold:

- (i)  $q_r^*(d)$  is strictly increasing with respect to d in  $(0, \infty)$ ;
- (ii)  $\lim_{d\to 0} q_r^*(d) = \max_{1 \le i \le n} r_i$ , and  $\lim_{d\to\infty} q_r^*(d) = \sum_{i=1}^n r_i$ ;
- (iii) If  $r_1 > r_2 \gg 0$ , then  $q_{r_1}^*(d) > q_{r_2}^*(d)$  for any d > 0.

**Proof** (i) Let  $d_1 > d_2 > 0$ . Then, by the definition of  $q_r^*(d)$ , we have

$$\lambda_1(d_1, q_r^*(d_1), r) = \lambda_1(d_2, q_r^*(d_2), r) = 0.$$

This, combined with Lemma 3.5, yields

$$\lambda_1 \left( d_1, q_{\boldsymbol{r}}^*(d_1), \boldsymbol{r} \right) - \lambda_1 \left( d_1, q_{\boldsymbol{r}}^*(d_2), \boldsymbol{r} \right) = \lambda_1 \left( d_2, q_{\boldsymbol{r}}^*(d_2), \boldsymbol{r} \right) - \lambda_1 \left( d_1, q_{\boldsymbol{r}}^*(d_2), \boldsymbol{r} \right) < 0.$$
(3.17)

By Lemma 3.1,  $\lambda_1(d, q, r)$  is strictly decreasing with respect to q. Therefore, we can see from (3.17) that  $q_r^*(d_1) > q_r^*(d_2)$ .

(ii) Since  $q_r^*(d)$  is strictly increasing with respect to d, the limit  $\lim_{d\to 0} q_r^*(d)$  exists in  $[0, \infty)$  and the limit  $\lim_{d\to\infty} q_r^*(d)$  exists in  $(0, \infty)$ . We denote

$$a_1 := \lim_{d \to 0} q_{\mathbf{r}}^*(d)$$
 and  $a_2 := \lim_{d \to \infty} q_{\mathbf{r}}^*(d)$ .

We first suppose that  $a_1 \neq 0$  (i.e.,  $a_1 > 0$ ). Then, for sufficiently small  $\epsilon > 0$ , there exists  $\bar{d} > 0$  such that  $0 < a_1 - \epsilon < q_r^*(d) < a_1 + \epsilon$  for all  $0 < d < \bar{d}$ . Since  $\lambda_1(d, q, r)$  is strictly decreasing in q, we have

$$\lambda_1(d, a_1 + \epsilon, \mathbf{r}) < \lambda_1(d, q_{\mathbf{r}}^*(d), \mathbf{r}) = 0 \le \lambda_1(d, a_1 - \epsilon, \mathbf{r})$$
(3.18)

for all  $0 < d < \overline{d}$ . Taking  $d \to 0$  in (3.18) and using Lemma 3.4, we have

$$\max_{1 \le i \le n} r_i - (a_1 + \epsilon) \le 0 \le \max_{1 \le i \le n} r_i - (a_1 - \epsilon).$$
(3.19)

This gives  $\max_{1 \le i \le n} r_i - \epsilon \le a_1 \le \max_{1 \le i \le n} r_i + \epsilon$ . Since  $\epsilon > 0$  is arbitrary, we have  $a_1 = \max_{1 \le i \le n} r_i$ . If  $a_1 = 0$ , then the first inequality of (3.19) still holds, which gives  $\max_{1 \le i \le n} r_i \le \epsilon$ . Since  $\epsilon > 0$  is arbitrary, we have  $\mathbf{r} = \mathbf{0}$ , which is a contradiction. This proves  $\lim_{d \to 0} q_{\mathbf{r}}^*(d) = \max_{1 \le i \le n} r_i$ .

Let  $\boldsymbol{\phi} = (\phi_1, \phi_2, \dots, \phi_n)^T \gg \mathbf{0}$  be the eigenvector corresponding to the eigenvalue  $\lambda_1(d, q_r^*(d), r) = 0$  with  $\sum_{i=1}^n \phi_i = 1$ . Then, we have

$$dD\boldsymbol{\phi} + q_{\boldsymbol{r}}^{*}(d)Q\boldsymbol{\phi} + \operatorname{diag}(r_{i})\boldsymbol{\phi} = \boldsymbol{0}.$$
(3.20)

Up to a subsequence, we may assume  $\lim_{d\to\infty} \phi = \phi^*$ , where  $\phi^* = (\phi_1^*, \dots, \phi_n^*)^T \ge 0$  and  $\sum_{i=1}^n \phi_i^* = 1$ . Now, we claim that  $a_2 \ne \infty$ . Suppose to the contrary that  $a_2 = \infty$ . Multiplying (3.20) by  $(1, \dots, 1)$  and dividing both sides by  $q_r^*(d)$ , we obtain

$$-\phi_n + \frac{1}{q_r^*(d)} \sum_{i=1}^n r_i \phi_i = 0, \qquad (3.21)$$

which yields  $\phi_n^* = \lim_{d\to\infty} \phi_n = 0$ . By virtue of (3.20) again, we obtain that

$$\phi_{n-1} - \phi_n = \frac{-r_n \phi_n}{d + q_r^*(d)},$$
  

$$\phi_{i-1} - \phi_i = \frac{d}{d + q_r^*(d)} (\phi_i - \phi_{i+1}) - \frac{r_i \phi_i}{d + q_r^*(d)}, \quad i = 2, \dots, n-1.$$
(3.22)

Taking  $d \to \infty$  in (3.22), we have  $\phi_1^* = \cdots = \phi_n^*$ , and consequently  $\phi^* = 0$ . This is a contradiction, and hence,  $a_2 \in (-\infty, \infty)$ . Dividing (3.20) by d and taking  $d \to \infty$ , we have  $D\phi^* = 0$ , which implies that

$$\boldsymbol{\phi}^* = \left(\phi_1^*, \dots, \phi_n^*\right)^T = \left(\frac{1}{n}, \dots, \frac{1}{n}\right)^T.$$

Then taking the limit of (3.21), we have  $a_2 = \sum_{i=1}^{n} r_i$ .

(iii) Clearly, if  $r_1 > r_2$ , then

$$\lambda_1(d, q, r_1) > \lambda_1(d, q, r_2) \text{ for any } d, q > 0.$$
 (3.23)

Note that  $\lambda_1(d, q_{r_1}^*(d), r_1) = \lambda_1(d, q_{r_2}^*(d), r_2) = 0$ . This, combined with (3.23), implies that

$$\lambda_1(d, q_{r_1}^*(d), r_1) - \lambda_1(d, q_{r_2}^*(d), r_1) = \lambda_1(d, q_{r_2}^*(d), r_2) - \lambda_1(d, q_{r_2}^*(d), r_1) < 0.$$

Since  $\lambda_1(d, q, r)$  is strictly decreasing in q, we have  $q_{r_1}^*(d) > q_{r_2}^*(d)$  as desired.

Next, we consider case (b).

**Lemma 3.8** Suppose that  $H1^*$  holds, and let  $q_r^*(d)$  and  $d^*$  be defined in Proposition 3.3. Then, the following statements hold:

(i) If  $\mathbf{r} = (r_1, ..., r_n)$  satisfies  $\max_{1 \le i \le n} r_i > 0$ , then

$$\lim_{d \to 0} q_{r}^{*}(d) = \max_{1 \le i \le n} r_{i} \text{ and } \lim_{d \to d^{*}} q_{r}^{*}(d) = 0;$$

- (ii) If  $\mathbf{r}_j = (r_{j,1}, \dots, r_{j,n})$  satisfies  $\mathbf{r}_1 > \mathbf{r}_2$  and  $\max_{1 \le i \le n} r_{j,i} > 0$  for j = 1, 2, then  $q_{\mathbf{r}_1}^*(d) > q_{\mathbf{r}_2}^*(d)$  for any  $d \in (0, \hat{d})$ . Here,  $\hat{d} = \min\{d_1^*, d_2^*\} = d_2^*$ , where  $\lambda_1(d_1^*, 0, \mathbf{r}_1) = \lambda_1(d_2^*, 0, \mathbf{r}_2) = 0$ ;
- (iii) If  $\mathbf{r} = (r, \ldots, r)$  with r > 0 and  $q_r^*(\bar{d}) < r$  for some  $\bar{d} \in (0, d^*)$ , then  $[q_r^*(d)]' < 0$  for  $d \in [\bar{d}, d^*)$ .

