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On the impact of spatial heterogeneity and drift rate in a three-patch two-species Lotka–Volterra competition model over a stream

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Abstract. In this paper, we study a three-patch two-species Lotka–Volterra competition patch model over a stream network. The individuals are subject to both random and directed movements, and the two species are assumed to be identical except for the movement rates. The environment is heterogeneous, and the carrying capacity is lager in upstream locations. We treat one species as a resident species and investigate whether the other species can invade or not. Our results show that the spatial heterogeneity of environment and the magnitude of the drift rates have a large impact on the competition outcomes of the stream species.

1. Introduction

The species living in stream environment is subject to both passive random movement and directed drift [47]. Intuitively, the drift will carry individuals to the downstream end, which may be crowded or hostile. However, random dispersal may drive the individuals to the upper stream locations, which are usually more favorable for the species [23]. Therefore, the joint impact of both undirectional and directed dispersal rates on the population dynamics of the species is usually complicated and has attracted increasing research interests recently [22,25,34,40–42,47].

Dispersal has profound effects on the distribution and abundance of organisms, and understanding the mechanisms for the evolution of dispersal is a fundamental question related to dispersal [26]. In the seminal works of Hastings [19] and Dockery et al. [15], it has been shown that in a spatially heterogeneous environment, when two competing species are identical except for the random dispersal rate, evolution of dispersal favors the species with a smaller dispersal rate. However, in an advective environment when individuals are subject to both undirectional random dispersal and directed movement, species with a faster dispersal rate can be selected [3,4,11].

Two-species reaction–diffusion–advection competition models of the following form have been proposed to study the evolution of dispersal for stream species [28,34–36,38,43,48,49,51–53]:
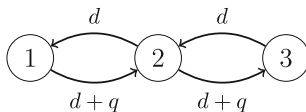
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FIG. 1. A stream with three patches, where d is the random movement rate and q is the directed drift rate. Patch 1 is the upstream end, and patch 3 is the downstream end

$$
\begin{cases}
u_t = d_1 u_{xx} - q_1 u_x + u[r(x) - u - v], & 0 < x < l, \ t > 0, \\
v_t = d_2 v_{xx} - q_2 v_x + v[r(x) - u - v], & 0 < x < l, \ t > 0, \\
d_1 u_x(0,t) - q_1 u(0,t) = d_2 v_x(0,t) - q_2 v(0,t) = 0, & t > 0, \\
d_1 u_x(l,t) - q_1 u(l,t) = d_2 v_x(l,t) - q_2 v(l,t) = 0, & t > 0, \\
u(x,0), v(x,0) \geq (\not\equiv)0, & 0 < x < l.
\end{cases}
\tag{1.1}
$$

In [28, 34, 49], the authors have treated species u as a resident species and studied the conditions under which the species u only semitrivial equilibrium is stable/unstable. Various results on the global dynamics of (1.1) are presented in [36, 38, 43, 52, 53]. In particular, if $r(x)$ is constant, the works [36, 38, 53] show that the species with a larger diffusion rate and/or a smaller advection rate wins the competition. If $r(x)$ is a decreasing function, the authors in [37, 52] use q_1 and q_2 as bifurcation parameters to study the global dynamics of (1.1) and the related results will be discussed later (see Remark 3.14).

To study the evolution of dispersal in a river network, the authors in [23, 24] propose and investigate three-patch two-species Lotka–Volterra competition models. Let $\boldsymbol{u} = (u_1, u_2, u_3)$ and $\boldsymbol{v} = (v_1, v_2, v_3)$ be the population density of two competing species, respectively, where u_i and v_i are the densities in patch i. Suppose that the dispersal patterns of the individuals and the configuration of the patches are shown in Fig. 1.

The competition patch model over the stream network in Fig. 1 (with $r_1 = r_2 = r_3$) in [23, 24] is:

$$
\begin{cases}
\dfrac{\mathrm{d}u_i}{\mathrm{d}t} = \displaystyle\sum_{j=1}^{3} (d_1 D_{ij} + q_1 Q_{ij}) u_j + r_i u_i \left(1 - \dfrac{u_i + v_i}{k_i}\right), & i = 1,2,3, \ t > 0, \\
\dfrac{\mathrm{d}v_i}{\mathrm{d}t} = \displaystyle\sum_{j=1}^{3} (d_2 D_{ij} + q_2 Q_{ij}) v_j + r_i v_i \left(1 - \dfrac{u_i + v_i}{k_i}\right), & i = 1,2,3, \ t > 0, \\
\boldsymbol{u}(0) = \boldsymbol{u}_0 \geq (\not\equiv) \ \boldsymbol{0}, \ \boldsymbol{v}(0) = \boldsymbol{v}_0 \geq (\not\equiv) \ \boldsymbol{0},
\end{cases}
\tag{1.2}
$$

where d_1 and d_2 are random movement rates; q_1 and q_2 are directed movement rates; $\boldsymbol{r} = (r_1, r_2, r_3)$ is the growth rate; $\boldsymbol{k} = (k_1, k_2, k_3)$ is the carrying capacity; and two 3×3 matrices $D = (D_{ij})$ and $Q = (Q_{ij})$ represent the random movement pattern and directed drift pattern of individuals, respectively, where

$$
D = \begin{bmatrix} -1 & 1 & 0 \\ 1 & -2 & 1 \\ 0 & 1 & -1 \end{bmatrix}, \quad Q = \begin{bmatrix} -1 & 0 & 0 \\ 1 & -1 & 0 \\ 0 & 1 & 0 \end{bmatrix}.
\tag{1.3}
$$

We can write the model as

$$\begin{cases}
\dfrac{\mathrm{d}u_1}{\mathrm{d}t} = -(d_1 + q_1)u_1 + d_1 u_2 + r_1 u_1 \left(1 - \dfrac{u_1 + v_1}{k_1}\right), \\[2mm]
\dfrac{\mathrm{d}u_2}{\mathrm{d}t} = (d_1 + q_1)u_1 - (2d_1 + q_1)u_2 + d_1 u_3 + r_2 u_2 \left(1 - \dfrac{u_2 + v_2}{k_2}\right), \\[2mm]
\dfrac{\mathrm{d}u_3}{\mathrm{d}t} = (d_1 + q_1)u_2 - d_1 u_3 + r_3 u_3 \left(1 - \dfrac{u_3 + v_3}{k_3}\right), \\[2mm]
\dfrac{\mathrm{d}v_1}{\mathrm{d}t} = -(d_2 + q_2)v_1 + d_2 v_2 + r_1 v_1 \left(1 - \dfrac{u_1 + v_1}{k_1}\right), \\[2mm]
\dfrac{\mathrm{d}v_2}{\mathrm{d}t} = (d_2 + q_2)v_1 - (2d_2 + q_2)v_2 + d_2 v_3 + r_2 v_2 \left(1 - \dfrac{u_2 + v_2}{k_2}\right), \\[2mm]
\dfrac{\mathrm{d}v_3}{\mathrm{d}t} = (d_2 + q_2)v_2 - d_2 v_3 + r_3 v_3 \left(1 - \dfrac{u_3 + v_3}{k_3}\right), \\[2mm]
\boldsymbol{u}(0) = \boldsymbol{u}_0 \geq (\not\equiv)\ \boldsymbol{0},\ \boldsymbol{v}(0) = \boldsymbol{v}_0 \geq (\not\equiv)\ \boldsymbol{0}.
\end{cases} \tag{1.4}$$

We assume $d_1, d_2, q_1, q_2 > 0$ and $r_i, k_i > 0$ for $i = 1, 2, 3$. We adopt the same assumption in [23] on $\boldsymbol{k} = (k_1, k_2, k_3)$:

(**H**) $k_1 > k_2 > k_3 > 0$.

Biologically, (**H**) means that the upstream locations are more favorable for both species.

Two-species Lotka–Volterra competition patch models have attracted many research interests recently. Model (1.2) with n patches in spatially homogeneous environment (i.e., $r_1 = \cdots = r_n$ and $k_1 = \cdots = k_n$) has been considered in our earlier papers [7,10], but many techniques and results there cannot be generalized to the situation when $k_1 = \cdots = k_n$ is not assumed. The authors in [18,45] have studied the global dynamics of model (1.2) with two patches and $q := q_1 = q_2$. They have showed that there exists a critical drift rate such that below it the species with a smaller dispersal rate wins the competition, while above it the species with a larger dispersal rate wins. In a competition model with two patches, the authors in [12,17,32] have showed that the species with more evenly distributed resources has less competition advantage. In [8], the global dynamics of a Lotka–Volterra competition patch model is classified under some assumptions on patches, which requires $d_1/q_1 = d_2/q_2$ in terms of (1.2). For more studies on competition patch models, we refer to the works [2,5,6,27,30,33,44,46,50].

We will take an adaptive dynamics approach [14,16] to analyze (1.4) by viewing species $\boldsymbol{u}$ as the resident species and species $\boldsymbol{v}$ as the mutant species. Model (1.4) has two semitrivial equilibria $(\boldsymbol{u}^*, \boldsymbol{0})$ and $(\boldsymbol{0}, \boldsymbol{v}^*)$. We fix parameters d_1 and q_1 and vary d_2 and q_2. We show that there exists a curve $q = q_{\boldsymbol{u}}^*(d)$ dividing the (d_2, q_2)-plane into two regions such that $(\boldsymbol{u}^*, \boldsymbol{0})$ is stable if and only if (d_2, q_2) is above the curve. Our results complement those in [23] by defining and analyzing the curve $q = q_{\boldsymbol{u}}^*(d)$ and obtaining the global dynamics of model (1.4). In particular, we show that if $q_1 < \underline{q}$ the curve $q = q_{\boldsymbol{u}}^*(d)$ is bounded (see Fig. 3) and if $q_1 > \overline{q}$ it is unbounded (see Fig. 4). This result is in sharp contrast with the corresponding one for the model in spatially homogeneous environment ($k_1 = k_2 = k_3$) [7], where the curve $q = q_{\boldsymbol{u}}^*(d)$ is always unbounded. We give explicitly parameter ranges for competitive exclusion and conditions for coexistence/bistability in three cases ($q_1 < \underline{q}$, $\underline{q} \leq q_1 \leq \overline{q}$ and $q_1 > \overline{q}$). Our results show that the magnitude of the drift rates and the spatial heterogeneity of environment have a large impact on the competition outcomes of the stream species.

Our paper is organized as follows. In Sect. 2, we list some preliminary results. In Sect. 3, we state the main results on model (1.4). We give some conclusive remarks and numerical simulations in Sect. 4. The proofs of the main results are presented in Sect. 5. In the Appendix, we show the relations of $\underline{q}$, $\overline{q}$, and q_0. These relations are implicitly included in the main results, and we prove them for reader's convenience.