**Proof** (i) By Proposition 3.3 and  $\max_{1 \le i \le n} r_i > 0$ ,  $q_r^*(d)$  is well-defined. Up to a subsequence, we have

$$a_1 := \lim_{d \to 0} q_r^*(d)$$
 and  $a_2 := \lim_{d \to d^*} q_r^*(d)$ ,

where  $a_1, a_2 \in [0, \infty]$ . Using the same argument as in the proof of Lemma 3.7, we can show  $a_1, a_2 \neq \infty$ . Then, similar to Lemma 3.7, we can use Lemma 3.6 to compute  $a_1 = \max_{1 \le i \le n} r_i$ .

Now, we claim that  $a_2 = 0$ . If it is not true, then for sufficiently small  $\epsilon > 0$ , there exists  $\bar{d} > 0$  such that  $0 < a_2 - \epsilon < q_r^*(d) < a_2 + \epsilon$  for all  $d \in (\bar{d}, d^*)$ . Since  $\lambda_1(d, q_r^*(d), r) = 0$  and  $\lambda_1(d, q, r)$  is strictly decreasing in q, we have

$$\lambda_1(d, a_2 + \epsilon, \mathbf{r}) < \lambda_1(d, q_{\mathbf{r}}^*(d), \mathbf{r}) = 0 < \lambda_1(d, a_2 - \epsilon, \mathbf{r}).$$

for all  $d \in (\bar{d}, d^*)$ . Taking  $d \to d^*$ , we have

$$\lambda_1(d^*, a_2 + \epsilon, \mathbf{r}) \le 0 \le \lambda_1(d^*, a_2 - \epsilon, \mathbf{r}).$$

Taking  $\epsilon \to 0$ , we have  $\lambda_1(d^*, a_2, \mathbf{r}) = 0$ , which contradicts with  $a_2 > 0$ .

The proof of (ii) is similar to the one for Lemma 3.7, so we omit it here.

(iii) Let  $\boldsymbol{\phi} = (\phi_1, \phi_2, \dots, \phi_n)^T \gg \mathbf{0}$  be the eigenvector corresponding to the eigenvalue  $\lambda_1(d, q_r^*(d), r) = 0$  with  $\sum_{i=1}^n \phi_i = 1$ . Then, we have

$$d\sum_{j=1}^{n} D_{ij}\phi_j + q_r^*(d)\sum_{j=1}^{n} Q_{ij}\phi_j + r\phi_i = 0.$$
(3.24)

Differentiating (3.24) with respect to d, we obtain

$$\sum_{j=1}^{n} D_{ij}\phi_j + \sum_{j=1}^{n} D_{ij}\phi'_j + [q_r^*(d)]' \sum_{j=1}^{n} Q_{ij}\phi_j + q_r^*(d) \sum_{j=1}^{n} Q_{ij}\phi'_j + r\phi'_i = 0.$$
(3.25)

Multiplying (3.25) by  $\phi_i$  and (3.24) by  $\phi'_i$  and taking the difference, we have

$$[q_{\mathbf{r}}^{*}(d)]' \sum_{j=1}^{n} Q_{ij}\phi_{i}\phi_{j} = -\sum_{j=1}^{n} (dD_{ij} + q_{\mathbf{r}}^{*}(d)Q_{ij})(\phi_{i}\phi_{j}' - \phi_{i}'\phi_{j}) - \sum_{j=1}^{n} D_{ij}\phi_{i}\phi_{j}.$$
(3.26)

Similar to the proof of Lemma 3.1, let

$$(\beta_1, \beta_2, \beta_3, \dots, \beta_n) = \left(1, \frac{d}{d + q_r^*(d)}, \left(\frac{d}{d + q_r^*(d)}\right)^2, \dots, \left(\frac{d}{d + q_r^*(d)}\right)^{n-1}\right).$$

Multiplying (3.26) by  $\beta_i$  and summing them over *i*, we obtain

$$[q_{\mathbf{r}}^{*}(d)]' \sum_{i=1}^{n} \sum_{j=1}^{n} \beta_{i} Q_{ij} \phi_{i} \phi_{j} = -\sum_{i=1}^{n} \sum_{j=1}^{n} \beta_{i} D_{ij} \phi_{i} \phi_{j}, \qquad (3.27)$$

where we have used

$$\sum_{i=1}^{n} \sum_{j=1}^{n} \beta_i \left( dD_{ij} + q_r^*(d)Q_{ij} \right) \left( \phi_i \phi'_j - \phi'_i \phi_j \right) = 0.$$

By (3.7), we have

$$\sum_{i=1}^{n} \sum_{j=1}^{n} \beta_i Q_{ij} \phi_i \phi_j < 0.$$
(3.28)

A direct computation gives

$$\sum_{i=1}^{n} \sum_{j=1}^{n} \beta_i D_{ij} \phi_i \phi_j = \sum_{i=1}^{n-1} \beta_i \left( \phi_{i+1} - \phi_i \right) \left[ \phi_i - \left( \frac{d}{d+q_r^*(d)} \right) \phi_{i+1} \right] - \beta_n \phi_n^2.$$
(3.29)

Suppose  $q_r^*(\bar{d}) < r$  for some  $\bar{d} \in (0, d^*)$ . We can rewrite (3.24) as

$$\bar{d}(\phi_1 - \phi_2) = (r - q_r^*(\bar{d}))\phi_1, 
\bar{d}(\phi_i - \phi_{i+1}) = (\bar{d} + q_r^*(\bar{d}))(\phi_{i-1} - \phi_i) + r\phi_i, \quad i = 2, \dots, n-1,$$

$$\bar{d}(\phi_{n-1} - 2\phi_n) + q_r^*(\bar{d})(\phi_{n-1} - \phi_n) + r\phi_n = 0.$$
(3.30)

It follows from (3.30) that  $\phi_1 > \cdots > \phi_n$ . So, by (3.29), we have

$$\sum_{i=1}^n \sum_{j=1}^n \beta_i D_{ij} \phi_i \phi_j < 0.$$

This combined with (3.27)–(3.28) gives  $[q_r^*(\bar{d})]' < 0$ . Therefore, we must have  $[q_r^*(d)]' < 0$  for  $d \in [\bar{d}, d^*)$ .

**Remark 3.9** The monotonicity of  $\lambda_1(d, q, r)$  in q for cases (a) and (b) of reaction–diffusion models was proved in Lou and Lutscher (2014). To our best knowledge, the properties of  $q_r^*(d)$  were not studied for reaction–diffusion models.

# 4 Invasion Analysis for Two Competing Species

In this section, we study the evolution of diffusion and advection rates by considering the two species competition model (1.4). Throughout this section, assume  $\mathbf{r} = (r, ..., r) \gg 0$ .

If we treat  $\boldsymbol{u} = (u_1, \ldots, u_n)^T$  as the resident species and  $\boldsymbol{v} = (v_1, \ldots, v_n)^T$  as the mutant species, our purpose is to find conditions under which  $\boldsymbol{v}$  can or cannot invade. To this aim, we suppose that species  $\boldsymbol{u}$  has been established, and model (1.4) has a unique semi-trivial equilibrium by  $(\boldsymbol{u}^*, \boldsymbol{0})$ , where  $\boldsymbol{u}^* = (u_1^*, \ldots, u_n^*)^T \gg \boldsymbol{0}$  satisfies

$$\sum_{j=1}^{n} (d_1 D_{ij} + q_1 Q_{ij}) u_j + u_i (r - u_i) = 0, \quad i = 1, \dots, n,$$
(4.1)

where r > 0 in this section. Then, we study the stability of  $(u^*, 0)$  when  $d_2$  and  $q_2$  are different from  $d_1$  and  $q_1$ , respectively. Biologically, if  $(u^*, 0)$  is stable, this means that an introduction of small amount of species v cannot invade species u; if  $(u^*, 0)$  is unstable, this means that a small amount of species v may be able to destabilize the system and the mutant species v may be established.

We denote the **v**-only semi-trivial equilibrium by  $(\mathbf{0}, \mathbf{v}^*)$  if it exists, where  $\mathbf{v}^* = (v_1^*, \ldots, v_n^*)^T \gg \mathbf{0}$  solves

$$\sum_{j=1}^{n} (d_2 D_{ij} + q_2 Q_{ij}) v_j + v_i (r - v_i) = 0, \quad i = 1, \dots, n.$$
(4.2)

#### 4.1 Invasion Analysis for Case (a)

By Proposition 3.2,  $q_r^*(d_1) > 0$  exists for any  $d_1 > 0$ . We suppose that species u is established, i.e.,

**H2**.  $q_1 < q_r^*(d_1)$ ,

where  $q_r^*(d_1)$  satisfies  $\lambda_1(d_1, q_r^*(d_1), r) = 0$ . If **H**2 is satisfies, model (1.4) admits a unique semi-trivial equilibrium ( $u^*, 0$ ) by Proposition 3.2.