2. Preliminary

Let $A = (a_{ij})_{n \times n}$ be a square matrix with real entries, $\sigma(A)$ be the set of all eigenvalues of A, and $s(A)$ be the *spectral bound* of A, i.e., $s(A) = \max\{\text{Re}\lambda : \lambda \in \sigma(A)\}$. The matrix A is called *irreducible* if it cannot be placed into block upper triangular form by simultaneous row and column permutations and *essentially nonnegative* if $a_{ij} \geq 0$ for all $1 \leq i, j \leq n$ and $i \neq j$. By the Perron–Frobenius theorem, if A is irreducible and essentially nonnegative, then $s(A)$ is an eigenvalue of A (called the *principal eigenvalue* of A), which is the unique eigenvalue associated with a nonnegative eigenvector. The following result on the monotonicity of spectral bound can be found in [1,9]:

Lemma 2.1. *Let $A = (a_{ij})_{n \times n}$ be an irreducible and essentially nonnegative matrix and $M = diag(m_i)$ be a real diagonal matrix. If $s(A) = 0$, then*

$$\frac{\mathrm{d}}{\mathrm{d}\mu} s(\mu A + M) \leq 0$$

for $\mu \in (0, \infty)$ and the inequality is strict except for the case $m_1 = \cdots = m_n$. Moreover,

$$\lim_{\mu \to 0} s(\mu A + M) = \max_{1 \leq i \leq n} \{m_i\} \ \ and \ \ \lim_{\mu \to \infty} s(\mu A + M) = \sum_{i=1}^{n} \theta_i m_i,$$

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

Let $\boldsymbol{m} = (m_1, m_2, m_3)$ be a real vector. We write $\boldsymbol{m} \gg \boldsymbol{0}$ if $m_i > 0$ for all $i = 1, 2, 3$, and $\boldsymbol{m} > \boldsymbol{0}$ if $\boldsymbol{m} \geq \boldsymbol{0}$ and $\boldsymbol{m} \neq \boldsymbol{0}$. Matrix $dD + qQ + diag(m_i)$ is irreducible and essentially nonnegative for any $d, q > 0$, where D and Q are defined by (1.3). By the Perron–Frobenius theorem, $s(dD + qQ + diag(m_i))$ is the principal eigenvalue of the following eigenvalue problem:

$$\sum_{j=1}^{3} (dD_{ij} + qQ_{ij})\phi_j + m_i\phi_i = \lambda\phi_i, \ \ i = 1, 2, 3. \tag{2.1}$$

We need to consider the following single-species patch model:

$$\begin{cases} \dfrac{\mathrm{d}u_i}{\mathrm{d}t} = \sum_{j=1}^{3} (dD_{ij} + qQ_{ij})u_j + r_i u_i \left(1 - \dfrac{u_i}{k_i}\right), & i = 1, 2, 3, \ \ t > 0, \\ \boldsymbol{u}(0) = \boldsymbol{u}_0 > \boldsymbol{0}. \end{cases} \tag{2.2}$$

The global dynamics of (2.2) is as follows:

Lemma 2.2. *Let D and Q be defined in (1.3), $\boldsymbol{r}, \boldsymbol{k} \gg \boldsymbol{0}$, $d > 0$, and $q \geq 0$. Then, model (2.2) admits a unique positive equilibrium $\boldsymbol{u}^* \gg \boldsymbol{0}$, which is globally asymptotically stable.*

Proof. By [13,31,39], it suffices to show that $\boldsymbol{0}$ is unstable, i.e.,

$$s := s(dD + qQ + diag(r_i)) > 0.$$

Let $\phi^T = (\phi_1, \phi_2, \phi_3)^T \gg \boldsymbol{0}$ with $\sum_{i=1}^{3} \phi_i = 1$ be the positive eigenvector of $dD + qQ + diag(r_i)$ corresponding to s. Multiplying $(1, 1, 1)$ to the left of $dD\phi + qQ\phi + diag(r_i)\phi = s\phi$, we get $s = \sum_{i=1}^{3} r_i\phi_i > 0$. This proves the result. $\qquad \square$

By Lemma 2.2, model (1.4) has two semitrivial equilibria $(\boldsymbol{u}^*, \boldsymbol{0})$ and $(\boldsymbol{0}, \boldsymbol{v}^*)$, where $\boldsymbol{u}^*$(resp., $\boldsymbol{v}^*$) $\gg \boldsymbol{0}$ is the positive equilibrium of (2.2) with (d, q) replaced by (d_1, q_1) (resp., (d_2, q_2)). Linearizing model (1.4)

at $(\boldsymbol{u}^*, \boldsymbol{0})$, we can easily see that its stability is determined by the sign of $\lambda_1(d_2, q_2, \boldsymbol{1} - \boldsymbol{u}^*/\boldsymbol{k})$, which is the principal eigenvalue of the following eigenvalue problem:

$$\begin{cases} \lambda\phi_1 = -(d_2 + q_2)\phi_1 + d_2\phi_2 + r_1\left(1 - \dfrac{u_1^*}{k_1}\right)\phi_1, \\ \lambda\phi_2 = (d_2 + q_2)\phi_1 - (2d_2 + q_2)\phi_2 + d_2\phi_3 + r_2\left(1 - \dfrac{u_2^*}{k_2}\right)\phi_2, \\ \lambda\phi_3 = (d_2 + q_2)\phi_2 - d_2\phi_3 + r_3\left(1 - \dfrac{u_3^*}{k_3}\right)\phi_3. \end{cases} \tag{2.3}$$

In particular, $(\boldsymbol{u}^*, \boldsymbol{0})$ is locally asymptotically stable if $\lambda_1(d_2, q_2, \boldsymbol{1} - \boldsymbol{u}^*/\boldsymbol{k}) < 0$ and unstable if $\lambda_1(d_2, q_2, \boldsymbol{1} - \boldsymbol{u}^*/\boldsymbol{k}) > 0$. Here, we abuse the notation by denoting $\boldsymbol{1} - \boldsymbol{u}^*/\boldsymbol{k} := (1 - u_1^*/k_1, 1 - u_2^*/k_2, 1 - u_3^*/k_3)$.

3. Main results

We fix $d_1, q_1 > 0, \boldsymbol{r}, \boldsymbol{k} \gg \boldsymbol{0}$ and view species $\boldsymbol{u}$ as the resident species and $\boldsymbol{v}$ as the mutant species. We investigate the dynamics of model (1.4) varying (d_2, q_2). For this purpose, we divide the first quadrant of the (d, q)-plane into six regions:

$$\begin{aligned} G_{11} &:= \left\{ (d, q) : \ d \geq d_1, q \geq \frac{q_1}{d_1}d, (d, q) \neq (d_1, q_1) \right\}, \\ G_{12} &:= \left\{ (d, q) : \ 0 < d < d_1, q \geq q_1 \right\}, \\ G_{13} &:= \left\{ (d, q) : \ d \geq d_1, q_1 \leq q < \frac{q_1}{d_1}d, (d, q) \neq (d_1, q_1) \right\}, \\ G_{21} &:= \left\{ (d, q) : \ 0 < d \leq d_1, 0 < q \leq \frac{q_1}{d_1}d, (d, q) \neq (d_1, q_1) \right\}, \\ G_{22} &:= \left\{ (d, q) : \ d > d_1, 0 < q \leq q_1 \right\}, \\ G_{23} &:= \left\{ (d, q) : \ 0 < d \leq d_1, \frac{q_1}{d_1}d < q \leq q_1, (d, q) \neq (d_1, q_1) \right\}. \end{aligned} \tag{3.1}$$

For readers' convenience, we graph the six regions in Fig. 2.

3.1. Invasion curve

We consider the local stability of $(\boldsymbol{u}^*, \boldsymbol{0})$ in this subsection. Biologically, if $(\boldsymbol{u}^*, \boldsymbol{0})$ is stable, then a small amount of species $\boldsymbol{v}$ cannot invade species $\boldsymbol{u}$; if $(\boldsymbol{u}^*, \boldsymbol{0})$ is unstable, then a small amount of species $\boldsymbol{v}$ may be able to invade species $\boldsymbol{u}$. We prove that there exists a curve $q = q_{\boldsymbol{u}}^*(d)$ in the (d, q)-plane such that $(\boldsymbol{u}^*, \boldsymbol{0})$ is locally asymptotically stable if (d_2, q_2) is above the curve and $(\boldsymbol{u}^*, \boldsymbol{0})$ is unstable if it is below the curve. To this end, we define

$$d^* = \begin{cases} \infty, & \text{if } \sum_{i=1}^{3} r_i\left(1 - \frac{u_i^*}{k_i}\right) \geq 0, \\ d_0, & \text{if } \sum_{i=1}^{3} r_i\left(1 - \frac{u_i^*}{k_i}\right) < 0, \end{cases} \tag{3.2}$$

where $d = d_0 > 0$ is the unique root of $\lambda_1(d, 0, \boldsymbol{1} - \boldsymbol{u}^*/\boldsymbol{k}) = 0$ if $\sum_{i=1}^{3} r_i(1 - u_i^*/k_i) < 0$ (see the existence of d_0 in Lemma 5.2). We have the following result about the local stability/instability of the semitrivial equilibrium $(\boldsymbol{u}^*, \boldsymbol{0})$:

Theorem 3.1. *Suppose that* (**H**) *holds,* $\boldsymbol{r} \gg \boldsymbol{0}$, *and* $d_1, q_1 > 0$. *Then, there exists a continuous function* $q = q_{\boldsymbol{u}}^*(d) : (0, d^*) \to \mathbb{R}_+$ *passing through* (d_1, q_1) *such that the following statements hold for model* (1.4):
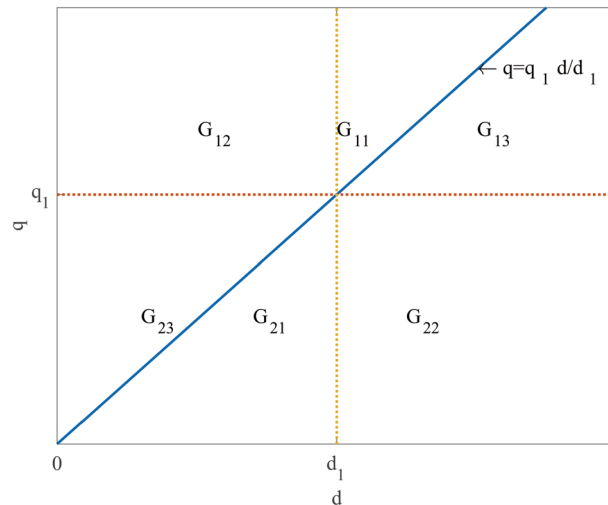
FIG. 2. Illustration of the six regions of (d, q)-plane

(i) If $(d_2, q_2) \in S_1$, then the semitrivial equilibrium $(\boldsymbol{u}^*, \boldsymbol{0})$ is locally asymptotically stable;

(ii) If $(d_2, q_2) \in S_2$, then the semitrivial equilibrium $(\boldsymbol{u}^*, \boldsymbol{0})$ is unstable.

Here, $S_1 \cup S_2$ is a partition of the first quadrant of the (d, q)-plane defined as follows:

$$
\begin{aligned}
S_1 &:= \{(d, q) : \ 0 < d < d^*, \ q > q_{\boldsymbol{u}}^*(d)\} \cup S_1^*, \\
S_2 &:= \{(d, q) : \ 0 < d < d^*, \ 0 < q < q_{\boldsymbol{u}}^*(d)\},
\end{aligned}
\tag{3.3}
$$

where

$$
S_1^* = \begin{cases} \{(d, q) : d \geq d^*, \ q > 0\}, & \text{if } d^* \neq \infty, \\ \emptyset, & \text{if } d^* = \infty. \end{cases}
\tag{3.4}
$$

Remark 3.2. We call the curve in the first quadrant of (d, q)-plane defined by the function $q = q_{\boldsymbol{u}}^*(d)$ in Theorem 3.1 the *invasion curve*. This curve consists with all the points $(d, q_{\boldsymbol{u}}^*(d))$ such that $\lambda_1(d, q_{\boldsymbol{u}}^*(d), \boldsymbol{1} - \boldsymbol{u}^*/\boldsymbol{k}) = 0$, i.e., $(\boldsymbol{u}^*, \boldsymbol{0})$ is linearly neutrally stable. The invasion curve divides the first quadrant into $S_1 \cup S_2$, where S_1 is the region above the curve and S_2 is the region below it. By Theorem 3.1, $(\boldsymbol{u}^*, \boldsymbol{0})$ is locally asymptotically stable if $(d_2, q_2) \in S_1$ and unstable if $(d_2, q_2) \in S_2$.