The following estimate about  $u^*$  will be useful later.

**Lemma 4.1** Suppose that H1 and H2 hold. Let  $\mathbf{u}^* = (u_1^*, \dots, u_n^*)^T$  be the unique positive solution of (4.1). Then,  $0 < u_1^* < \dots < u_n^* < r$ .

*Proof* It follows from (4.1) that

$$(d+q)(u_{n-1}^* - u_n^*) = -u_n^*(r - u_n^*),$$
  

$$(d+q)(u_{i-1}^* - u_i^*) = d(u_i^* - u_{i+1}^*) - u_i^*(r - u_i^*), \quad i = 2, \dots, n-1, \quad (4.3)$$
  

$$qu_1^* = d(u_2^* - u_1^*) + u_1^*(r - u_1^*).$$

We first claim that  $u_n^* < r$ . If it is not true, then we see from the first equation of (4.3) that  $u_{n-1}^* \ge u_n^* \ge r$ . By induction, we obtain from the second equation of (4.3) that

$$u_1^* \ge u_2^* \ge \cdots \ge u_n^* \ge r.$$

By the third equation of (4.3),

$$qu_1^* = d(u_2^* - u_1^*) + u_1^*(r - u_1^*) \le 0,$$

which contradicts with  $u_1^* > 0$ . Therefore,  $u_n^* < r$ . Then, by virtue of (4.3), we obtain that  $u_1^* < u_2^* < \cdots < u_n^* < r$ . This completes the proof.

By Lemma 4.1, we have  $r - u^* \gg 0$ . Therefore, the function  $q_{r-u^*}^*(d)$  is well-defined for  $d \in (0, \infty)$  by Lemma 3.2. Moreover, by Lemma 3.7 (iii), we have  $q_{r-u^*}^*(d) < q_r^*(d)$  for all d > 0.

**Proposition 4.2** Suppose that H1 and H2 hold. Then,  $q_{r-u^*}^*(d)$  is strictly increasing for  $d \in (0, \infty)$  with

$$\lim_{d \to 0} q_{r-u^*}^*(d) = r - u_1^* > 0 \text{ and } \lim_{d \to \infty} q_{r-u^*}^*(d) = \sum_{i=1}^n (r - u_i^*) > 0.$$

**Proof** By Lemma 4.1, we have  $0 < u_1^* < \cdots < u_n^* < r$ . Then, the results follow from Lemma 3.7.

We partition the first quadrant of the d - q plane into two disjoint subsets:

$$S_{1} := \{ (d, q) : q, d > 0, q > q_{r-u^{*}}^{*}(d) \},$$
  

$$S_{2} := \{ (d, q) : q, d > 0, q < q_{r-u^{*}}^{*}(d) \}.$$
(4.4)

We have the following result about the local stability of the semi-trivial equilibrium  $(u^*, 0)$  of model (1.4).

**Proposition 4.3** Suppose that H1 and H2 hold. Then, the following statements about the semi-trivial equilibrium  $(u^*, 0)$  of (1.4) hold:

- (i) If  $(d_2, q_2) \in S_1$ , then  $(\boldsymbol{u}^*, \boldsymbol{0})$  is locally asymptotically stable.
- (ii) If  $(d_2, q_2) \in S_2$ , then  $(\mathbf{u}^*, \mathbf{0})$  is unstable.

To characterize the set  $S_1$  and  $S_2$  more precisely, we first prove the following property about  $q = q_{r-n^*}^*(d)$ .

**Lemma 4.4** Suppose that H1 and H2 hold. Then, the two functions  $q = q_{r-u^*}^*(d)$  and  $q = \frac{q_1}{d_1}d$  have exactly one intersection point  $(d_1, q_1)$  in the first quadrant.

**Proof** Since  $\lambda_1(d_1, q_1, \mathbf{r} - \mathbf{u}^*) = 0$ , we have  $q_1 = q_{\mathbf{r}-\mathbf{u}^*}^*(d_1)$ . Therefore,  $d = d_1$  is a root of the equation  $q_{\mathbf{r}-\mathbf{u}^*}^*(d) - \frac{q_1}{d_1}d = 0$ . To see this is the only root, we suppose to the contrary that  $\bar{d}_1 \neq d_1$  is another root. Without loss of generality, we assume  $\bar{d}_1 = \bar{\mu}d_1$  for some  $\bar{\mu} > 1$ . So, we have  $q_{\mathbf{r}-\mathbf{u}^*}^*(\bar{d}_1) = \frac{q_1}{d_1}\bar{d}_1 = \bar{\mu}q_1$ . By Lemma 2.2, we have

$$\frac{d}{d\mu}\lambda_1(\mu d_1, \mu q_1, \boldsymbol{r} - \boldsymbol{u^*}) < 0.$$

Therefore, we obtain

 $0 = \lambda_1(d_1, q_1, \boldsymbol{r} - \boldsymbol{u^*}) > \lambda_1(\bar{\mu}d_1, \bar{\mu}q_1, \boldsymbol{r} - \boldsymbol{u^*}) = \lambda_1(\bar{d}_1, q_{\boldsymbol{r}-\boldsymbol{u^*}}^*(\bar{d}_1), \boldsymbol{r} - \boldsymbol{u^*}) = 0,$ 

which is a contradiction.

Next, we define two subsets of the first quadrant of the d - q plane:

$$G_1 := \{ (d,q) : 0 < d \le \frac{d_1}{q_1} q, q \ge q_1, (d,q) \ne (d_1,q_1) \},$$
  
$$G_2 := \{ (d,q) : d \ge \frac{d_1}{q_1} q, 0 < q \le q_1, (d,q) \ne (d_1,q_1) \}.$$

By Proposition 4.2, function  $q_{r-u^*}^*(d)$  is strictly increasing in *d*. By Lemma 4.4, we have:

$$G_1 \subset S_1 \quad \text{and} \quad G_2 \subset S_2.$$
 (4.5)

It turns out that we are able to completely understand the dynamics of model (1.4) for  $(d_2, q_2) \in G_1 \cup G_2$ . The key ingredient is the following result:

**Lemma 4.5** Suppose that H1 and H2 hold. Then, if  $(d_2, q_2) \in G_1 \cup G_2$ , model (1.4) has no positive equilibrium.

**Proof** Let  $(d_2, q_2) \in G_1 \cup G_2$ . Suppose to the contrary that model (1.4) admits a positive equilibrium  $(\hat{\boldsymbol{u}}, \hat{\boldsymbol{v}})$ , where  $\hat{\boldsymbol{u}} = (\hat{u}_1, \dots, \hat{u}_n) \gg \boldsymbol{0}$  and  $\hat{\boldsymbol{v}} = (\hat{v}_1, \dots, \hat{v}_n) \gg \boldsymbol{0}$ .

Then, we have

$$(d_1 + q_1)(\hat{u}_{n-1} - \hat{u}_n) = -\hat{u}_n(r - \hat{u}_n - \hat{v}_n),$$
  

$$(d_1 + q_1)(\hat{u}_{i-1} - \hat{u}_i) = d_1(\hat{u}_i - \hat{u}_{i+1}) - \hat{u}_i(r - \hat{u}_i - \hat{v}_i), \quad i = 2, \dots, n-1,$$
  

$$q_1\hat{u}_1 = d_1(\hat{u}_2 - \hat{u}_1) + \hat{u}_1(r - \hat{u}_1 - \hat{v}_1).$$

and

$$\begin{aligned} (d_2 + q_2)(\hat{v}_{n-1} - \hat{v}_n) &= -\hat{v}_n(r - \hat{u}_n - \hat{v}_n), \\ (d_2 + q_2)(\hat{v}_{i-1} - \hat{v}_i) &= d_2(\hat{v}_i - \hat{v}_{i+1}) - \hat{v}_i(r - \hat{u}_i - \hat{v}_i), \quad i = 2, \dots, n-1, \\ q_2\hat{v}_1 &= d_2(\hat{v}_2 - \hat{v}_1) + \hat{v}_1(r - \hat{u}_1 - \hat{v}_1). \end{aligned}$$

Then, using similar arguments as in the proof of Lemma 4.1, we can show that  $\hat{z}_1 < \hat{z}_2 < \cdots < \hat{z}_n$  for z = u, v and  $\hat{u}_i + \hat{v}_i < r$  for  $1 \le i \le n$ . Therefore,  $\mathbf{r} - \hat{\mathbf{u}} - \hat{\mathbf{v}} \gg \mathbf{0}$ . By Proposition 3.2, function  $q = q^*_{\mathbf{r}-\hat{\mathbf{u}}-\hat{\mathbf{v}}}(d)$  is well-defined for  $d \in (0, \infty)$ . Moreover, by Lemma 3.7, it is strictly increasing in  $(0, \infty)$ .