In the following of this paper, we denote

$$
\begin{aligned}
\underline{q} &:= \min\left\{\frac{r_1}{k_1}(k_1 - k_2), \frac{r_3}{k_3}(k_2 - k_3)\right\}, \\
\overline{q} &:= \max\left\{\frac{r_1}{k_1}(k_1 - k_2), \frac{r_3}{k_3}(k_2 - k_3)\right\}.
\end{aligned}
\tag{3.5}
$$

We take $\underline{q}$ and $\overline{q}$ as the threshold values for the drift rates. Specifically, if a drift rate is below $\underline{q}$ (above $\overline{q}$), we call it a *slow (large) drift*; if a drift rate is between $\underline{q}$ and $\overline{q}$, we call it an *intermediate drift*. These definitions coincide with those in [23] if $r_1 = r_2 = r_3$. It turns out that the magnitude of drift rate q_1 will have a large impact on the shape of the invasion curve and the dynamics of the model.

We have the following result about the invasion curve:

Proposition 3.3. *Suppose that* (**H**) *holds,* $\boldsymbol{r} \gg \boldsymbol{0}$, *and* $d_1, q_1 > 0$. *Let* S_1 *and* S_2 *be defined in Theorem 3.1. Then, the following statements hold:*

(i) $G_{11} \subset S_1$ and $G_{21} \subset S_2$;
(ii) If $q_1 > \overline{q}$, then $G_{12} \subset S_1$ and $G_{22} \subset S_2$;
(iii) If $q_1 < \underline{q}$, then $G_{13} \subset S_1$ and $G_{23} \subset S_2$

We explore further properties of the invasion curve:

Proposition 3.4. *Suppose that* (**H**) *holds,* $r \gg 0$, *and* $d_1, q_1 > 0$. *Let* $q = q_u^*(d) : (0, d^*) \to \mathbb{R}_+$ *be defined in Theorem* 3.1. *Then, the following statements hold:*

(i) $\lim_{d \to 0} q_u^*(d) = q_0$, *where*

$$q_0 = \max \left\{ r_1 \left(1 - \frac{u_1^*}{k_1} \right), \ r_2 \left(1 - \frac{u_2^*}{k_2} \right) \right\}; \tag{3.6}$$

(ii) *If* $q_1 < \underline{q}$, *then*

$$d^* = d_0 \quad and \quad \lim_{d \to d^*} q_u^*(d) = 0; \tag{3.7}$$

(iii) *If* $q_1 > \overline{q}$, *then*

$$d^* = \infty \quad and \quad \lim_{d \to \infty} \frac{q_u^*(d)}{d} = \theta \tag{3.8}$$

for some $\theta \in (0, q_1/d_1)$;

(iv) *If* $\underline{q} \leq q \leq \overline{q}$, *then* (3.7) *holds when* $\sum_{i=1}^3 r_i \left(1 - u_i^*/k_i \right) < 0$, (3.8) *holds with* $\theta \in (0, q_1/d_1)$ *when* $\sum_{i=1}^3 r_i \left(1 - u_i^*/k_i \right) > 0$, *and* (3.8) *holds with* $\theta = 0$ *when* $\sum_{i=1}^3 r_i \left(1 - u_i^*/k_i \right) = 0$.

Remark 3.5. By Propositions 3.3 and 3.4, the invasion curve lies in $G_{12} \cup G_{22}$ when the drift rate q_1 is small, and it lies in $G_{13} \cup G_{23}$ when q_1 is large. Moreover, if q_1 is small, the invasion curve is defined on a bounded interval $(0, d_0)$; if q_1 is large, it is defined on $(0, \infty)$ and has a slant asymptote $q = \theta d$ for some $\theta \in (0, q_1/d_1)$.

3.2. Competitive exclusion

In this subsection, we study the global dynamics of model (1.4) and find some parameter ranges of (d_2, q_2) such that competitive exclusion happens. The relations of $\underline{q}$, $\overline{q}$ and q_0 are implicitly included in the results below. However, for reader's convenience, we include the proof in the Appendix.

Firstly, we consider the small drift case, i.e., $q_1 < \underline{q}$.

Theorem 3.6. *Suppose that* (**H**) *holds,* $r \gg 0$, *and* $d_1, q_1 > 0$ *with* $q_1 < \underline{q}$. *Then, the following statements hold:*

(i) *If* $(d_2, q_2) \in G_{21} \cup G_{23}$, *then the semitrivial equilibrium* $(\mathbf{0}, v^*)$ *of* (1.4) *is globally asymptotically stable;*

(ii) *If* $(d_2, q_2) \in G_{11} \cup G_{12}^* \cup G_{13}$, *then the semitrivial equilibrium* $(u^*, \mathbf{0})$ *of* (1.4) *is globally asymptotically stable.*

Here, G_{12}^* *is defined by*

$$G_{12}^* = \{ (d_2, q_2) : (d_2, q_2) \in G_{12}, q_2 > \overline{q} \}. \tag{3.9}$$

Remark 3.7. Our results on model (1.4) for the small drift rate case are summarized in Fig. 3. We have proved that competitive exclusion appears if (d_2, q_2) falls into the blue and yellow regions of Fig. 3.

Next, we consider the large drift case, i.e., $q_1 > \overline{q}$.

Theorem 3.8. *Suppose that* (**H**) *holds,* $r \gg 0$, *and* $d_1, q_1 > 0$ *with* $q_1 > \overline{q}$. *Then, the following statements hold:*
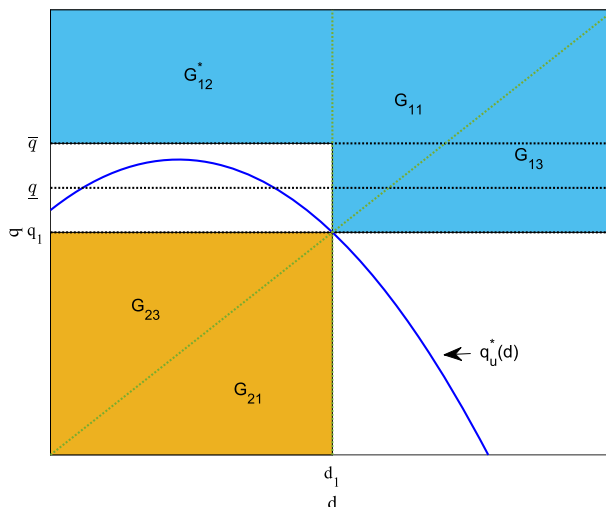
FIG. 3. Illustration of the results for the case $q_1 < \underline{q}$. If (d_2, q_2) is above the curve $q = q_u^*(d)$, then $(\boldsymbol{u}^*, \boldsymbol{0})$ is stable; and if (d_2, q_2) is under the curve, then $(\boldsymbol{u}^*, \boldsymbol{0})$ is unstable. If $(d_2, q_2) \in G_{21} \cup G_{23}$, $(\boldsymbol{0}, \boldsymbol{v}^*)$ is globally asymptotically stable; if $(d_2, q_2) \in G_{11} \cup G_{12}^* \cup G_{13}$, $(\boldsymbol{u}^*, \boldsymbol{0})$ is globally asymptotically stable

(i) If $(d_2, q_2) \in G_{21} \cup G_{22} \cup G_{23}^*$, then the semitrivial equilibrium $(\boldsymbol{0}, \boldsymbol{v}^*)$ is globally asymptotically stable;

(ii) If $(d_2, q_2) \in G_{11} \cup G_{12}$, then the semitrivial equilibrium $(\boldsymbol{u}^*, \boldsymbol{0})$ is globally asymptotically stable.

Here, G_{23}^* is defined by

$$G_{23}^* = \{(d_2, q_2) : (d_2, q_2) \in G_{23}, q_2 < \underline{q}\}. \tag{3.10}$$

Remark 3.9. Our results on model (1.4) for the large drift rate case are summarized in Fig. 4. Different from the small drift rate case, the invasion curve is unbounded. Again, we are able to prove that competitive exclusion happens if (d_2, q_2) falls into the blue and yellow regions of Fig. 4.

Then, we consider the intermediate drift case, i.e., $\underline{q} \leq q_1 \leq \overline{q}$, and we have the following results on the global dynamics of model (1.4).

Theorem 3.10. *Suppose that* (**H**) *holds,* $\boldsymbol{r} \gg \boldsymbol{0}$, *and* $d_1, q_1 > 0$ *with* $\underline{q} \leq q_1 \leq \overline{q}$. *Let* G_{12}^* *be defined by* (3.9) *and* G_{23}^* *be defined by* (3.10). *Then, the following statements hold:*

(i) *If* $(d_2, q_2) \in G_{21} \cup G_{23}^*$, *then the semitrivial equilibrium* $(\boldsymbol{0}, \boldsymbol{v}^*)$ *is globally asymptotically stable;*

(ii) *If* $(d_2, q_2) \in G_{11} \cup G_{12}^*$, *then the semitrivial equilibrium* $(\boldsymbol{u}^*, \boldsymbol{0})$ *is globally asymptotically stable.*

Remark 3.11. Our results on model (1.4) for the intermediate drift rate case are summarized in Fig. 5. In this case, the invasion curve may be defined on either a bounded or an unbounded interval. However, we know that it must locate between the yellow and blue regions in Fig. 5, where competitive exclusion happens.

In view of Theorems 3.6, 3.8, and 3.10, the global dynamics of model (1.4) in $G_{11} \cup G_{21}$ is independent of q_1:

Corollary 3.12. *Suppose that* (**H**) *holds,* $\boldsymbol{r} \gg \boldsymbol{0}$, *and* $d_1, q_1 > 0$. *Then, the following statements hold:*

(i) *If* $(d_2, q_2) \in G_{11}$, *then the semitrivial equilibrium* $(\boldsymbol{u}^*, \boldsymbol{0})$ *is globally asymptotically stable;*