Noticing that  $(\hat{u}, \hat{v})$  is a positive equilibrium, we have  $\lambda_1(d_1, q_1, \mathbf{r} - \hat{u} - \hat{v}) = \lambda_1(d_2, q_2, \mathbf{r} - \hat{u} - \hat{v}) = 0$ . By virtue of similar arguments as in the proof of Lemma 4.4, the functions  $q = q_{\mathbf{r}-\hat{u}-\hat{v}}^*(d)$  and  $q = \frac{q_1}{d_1}d$  have exactly one intersection point  $(d_1, q_1)$  in the first quadrant of the d - q plane. It follows that

$$G_1 \subset \{(d,q): q, d > 0, q > q_{r-\hat{u}-\hat{v}}^*(d)\}$$

and

$$G_2 \subset \{(d,q): q, d > 0, q < q^*_{r-\hat{u}-\hat{v}}(d)\}.$$

By Lemma 3.1, we have  $\lambda_1(d_2, q_2, \mathbf{r} - \hat{\boldsymbol{u}} - \hat{\boldsymbol{v}}) < 0$  for  $(d_2, p_2) \in G_1$  and  $\lambda_1(d_2, q_2, \mathbf{r} - \hat{\boldsymbol{u}} - \hat{\boldsymbol{v}}) > 0$  for  $(d_2, p_2) \in G_2$ , which contradicts with  $\lambda_1(d_2, q_2, \mathbf{r} - \hat{\boldsymbol{u}} - \hat{\boldsymbol{v}}) = 0$ . Therefore, model (1.4) has no positive equilibrium if  $(d_2, q_2) \in G_1 \cup G_2$ .

By virtue of Proposition 4.3, Lemma 4.5 and the monotone dynamical system theory, we have the following main result about the global dynamics of model (1.4):

**Theorem 4.6** Suppose that **H**1 and **H**2 hold. Then, the following statements hold:

- (i) If  $(d_2, q_2) \in G_1$ , then  $(\mathbf{u}^*, \mathbf{0})$  is globally asymptotically stable for (1.4);
- (ii) If  $(d_2, q_2) \in G_2$ , then the semi-trivial equilibrium  $(\mathbf{0}, \mathbf{v}^*)$  exists and is globally asymptotically stable for (1.4).

**Proof** (i) Suppose  $(d_2, q_2) \in G_1$ . We claim that semi-trivial equilibrium  $(\mathbf{0}, \mathbf{v}^*)$  is either unstable or does not exist. Indeed, if  $q_2 < q_r^*(d_2)$ , then  $(\mathbf{0}, \mathbf{v}^*)$  exists. Since the nonlinear terms of the model are symmetric and  $(\mathbf{u}^*, \mathbf{0})$  is unstable when  $(d_2, q_2) \in G_2$ ,  $(\mathbf{0}, \mathbf{v}^*)$  is unstable when  $(d_2, q_2) \in G_1$ . If  $q_2 \ge q_r^*(d_2)$ , then  $(\mathbf{0}, \mathbf{v}^*)$  does not exist. Since model (1.4) has no positive equilibrium for  $(d_2, q_2) \in G_1$ , by the monotone dynamical system theory (Hess 1991; Hsu et al. 1996; Lam and Munther 2016; Smith 1995),  $(\mathbf{u}^*, \mathbf{0})$  is globally asymptotically stable.



**Fig. 2** Illustration of Proposition 4.3 and Theorem 4.6 for model (1.4)-case (a). Here,  $d_1$  and  $q_1$  are fixed and satisfy H2 such that  $(u^*, 0)$  exists. If  $(d_2, q_2)$  is above the curve  $q = q^*_{r-u^*}(d)$ , then  $(u^*, 0)$  is stable; if  $(d_2, q_2)$  is under the curve, then  $(u^*, 0)$  is unstable. If  $(d_2, q_2) \in G_1$ ,  $(u^*, 0)$  is globally asymptotically stable; and if  $(d_2, q_2) \in G_2$ ,  $(0, v^*)$  exists and is globally asymptotically stable

(ii) By Lemma 3.7, we have  $q_{r-u^*}^*(d) < q_r^*(d)$  for all d > 0. So if  $(d_2, q_2) \in G_2 \subset \{(d, q) : q, d > 0, q < q_r^*(d)\}$ , semi-trivial equilibrium  $(\mathbf{0}, \mathbf{v}^*)$  exists. Since  $(\mathbf{u}^*, \mathbf{0})$  is unstable and model (1.4) has no positive equilibrium for  $(d_2, q_2) \in G_2$ , the desired result follows from the monotone dynamical system theory (Hess 1991; Hsu et al. 1996; Lam and Munther 2016; Smith 1995).

**Remark 4.7** Theorem 4.6 is illustrated in Fig. 2. We are able to completely understand the global dynamics of model (1.4) in the colored regions  $(G_1 \text{ and } G_2)$ , in which the competitive exclusion happens.

We have the following observations from Theorem 4.6:

#### **Corollary 4.8** Suppose that H1 and H2 hold. Then, the following statements hold:

- (i) Fix  $q_2 = q_1$ . If  $d_2 < d_1$ ,  $(\boldsymbol{u}^*, \boldsymbol{0})$  is globally asymptotically stable for (1.4); and if  $d_2 > d_1$ ,  $(\boldsymbol{0}, \boldsymbol{v}^*)$  is globally asymptotically stable;
- (ii) Fix  $d_2 = d_1$ . If  $q_2 > q_1$ ,  $(\boldsymbol{u}^*, \boldsymbol{0})$  is globally asymptotically stable for (1.4); and if  $q_2 < q_1$ ,  $(\boldsymbol{0}, \boldsymbol{v}^*)$  is globally asymptotically stable.

**Remark 4.9** By Corollary 4.8, the species with a larger diffusion rate or a smaller advection rate can invade and replace the resident species. Moreover, Corollary 4.8 (i) resolves a conjecture in Lou (2019), which was originally proposed for a two-patch model.

To study the dynamics of model (1.4) with  $(d_2, q_2)$  in the region other than  $G_1$ ,  $G_2$  in Fig. 2, we first show that there exists a curve which determines the stability of the semi-trivial equilibrium (**0**,  $v^*$ ). We recall that (**0**,  $v^*$ ) exists if and only if  $0 < q_2 < q_r^*(d_2)$ .

**Proposition 4.10** Suppose that **H**1 and **H**2 hold. Then, the following statements hold:

- (i) For any  $d_2 > 0$ ,  $\lambda_1(d_1, q_1, \mathbf{r} \mathbf{v}^*(d_2, q_2))$  is strictly increasing in  $q_2$  for  $q_2 \in (0, q_r^*(d_2))$ ;
- (ii) For any  $d_2 > 0$ , there exists a unique  $q_2^*(d_2) \in (0, q_r^*(d_2))$  such that

$$\lambda_1(d_1, q_1, \mathbf{r} - \mathbf{v}^*(d_2, q_2^*(d_2))) = 0;$$
(4.6)

*Moreover*,  $q_2^*(d_1) = q_1$ , and

$$q_{1} < q_{2}^{*}(d_{2}) < \min\left\{\frac{q_{1}}{d_{1}}d_{2}, q_{r}^{*}(d_{2})\right\} \text{ for } d_{2} > d_{1},$$

$$\frac{q_{1}}{d_{1}}d_{2} < q_{2}^{*}(d_{2}) < \min\left\{q_{1}, q_{r}^{*}(d_{2})\right\} \text{ for } d_{2} < d_{1}.$$

$$(4.7)$$

(iii) Semi-trivial equilibrium (0,  $v^*(d_2, q_2)$ ) is stable if  $0 < q_2 < q_2^*(d_2)$  and unstable if  $q_2^*(d_2) < q_2 < q_r^*(d_2)$ .