(ii) *If* $(d_2, q_2) \in G_{21}$, *then the semitrivial equilibrium* $(\boldsymbol{0}, \boldsymbol{v}^*)$ *is globally asymptotically stable.*
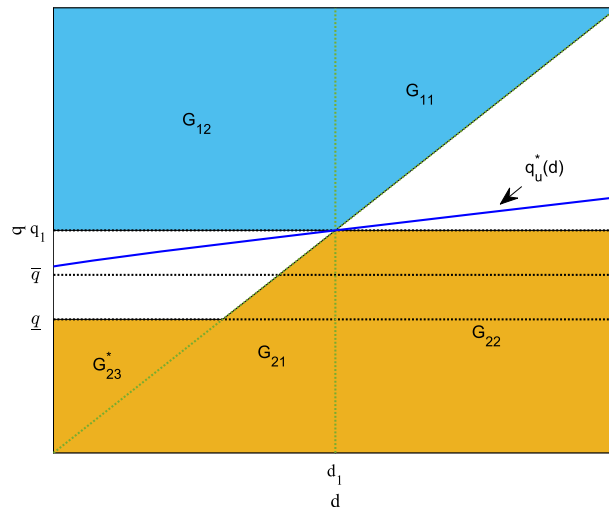
FIG. 4. Illustration of the results for the case $q_1 > \bar{q}$. If (d_2, q_2) is above the curve $q = q_u^*(d)$, then $(\boldsymbol{u}^*, \boldsymbol{0})$ is stable; and if (d_2, q_2) is under the curve, then $(\boldsymbol{u}^*, \boldsymbol{0})$ is unstable. If $(d_2, q_2) \in G_{21} \cup G_{22} \cup G_{23}^*$, $(\boldsymbol{0}, \boldsymbol{v}^*)$ is globally asymptotically stable; and if $(d_2, q_2) \in G_{11} \cup G_{12}$, $(\boldsymbol{u}^*, \boldsymbol{0})$ is globally asymptotically stable
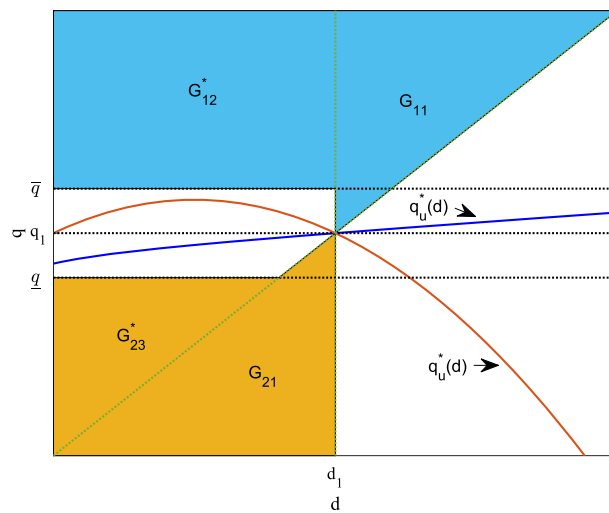

FIG. 5. Illustration of the results for the case $\underline{q} \leq q_1 \leq \bar{q}$. If $(d_2, q_2) \in G_{21} \cup G_{23}^*$, $(\boldsymbol{0}, \boldsymbol{v}^*)$ is globally asymptotically stable; and if $(d_2, q_2) \in G_{11} \cup G_{12}^*$, $(\boldsymbol{u}^*, \boldsymbol{0})$ is globally asymptotically stable

More importantly, we have the following result about the evolution of random dispersal and directed drift rates.

Corollary 3.13. *Suppose that* (**H**) *holds,* $\boldsymbol{r} \gg \boldsymbol{0}$*, and* $d_1, q_1 > 0$*. Then, the following statements hold:*

(i) *Fix* $d_1 = d_2$*. If* $q_1 < q_2$*, then the semitrivial equilibrium* $(\boldsymbol{u}^*, \boldsymbol{0})$ *is globally asymptotically stable; If* $q_1 > q_2$*, then the semitrivial equilibrium* $(\boldsymbol{0}, \boldsymbol{v}^*)$ *is globally asymptotically stable;*

(ii) *Fix* $q_1 = q_2 < \underline{q}$*. If* $d_1 < d_2$*, then the semitrivial equilibrium* $(\boldsymbol{u}^*, \boldsymbol{0})$ *is globally asymptotically stable; If* $d_1 > d_2$*, then the semitrivial equilibrium* $(\boldsymbol{0}, \boldsymbol{v}^*)$ *is globally asymptotically stable;*

(iii) *Fix $q_1 = q_2 > \overline{q}$. If $d_1 < d_2$, then the semitrivial equilibrium $(\mathbf{0}, \mathbf{v}^*)$ is globally asymptotically stable; If $d_1 > d_2$, then the semitrivial equilibrium $(\mathbf{u}^*, \mathbf{0})$ is globally asymptotically stable.*

Remark 3.14. By Corollary 3.13, the species with a smaller drift rate tends to have competitive advantage. If the drift rate is small, the species with smaller random dispersal rate has competitive advantage; if the drift rate is large, larger random dispersal rate is favored. We remark that Corollary 3.13 (i) was proved in [37] for the PDE case, and the corresponding results of 3.13 (ii)–(iii) for the PDE case in [37] are as follows: if $d_1 > d_2$, then there exists $\overline{q}(d_1, d_2)$ (resp. $\underline{q}(d_1, d_2)$) such that $(\mathbf{u}^*, \mathbf{0})$ (resp. $(\mathbf{0}, \mathbf{v}^*)$) is globally asymptotically stable for $q_1 = q_2 > \overline{q}(d_1, d_2)$ (resp. $q_1 = q_2 < \underline{q}(d_1, d_2)$).

3.3. Coexistence and bistability

If (d_2, q_2) is in the blank regions of Figs. 3, 4 and 5, we show that bistability and coexistence may occur. To this end, we explore the stability/instability of the semitrivial equilibrium $(\mathbf{0}, \mathbf{v}^*(d_2, q_2))$ along the invasion curve $q_2 = q_{\mathbf{u}}^*(d_2)$. Let

$$\hat{\lambda}_1(d_2) := \lambda_1\left(d_1, q_1, \mathbf{1} - \frac{\mathbf{v}^*(d_2, q_{\mathbf{u}}^*(d_2))}{\mathbf{k}}\right). \tag{3.11}$$

Then, $\hat{\lambda}_1(d_1) = 0$, the semitrivial equilibrium $(\mathbf{0}, \mathbf{v}^*(d_2, q_{\mathbf{u}}^*(d_2)))$ is stable if $\hat{\lambda}_1(d_2) < 0$, and $(\mathbf{0}, \mathbf{v}^*(d_2, q_{\mathbf{u}}^*(d_2)))$ is unstable if $\hat{\lambda}_1(d_2) > 0$. The following result for the large drift case can be proved similarly as [7, Theorem 5.4], so we omit the proof here.