**Proof** (i) Clearly,  $v^*(d_2, q_2)$  satisfies

$$\sum_{j=1}^{n} (d_2 D_{ij} + q_2 Q_{ij}) v_j + v_i (r - v_i) = 0, \quad i = 1, \dots, n,$$
(4.8)

Differentiating (4.8) with respect to  $q_2$  yields

$$-\sum_{j=1}^{n} (d_2 D_{ij} + q_2 Q_{ij}) v'_j - (r - 2v_i) v'_i = \sum_{j=1}^{n} Q_{ij} v_j, \quad i = 1, \dots, n,$$
(4.9)

Denote  $\tilde{L} = d_2D + q_2Q + \text{diag}(r - 2v_i)$ , and we have  $s(\tilde{L}) < s(d_2D + q_2Q + \text{diag}(r - v_i)) = 0$ . So  $-\tilde{L}$  is an irreducible non-singular *M*-matrix, and red each entry of  $-\tilde{L}^{-1}$  is positive (Berman and Plemmons 1994). By Lemma 4.1, we have  $v_1 < \cdots < v_n$ . Therefore, the right hand side of (4.9) is negative. This implies that  $v'_i < 0$  for  $i = 1, \ldots, n$  and each entry of  $v^*(d_2, q_2)$  is strictly decreasing in  $q_2$  for  $q \in (0, q^*_r(d_2))$ . Then, it follows from Lemma 3.1 that (i) holds.

(ii) We only consider the case  $0 < d_2 < d_1$ , since the other case  $d_2 > d_1$  is similar. It follows from Theorem 4.6 that  $(\mathbf{0}, \mathbf{v}^*)$  is stable for  $q_2 \leq \frac{q_1}{d_1}d_2$  and unstable for  $q_2 \geq q_1$ . Hence, we have  $\lambda_1(d_1, q_1, \mathbf{r} - \mathbf{v}^*(d_2, q_2)) < 0$  for  $q_2 \leq \frac{q_1}{d_1}d_2$  and  $\lambda_1(d_1, q_1, \mathbf{r} - \mathbf{v}^*(d_2, q_2)) > 0$  for  $q_2 \geq q_1$ . Note that

$$\lim_{q_2 \to q_2^*(d_2)^-} \lambda_1(d_1, q_1, \boldsymbol{r} - \boldsymbol{v}^*(d_2, q_2)) = \lambda_1(d_1, q_1, \boldsymbol{r}) > 0.$$

Since  $\lambda_1(d_1, q_1, \mathbf{r} - \mathbf{v}^*(d_2, q_2))$  is strictly increasing in  $q_2$ , there exists unique  $q_2^*(d_2)$  satisfying (4.6)–(4.7). Clearly,  $q_2^*(d_1) = q_1$ , and (iii) follows from (i)–(ii). This completes the proof.

By Propositions 4.2 and 4.10 and the monotone dynamical system theory, we have the following result.

**Theorem 4.11** Suppose that H1 and H2 hold. Let  $q_2^*(d_2)$  be defined in Proposition 4.10. Then, the following statements hold:

- (i) If  $q_2^*(d_2) < q_{r-u^*}^*(d_2)$ , then for any  $q_2 \in (q_2^*(d_2), q_{r-u^*}^*(d_2))$  both  $(u^*, 0)$  and  $(0, v^*)$  are unstable, and system (1.4) admits a stable positive equilibrium;
- (ii) If  $q_2^*(d_2) > q_{r-u^*}^*(d_2)$ , then for any  $q_2 \in (q_{r-u^*}^*(d_2), q_2^*(d_2))$  both  $(u^*, 0)$  and  $(0, v^*)$  are stable, and system (1.4) admits an unstable positive equilibrium.

**Remark 4.12** Since  $\lambda_1(d_1, q_1, \mathbf{r} - \boldsymbol{v}^*(d_2, q_2))$  is strictly increasing in  $q_2$ , the sign of  $q_2^*(d_2) - q_{\mathbf{r}-\mathbf{u}^*}^*(d_2)$  is determined by the sign of

$$\lambda_1^*(d_2) := \lambda_1 \left( d_1, q_1, \mathbf{r} - \mathbf{v}^*(d_2, q_{\mathbf{r}-\mathbf{u}^*}^*(d_2)) \right).$$
(4.10)

If  $\lambda_1^*(d_2) > (<)0$ , then  $q_2^*(d_2) < (>)q_{r-u^*}^*(d_2)$ .

**Remark 4.13** Some of our results were known for the corresponding reaction–diffusion models. A similar result of Lemma 4.1 was obtained in Vasilyeva and Lutscher (2010), a similar result of Corollary 4.8 (i) was presented in Lou and Lutscher (2014), and similar results of Lemma 4.5 and Theorem 4.6 were proved in Zhou and Zhao (2018) using a more sophisticated method. We used the monotonicity property of  $u^*$  in q in the proof of Proposition 4.10, which was also known for reaction–diffusion models (Vasilyeva and Lutscher 2010). Similar results of Proposition 4.10 and Theorem 4.11 were proved in Lou et al. (2018) with respect to some other parameters. To our best knowledge, similar results of Propositions 4.2, 4.3 and Lemma 4.4 were not proved for reaction–diffusion models.

# 4.2 Invasion Analysis for Case (b)

In this subsection, we suppose that H1\* holds. By Lemma 2.2, there exists a unique  $d^* > 0$  such that  $\lambda_1(d^*, 0, \mathbf{r}) = 0$ . By Theorem 3.3, for any  $d_1 \in (0, d^*)$ , there exists  $q_{\mathbf{r}}^*(d_1) > 0$  such that  $\lambda_1(d_1, q_1, \mathbf{r}) > 0$  for  $q_1 < q_{\mathbf{r}}^*(d_1)$  and  $\lambda_1(d_1, q_1, \mathbf{r}) < 0$  for  $q_1 > q_{\mathbf{r}}^*(d_1)$ . We suppose that species  $\mathbf{u}$  is established, i.e.,

**H**2<sup>\*</sup>.  $0 < d_1 < d^*$  and  $q_1 < q_r^*(d_1)$ .

Under assumptions  $H1^*$  and  $H2^*$ , model (1.4) admits a unique species *u*-only semitrivial equilibrium ( $u^*$ , **0**).

We first prove an estimate of  $u^*$ , which will be useful later.

**Lemma 4.14** Suppose that  $H1^*$  and  $H2^*$  hold. Let  $u^* = (u_1^*, \ldots, u_n^*)^T$  be the unique positive solution of (4.1). Then, we have  $0 \ll u^* \ll r$ .

**Proof** Let  $\hat{u} = r$ . It is easy to check that  $\hat{u}$  is an upper solution of (4.1). By the method of upper and lower solutions and the uniqueness of the positive solution of (4.1), we have  $0 \ll u^* \ll r$ .

By Lemma 2.2, there exists a unique  $d^{**} > 0$  such that  $\lambda_1(d^{**}, 0, \mathbf{r} - \mathbf{u}^*) = 0$ . By Proposition 3.3, for any  $d_2 \in (0, d^{**})$  there exists  $q^*_{\mathbf{r}-\mathbf{u}^*}(d_2) > 0$  such that  $\lambda_1(d_2, q_2, \mathbf{r} - \mathbf{u}^*) > 0$  for  $q_2 < q^*_{\mathbf{r}-\mathbf{u}^*}(d_2)$  and  $\lambda_1(d_2, q_2, \mathbf{r} - \mathbf{u}^*) < 0$  for  $q_2 > q^*_{\mathbf{r}-\mathbf{u}^*}(d_2)$ . Moreover, if  $d_2 \ge d^{**}$ , then  $\lambda_1(d_2, q_2, \mathbf{r} - \mathbf{u}^*) \le 0$  for all  $q_2 > 0$ . This suggests us to define the following parameter sets:

$$\begin{split} S_1^* &:= \{ (d,q) : \ q > q_{r-u^*}^*(d), \ 0 < d < d^{**} \} \cup \{ (d,q) : q > 0, \ d \ge d^{**} \}, \\ S_2^* &:= \{ (d,q) : 0 < q < q_{r-u^*}^*(d), \ 0 < d < d^{**} \}. \end{split}$$

We have the following result about the local stability of semi-trivial equilibrium  $(u^*, 0)$  of model (1.4), and its proof is omitted as it is similar to Proposition 4.3.

**Proposition 4.15** Suppose that  $H1^*$  and  $H2^*$  hold. The the following statements about semi-trivial equilibrium  $(u^*, 0)$  of (1.4) hold:

(i) *If* (*d*<sub>2</sub>, *q*<sub>2</sub>) ∈ *S*<sup>\*</sup><sub>1</sub>, *then* (*u*<sup>\*</sup>, **0**) *is locally asymptotically stable;*(ii) *If* (*d*<sub>2</sub>, *q*<sub>2</sub>) ∈ *S*<sup>\*</sup><sub>2</sub>, *then* (*u*<sup>\*</sup>, **0**) *is unstable.*

We also have the following property about the function  $q = q_{r-u^*}^*(d)$ , and its proof is exactly the same as that of Lemma 4.4 so we omit it.

**Lemma 4.16** Suppose that  $H1^*$  and  $H2^*$  hold. Then, the two functions  $q = q_{r-u^*}^*(d)$  and  $q = \frac{q_1}{d_1}d$  have exactly one intersection point  $(d_1, q_1)$  in the first quadrant.

Again we define parameter sets:

$$G_1^* := \{(d,q) : d_1 < d \le \frac{d_1}{q_1}q, (d,q) \ne (d_1,q_1)\},\$$
  
$$G_2^* := \{(d,q) : \frac{d_1}{q_1}q \le d \le d_1, q > 0, (d,q) \ne (d_1,q_1)\}.$$

Since the two functions  $q = q_{r-u^*}^*(d)$  and  $q = \frac{q_1}{d_1}d$  have exactly one intersection point  $(d_1, q_1)$  in the first quadrant, we have that  $G_1^* \subset S_1^*$  and  $G_2^* \subset S_2^*$ . The following result is similar to Lemma 4.5.

**Lemma 4.17** Suppose that  $H1^*$  and  $H2^*$  hold. Then, if  $(d_2, q_2) \in G_1^* \cup G_2^*$ , model (1.4) has no positive equilibrium.

**Proof** Let  $(d_2, q_2) \in G_1^* \cup G_2^*$ . Suppose to the contrary that model (1.4) admits a positive equilibrium  $(\hat{\boldsymbol{u}}, \hat{\boldsymbol{v}})$ , where  $\hat{\boldsymbol{u}} = (\hat{u}_1, \dots, \hat{u}_n) \gg \boldsymbol{0}$  and  $\hat{\boldsymbol{v}} = (\hat{v}_1, \dots, \hat{v}_n) \gg \boldsymbol{0}$ . Then, we have

$$(d_1 + q_1)(\hat{u}_{n-1} - \hat{u}_n) = d_1\hat{u}_n - \hat{u}_n(r - \hat{u}_n - \hat{v}_n),$$
  

$$(d_1 + q_1)(\hat{u}_{i-1} - \hat{u}_i) = d_1(\hat{u}_i - \hat{u}_{i+1}) - \hat{u}_i(r - \hat{u}_i - \hat{v}_i), \quad i = 2, \dots, n-1,$$
  

$$q_1\hat{u}_1 = d_1(\hat{u}_2 - \hat{u}_1) + \hat{u}_1(r - \hat{u}_1 - \hat{v}_1).$$
  
(4.11)

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(4.12)

and

$$(d_2 + q_2)(\hat{v}_{n-1} - \hat{v}_n) = d_2\hat{v}_n - \hat{v}_n(r - \hat{u}_n - \hat{v}_n),$$
  

$$(d_2 + q_2)(\hat{v}_{i-1} - \hat{v}_i) = d_2(\hat{v}_i - \hat{v}_{i+1}) - \hat{v}_i(r - \hat{u}_i - \hat{v}_i), \quad i = 2, \dots, n-1,$$
  

$$q_2\hat{v}_1 = d_2(\hat{v}_2 - \hat{v}_1) + \hat{v}_1(r - \hat{u}_1 - \hat{v}_1).$$

We claim  $\max_{1 \le i \le n} \{r - \hat{u}_i - \hat{v}_i\} > 0$ . Suppose to the contrary that  $r - \hat{u}_i - \hat{v}_i \le 0$  for all  $1 \le i \le n$ . Then, by the first two equations in both (4.11) and (4.12), we obtain that  $\hat{z}_1 > \hat{z}_2 > \cdots > \hat{z}_n$  for z = u, v. Then, by the third equation in (4.11), we get  $q\hat{u}_1 = d(\hat{u}_2 - \hat{u}_1) + \hat{u}_1(r - \hat{u}_1 - \hat{v}_1) < 0$ , which is a contradiction. Therefore,  $\max_{1 \le i \le n} \{r - \hat{u}_i - \hat{v}_i\} > 0$ . By Proposition 3.3, function  $q = q_{r-\hat{u}-\hat{v}}^*(d)$  is well-defined. Similar to Lemma 4.16, functions  $q = q_{r-\hat{u}-\hat{v}}^*(d)$  and  $q = \frac{q_1}{d_1}d$  have exactly one intersection point  $(d_1, q_1)$  in the first quadrant of the d - q plane. The rest of the proof is similar to that of Lemma 4.5, so we omit it here.

By Proposition 4.15, Lemma 4.17 and the monotone dynamical system theory, we have the following result about the global dynamics of model (1.4). We omit the proof as it is similar to Theorem 4.6.

**Theorem 4.18** Suppose that  $H1^*$  and  $H2^*$  hold. Then, the following statements hold:

- (i) If (d<sub>2</sub>, q<sub>2</sub>) ∈ G<sup>\*</sup><sub>1</sub>, semi-trivial equilibrium (u<sup>\*</sup>, 0) is globally asymptotically stable for model (1.4);
- (ii) If  $(d_2, q_2) \in G_2^*$ , semi-trivial equilibrium  $(\mathbf{0}, \mathbf{v}^*)$  exists and is globally asymptotically stable for model (1.4).

**Remark 4.19** Theorem 4.18 is illustrated in Fig. 3. We are able to completely understand the global dynamics of model (1.4) in the colored regions, in which competitive exclusion occurs.

We have the following observations from Theorem 4.18:

**Corollary 4.20** Suppose that  $H1^*$  and  $H2^*$  hold. Fix  $d_2 = d_1$ . If  $q_2 > q_1$ ,  $(u^*, 0)$  is globally asymptotically stable for (1.4); if  $q_2 < q_1$ ,  $(0, v^*)$  is globally asymptotically stable.

By Corollary 4.20, the species with a smaller advection rate can invade and replace the resident species in this case. However, whether a smaller or larger diffusion rate is favored seems to be more complicated in case (b). If we treat  $\boldsymbol{v}$  as the mutant species such that  $d_2$  is close to  $d_1$  and  $q_1 = q_2$ , then  $[q_{r-u^*}^*(d)]'|_{d=d_1} > 0$  means that  $\boldsymbol{v}$  can invade if and only if  $d_2 > d_1$ ;  $[q_{r-u^*}^*(d)]'|_{d=d_1} < 0$  means that  $\boldsymbol{v}$  can invade if and only if  $d_2 < d_1$ . We will show that the sign  $[q_{r-u^*}^*(d)]'|_{d=d_1}$  is not definite.

Define  $S := \{(d, q) : 0 < d < d^*, 0 < q < q_r^*(d)\}$ , and recall that  $(\boldsymbol{u}^*, \boldsymbol{0})$  exists if and only if  $(d_1, q_1) \in S$ . Let  $S' := \{(d, q) : 0 < q < r, q = q_r^*(d)\}$ . By Lemma 3.8, S' is non-empty and it is a curve  $q = q_r^*(d)$  connecting to  $(d^*, 0)$ .

**Proposition 4.21** Suppose that  $H1^*$  and  $H2^*$  holds. Then,  $[q^*_{r-u^*}(d)]'|_{d=d_1}$  changes sign for  $(d_1, q_1) \in S$ . Moreover,



**Fig. 3** Illustration of Proposition 4.15 and Theorem 4.18 for model (1.4)-case (b). Here,  $d_1$  and  $q_1$  are fixed and satisfy **H**2\* such that  $(u^*, 0)$  exists. If  $(d_2, q_2)$  is above the curve  $q = q^*_{r-u^*}(d)$ , then  $(u^*, 0)$  is stable; if  $(d_2, q_2)$  is under the curve, then  $(u^*, 0)$  is unstable. If  $(d_2, q_2) \in G_1^*$ ,  $(u^*, 0)$  is globally asymptotically stable; and if  $(d_2, q_2) \in G_2^*$ ,  $(0, v^*)$  is globally asymptotically stable

- (i)  $\lim_{(d_1,q_1)\to(d_0,0)} \left[q_{r-u^*}^*(d)\right]'|_{d=d_1} < 0$  for any  $d_0 \in (0, d^*)$ ;
- (ii)  $\lim_{(d_1,q_1)\to(0,q_0)} \left[ q_{r-u^*}^*(d) \right]' |_{d=d_1} > 0 \text{ for any } q_0 \in (0,r);$

(iii)  $\lim_{(d_1,q_1)\to(d_0,q_0)} \left[q_{r-u^*}^*(d)\right]'|_{d=d_1} < 0$  for any  $(d_0,q_0) \in \mathcal{S}'$ .

**Proof** For simplicity, we denote  $q_{r-u^*}^*(d)$  by  $q_1^*(d)$ . Let  $\boldsymbol{\phi} = (\phi_1, \phi_2, \dots, \phi_n)^T \gg \mathbf{0}$  be the eigenvector corresponding to the eigenvalue  $\lambda_1(d, q_1^*(d), \boldsymbol{r} - \boldsymbol{u^*}) = 0$  with  $\sum_{i=1}^n \phi_i = 1$ . Then, we have

$$d\sum_{j=1}^{n} D_{ij}\phi_j + q_1^*(d)\sum_{j=1}^{n} Q_{ij}\phi_j + (r - u_i^*)\phi_i = 0, \quad i = 1, \dots, n.$$
(4.13)

Similar to the proof of Lemma 3.8 (iii), we can show

$$\left[q_{1}^{*}(d)\right]' = -\frac{\sum_{i=1}^{n} \sum_{j=1}^{n} \beta_{i} D_{ij} \phi_{i} \phi_{j}}{\sum_{i=1}^{n} \sum_{j=1}^{n} \beta_{i} Q_{ij} \phi_{i} \phi_{j}},$$
(4.14)

where

$$(\beta_1, \beta_2, \beta_3, \dots, \beta_n) = \left(1, \frac{d}{d + q_1^*(d)}, \left(\frac{d}{d + q_1^*(d)}\right)^2, \dots, \left(\frac{d}{d + q_1^*(d)}\right)^{n-1}\right).$$

Since  $u^*$  is an eigenvector corresponding to  $\lambda_1(d_1, q_1, r - u^*) (= 0)$ ,  $q_1^*(d_1) = q_1$ and  $\phi$  is a multiple of  $u^*$  when  $d = d_1$ .

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It is easy to see that

$$\lim_{\substack{(d_1,q_1)\to(d_0,0)\\(d_1,q_1)\to(0,q_0)}} (\beta_1,\ldots,\beta_n) = (1,\ldots,1),$$
(4.15)

and

$$\lim_{(d_1,q_1)\to(d_0,0)} u^* = \tilde{u}^*, \text{ and } \lim_{(d_1,q_1)\to(0,q_0)} u^* = \hat{u}^*,$$

where  $\tilde{u}^*$  and  $\hat{u}^*$  satisfy (4.1) with  $(d_1, q_1) = (d_0, 0)$  and  $(d_1, q_1) = (0, q_0)$ , respectively. A direct computation implies that

$$\tilde{u}_1^* > \dots > \tilde{u}_n^* > 0$$
, and  $0 < r - q_0 = \hat{u}_1^* < \dots < \hat{u}_n^*$ .

(The left inequalities can be proved similarly as Lemma 4.1 starting with  $\tilde{u}_1^* > \tilde{u}_2^*$ ; We can show  $\hat{u}^* \ll r$  as Lemma 4.14, and then, the right inequalities follow easily from (4.1) with  $(d_1, q_1) = (0, q_0)$ .) This combined with (4.14)–(4.15) implies (i)–(ii).

Finally, we prove (iii). We claim that  $\lim_{(d_1,q_1)\to(d_0,q_0)} \boldsymbol{u}^* = \boldsymbol{0}$ . To see it, suppose to the contrary that, up to a subsequence,  $\boldsymbol{u}^* \to \boldsymbol{\check{u}}^* \neq \boldsymbol{0}$  as  $(d_1,q_1) \to (d_0,q_0)$ . Then, we have  $\boldsymbol{0} < \boldsymbol{\check{u}}^* \leq \boldsymbol{r}$  and  $\lambda_1(d_0,q_0,\boldsymbol{r}-\boldsymbol{\check{u}}^*) = \lim_{(d_1,q_1)\to(d_0,q_0)} \lambda_1(d_1,q_1,\boldsymbol{r}-\boldsymbol{u}^*) = 0$ . Since  $(d_0,q_0) \in S'$ , we have  $\lambda_1(d_0,q_0,\boldsymbol{r}) = 0$ . This implies  $\lambda_1(d_0,q_0,\boldsymbol{r}-\boldsymbol{\check{u}}^*) < \lambda_1(d_0,q_0,\boldsymbol{r}) = 0$ , which is a contradiction.

Letting  $d = d_1$  in (4.13) and using  $q_1^*(d_1) = q_1$  and  $u^* \to 0$ , we obtain  $\phi \to \check{\phi}$  as  $(d_1, q_1) \to (d_0, q_0)$ , where  $\check{\phi}$  satisfies

$$d_0 \sum_{j=1}^n D_{ij} \check{\phi}_j + q_0 \sum_{j=1}^n Q_{ij} \check{\phi}_j + r \check{\phi}_i = 0, \quad i = 1, \dots, n.$$
(4.16)

We rewrite (4.16) as

$$d_{0}(\check{\phi}_{1} - \check{\phi}_{2}) = (r - q_{0})\check{\phi}_{1},$$
  

$$d_{0}(\check{\phi}_{i} - \check{\phi}_{i+1}) = (d_{0} + q_{0})(\check{\phi}_{i-1} - \check{\phi}_{i}) + r\check{\phi}_{i}, \quad i = 2, \dots, n-1,$$
  

$$d_{0}(\check{\phi}_{n-1} - 2\check{\phi}_{n}) + q_{0}(\check{\phi}_{n-1} - \check{\phi}_{n}) + r\check{\phi}_{n} = 0.$$
  
(4.17)

This combined with  $q_0 < r$  implies  $\check{\phi}_1 > \cdots > \check{\phi}_n$ . Therefore,

$$\sum_{i=1}^{n} \sum_{j=1}^{n} \check{\beta}_{i} D_{ij} \check{\phi}_{i} \check{\phi}_{j} = \sum_{i=1}^{n-1} \check{\beta}_{i} \left( \check{\phi}_{i+1} - \check{\phi}_{i} \right) \left[ \check{\phi}_{i} - \left( \frac{d_{0}}{d_{0} + q_{0}} \right) \check{\phi}_{i+1} \right] - \check{\beta}_{n} \check{\phi}_{n}^{2} < 0,$$
(4.18)

where  $(\check{\beta}_1, ..., \check{\beta}_n) = (1, ..., (\frac{d_0}{d_0 + q_0})^{n-1})$ . Similar to (3.7), we can show

$$\sum_{i=1}^{n} \sum_{j=1}^{n} \check{\beta}_{i} Q_{ij} \check{\phi}_{i} \check{\phi}_{j} < 0.$$
(4.19)

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Evaluating (4.14) at  $d = d_1$ , taking  $(d_1, q_1) \rightarrow (d_0, q_0)$ , and using (4.18)–(4.19), we obtain (iii).

**Remark 4.22** By Proposition 4.21 and Lemma 3.8, for each  $q_1 \in (0, r)$ , there exists at least one  $\bar{d}_1 > 0$  such that  $[q_{r-u^*}^*(d)]'|_{d=\bar{d}_1} = 0$ . Moreover, the sign of  $[q_{r-u^*}^*(d)]'|_{d=d_1}$  switches from positive to negative at  $d_1 = \bar{d}_1$ . This suggests that the evolutionary singular strategy  $d_1 = \bar{d}_1$  may be a locally convergent stable strategy (A strategy is convergent stable if the species with the strategy closer to it can win the competition Apaloo et al. 2009; Lam and Lou 2014).

*Remark 4.23* For corresponding reaction–diffusion models, a similar result of Theorem 4.18 was proved in a very recent paper (Yan et al. 2022). To our best knowledge, similar results of Propositions 4.15 and 4.21 were not proved for reaction–diffusion models.

# **5** Simulations and Discussions

In this section, we perform some numerical simulations when model (1.4) is coupled with free-flow (case (a)) or hostile (case (b)) boundary conditions. We consider four patches, i.e., n = 4 and set r = 2.

# 5.1 Simulations for Case (a)

We choose  $d_1 = 1, q_1 = 0.5$  such that  $(\boldsymbol{u}^*, \boldsymbol{0})$  exists for case (a). We first plot the curve  $q = q_{r-\boldsymbol{u}^*}^*(d)$ , which divide the first quadrant into two subregions. In Fig. 4, we see that the curve  $q = q_{r-\boldsymbol{u}^*}^*(d)$  is monotone increasing, which is expected due to Lemma 3.7. By Propositions 4.3,  $E_1 = (\boldsymbol{u}^*, \boldsymbol{0})$  is stable if  $(d_2, q_2)$  is above the curve  $q = q_{r-\boldsymbol{u}^*}^*(d)$  and unstable if it is below the curve.

We further consider the stability of  $E_2 = (\mathbf{0}, \mathbf{v}^*)$  when  $(d_2, q_2) = (d, q_{\mathbf{r}-\mathbf{u}^*}^*(d))$ , which is determined by the sign of the principal eigenvalue

$$\lambda_1^*(d_2) = \lambda_1 \left( d_1, q_1, \mathbf{r} - \mathbf{v}^*(d_2, q_{\mathbf{r}-\mathbf{u}^*}^*(d_2)) \right).$$

In Fig. 4, the curve  $\lambda_1^*(d)$  seems to be below zero. Therefore, if we choose  $(d_2, q_2)$  sufficiently close to but above the curve  $q = q_{r-u^*}^*(d)$ , then both  $(u^*, 0)$  and  $(0, v^*)$  are stable and we have bi-stability. To confirm this, we choose  $(d_2, q_2) = (0.08, 0.44)$ , which is slightly above the curve  $q = q_{r-u^*}^*(d)$ . In Fig. 5, we plot the solutions of (1.4) with different initial data. If the initial data are u(0) = (0.1, 0.1, 0.1, 0.1) and v(0) = (2, 2, 2, 2), then species v wins the competition; if the initial data are u(0) = (5, 5, 5, 5), v(0) = (1, 1, 1, 1), then species u wins the competition. This confirms that it is possible to have bi-stability in case (a). We conjecture that for case (a) we always have  $\lambda_1^*(d_2) < 0$  for all  $d_2 \neq d_1$  and the model has no stable coexistence equilibrium.



**Fig. 4** Curves  $q = q_{r-u^*}^*(d)$  and  $\lambda_1^*(d)$  with  $n = 4, r = 2, d_1 = 1, q_1 = 0.5$  for case (a). The sign of the curve  $q = \lambda_1^*(d)$  determines the stability of  $E_2$  when  $d_2 = d$  and  $q_2 = q_{r-u^*}^*(d)$ 

#### 5.2 Simulations for Case (b)

We choose  $d_1 = 1$ ,  $q_1 = 0.5$  or 3 such that  $E_1$  exists for case (b), and we plot the curve  $q = q_{r-n^*}^*(d)$  in Fig. 6.

By Proposition 4.15,  $E_1$  is stable if  $(d_2, q_2)$  is above the curve  $q = q_{r-u^*}^*(d)$  and unstable if it is below the curve. In Fig. 6, the sign of  $\lambda_1^*(d)$  seems to be positive for  $q_1 = 0.5$  and negative for  $q_1 = 3$ . If  $q_1 = 0.5$  and  $(d_2, q_2)$  is sufficiently close to but below the curve  $q = q_{r-u^*}^*(d)$ , then both  $E_1$  and  $E_2$  are unstable and we should have coexistence. To confirm this, we choose  $(d_2, q_2) = (0.05, 0.555)$ . In Fig. 7, we plot the solutions of (1.4), and it appears that the two species coexist. If  $q_1 = 3$  and  $(d_2, q_2)$ is sufficiently close to but above the curve  $q = q_{r-u^*}^*(d)$ , we should have bi-stability (we omit the graphs here since they are similar to the ones in case (a) shown in Fig. 5). Our simulations show that both bi-stability and coexistence can occur for case (b).

#### 5.3 Evolution of Dispersal for Case (a) and (b)

Suppose that species v is the mutant species, and  $(d_2, q_2)$  is close to but not equal to  $(d_1, q_1)$ . When the model is coupled with free-flow boundary conditions (case (a)), we always have  $[q_{r-u}^*(d)]'|_{d=d_1} > 0$ . Biologically, this means that the mutant species can invade if and only if it has a larger diffusion rate.

If the model is coupled with hostile boundary conditions (case (b)), the dynamics of the model is more complicated. In Fig. 6, we can see that the sign of  $\left[q_{r-u^*}^*(d)\right]'|_{d=d_1}$ 



**Fig. 5** Solutions of (1.4) with n = 4 for case (a). The parameters are r = 2,  $d_1 = 1$ ,  $q_1 = 0.5$ ,  $d_2 = 0.08$  and  $q_2 = 0.44$ . **a** and **b** Initial data:  $\boldsymbol{u}(0) = (0.1, 0.1, 0.1, 0.1)$ ,  $\boldsymbol{v}(0) = (2, 2, 2, 2)$ , and species  $\boldsymbol{v}$  wins the competition; **c** and **d** Initial data:  $\boldsymbol{u}(0) = (5, 5, 5, 5)$ ,  $\boldsymbol{v}(0) = (1, 1, 1, 1)$ , and species  $\boldsymbol{u}$  wins the competition. This shows that the model has bi-stability in case (a)



**Fig. 6** Curves  $q = q_{r-u^*}^*(d)$  and  $\lambda_1^*(d)$  with  $n = 4, r = 2, d_1 = 1$  for case (b). (Left) q = 0.5; (right) q = 3. The sign of the curve  $\lambda_1^*(d)$  determines the stability of  $E_2$  when  $d_2 = d$  and  $q_2 = q_{r-u^*}^*(d)$ 



Fig. 7 Solutions of (1.4) with n = 4 for case (b). The parameters are r = 2,  $d_1 = 1$ ,  $q_1 = 0.5$ ,  $d_2 = 0.05$  and  $q_2 = 0.555$ . The two species seem to coexist



**Fig. 8** Curves  $q = q_{r-u^*}^*(d)$  and  $\lambda_1^*(d)$  with n = 4, r = 2,  $q_1 = 2$  for case (b). The first figure is for  $d_1 = 0.5$  and the second one for  $d_1 = 2$ . The sign of the curve  $\lambda_1^*(d)$  determines the stability of  $(0, v^*)$  when  $d_2 = d$  and  $q_2 = q_{r-u^*}^*(d)$ 

changes from negative to positive when q increased from 0.5 to 3. Biologically, when the advection rate is small ( $q_1 = 0.5$ ), the mutant species v can invade if it has a smaller diffusion rate; however, when the advection rate is large ( $q_1 = 3$ ), the mutant species v may need to have a larger diffusion rate than the resident species u to invade it. Therefore, if the downstream end is coupled with hostile boundary conditions, whether smaller or larger diffusion rate is a better strategy for the species depends on the advection rate. We conjecture that when  $d_1$  is small the sign of  $\left[q_{r-u^*}^*(d)\right]'|_{d=d_1}$ for case (b) changes from negative to positive as q increases, i.e., smaller diffusion rate is better when the advection rate is small, while larger diffusion rate is favored when advection rate is large. We also conjecture that when  $d_1$  is sufficiently large, then the sign of  $\left[q_{r-u^*}^*(d)\right]'|_{d=d_1}$  for case (b) is always negative, i.e., smaller diffusion rate is always better.

If we fix  $q_1 = 2$  for case (b), as shown in Fig. 8, the sign of  $[q_{r-u^*}^*(d)]'|_{d=d_1}$  changes from positive to negative when  $d_1$  increased from 0.5 to 2. Therefore, there exists  $\bar{d}_1 \in (0.5, 2)$  such that  $[q_{r-u^*}^*(d)]'|_{d=\bar{d}_1} = 0$ . Moreover, the sign of  $[q_{r-u^*}^*(d)]'|_{d=\bar{d}_1}$ 

switches from positive to negative at  $d_1 = \overline{d}_1$ . This suggests that  $d_1 = \overline{d}_1$  may be a convergence stable strategy. We conjecture that for each advection rate  $q_1 \in (0, r)$ , there exists a unique intermediate diffusion rate, which is a convergence stable strategy. We remark that if n = 2 the authors in Xiang and Fang (2019) have shown that for each  $q_1 \in (0, r)$  there exists a unique evolutionary stable strategy for  $d_1$ .

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**Data Availability** The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

# Declarations

Conflict of interest The authors declare they have no conflict of interest.

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