Theorem 3.15. *Suppose that* (**H**) *holds, $\mathbf{r} \gg \mathbf{0}$, and $d_1, q_1 > 0$ with $q_1 > \overline{q}$. Let $q = q_{\mathbf{u}}^*(d) : (0, \infty) \to \mathbb{R}_+$ be defined in Theorem 3.1 and Proposition 3.4 (iii). Then, for any $d_2 > 0$, the following statements hold:*

(i) *If $\hat{\lambda}_1(d_2) < 0$, then*

$$\hat{q}(d_2) := \inf\left\{q > 0 : \ q > q_{\mathbf{u}}^*(d_2) \ and \ \lambda_1\left(d_1, q_1, \mathbf{1} - \frac{\mathbf{v}^*(d_2, q)}{\mathbf{k}}\right) \geq 0\right\}$$

exists and satisfies

$$\begin{cases} \hat{q}(d_2) \in (q_{\mathbf{u}}^*(d_2), q_1) & for \ d_2 < d_1, \\ \hat{q}(d_2) \in \left(q_{\mathbf{u}}^*(d_2), \dfrac{q_1}{d_1}d_2\right) & for \ d_2 > d_1. \end{cases} \tag{3.12}$$

Moreover, for any $q_2 \in (q_{\mathbf{u}}^*(d_2), \hat{q}(d_2))$, both semitrivial equilibria $(\mathbf{u}^*, \mathbf{0})$ and $(\mathbf{0}, \mathbf{v}^*)$ are locally asymptotically stable and model (1.4) admits an unstable positive equilibrium.

(ii) *If $\hat{\lambda}_1(d_2) > 0$, then*

$$\hat{q}(d_2) := \sup\left\{q > 0 : \ q < q_{\mathbf{u}}^*(d_2) \ and \ \lambda_1\left(d_1, q_1, \mathbf{1} - \frac{\mathbf{v}^*(d_2, q)}{\mathbf{k}}\right) \leq 0\right\}$$

exists and satisfies

$$\begin{cases} \hat{q}(d_2) \in \left(\dfrac{q_1}{d_1}d_2, q_{\mathbf{u}}^*(d_2)\right) & for \ d_2 < d_1, \\ \hat{q}(d_2) \in (q_1, q_{\mathbf{u}}^*(d_2)) & for \ d_2 > d_1. \end{cases}$$

Moreover, for any $q_2 \in (\hat{q}(d_2), q_{\mathbf{u}}^*(d_2))$, both semitrivial equilibria $(\mathbf{u}^*, \mathbf{0})$ and $(\mathbf{0}, \mathbf{v}^*)$ are unstable and model (1.4) admits a stable positive equilibrium.

Remark 3.16. In (ii) when both semitrivial equilibria are unstable, we may conclude that the solutions are uniform persistent. If $\underline{q} \leq q_1 \leq \overline{q}$ (the intermediate drift case), Theorem 3.15 (i)–(ii) holds for any $d_2 < d_1$, and we omit the statement to save space here.

The small drift rate case will be handled slightly different from the large drift rate case. For any $\theta > 0$, by Lemma 2.1 and Proposition 3.3 (ii), the line $q = d\theta$ and the invasion curve $q = q_{\boldsymbol{u}}^*(d)$ have exactly one intersection point $(d^*(\theta), d^*(\theta)\theta)$. So we can reparameterize the invasion curve as follows:

$$\begin{cases} d = d^*(\theta), \\ q = q^*(\theta) = d^*(\theta)\theta, \end{cases} \quad \theta > 0. \tag{3.13}$$

Let

$$\tilde{\lambda}_1(\theta) := \lambda_1\left(d_1, q_1, \boldsymbol{1} - \frac{\boldsymbol{v}^*\left(d^*(\theta), q^*(\theta)\right)}{\boldsymbol{k}}\right), \quad \theta > 0. \tag{3.14}$$

Then, the semitrivial equilibrium $(\boldsymbol{0}, \boldsymbol{v}^*\left(d^*(\theta), q^*(\theta)\right))$ is stable if $\tilde{\lambda}_1(\theta) < 0$ and unstable if $\tilde{\lambda}_1(\theta) > 0$. Noticing that $q_{\boldsymbol{u}}^*(d_1) = q_1$, we have $d^*(q_1/d_1) = d_1$ and

$$\tilde{\lambda}_1\left(q_1/d_1\right) = \lambda_1\left(d_1, q_1, \boldsymbol{1} - \frac{\boldsymbol{v}^*\left(d_1, q_1\right)}{\boldsymbol{k}}\right) = 0.$$

Theorem 3.17. *Suppose that* (**H**) *holds,* $\boldsymbol{r} \gg \boldsymbol{0}$, *and* $d_1, q_1 > 0$ *with* $0 < q_1 < \underline{q}$. *Then, for any* $\theta > 0$, *the following statements hold:*

(i) *If* $\tilde{\lambda}_1(\theta) < 0$, *then*

$$\tilde{d}^*(\theta) := \inf\left\{d > 0: \ d > d^*(\theta) \ and \ \lambda_1\left(d_1, q_1, \boldsymbol{1} - \frac{\boldsymbol{v}^*\left(d, d\theta\right)}{\boldsymbol{k}}\right) \geq 0\right\}$$

exists with $d^*(\theta) < \tilde{d}^*(\theta)$ *such that for any* (d_2, q_2) *with* $q_2 = d_2\theta$ *and* $d^*(\theta) < d_2 < \tilde{d}^*(\theta)$ *both semitrivial equilibria* $(\boldsymbol{u}^*, \boldsymbol{0})$ *and* $(\boldsymbol{0}, \boldsymbol{v}^*)$ *are locally asymptotically stable and model* (1.4) *admits an unstable positive equilibrium.*

(ii) *If* $\tilde{\lambda}_1(\theta) > 0$, *then*

$$\tilde{d}^*(\theta) := \sup\left\{d > 0: \ d < d^*(\theta) \ and \ \lambda_1\left(d_1, q_1, \boldsymbol{1} - \frac{\boldsymbol{v}^*\left(d, d\theta\right)}{\boldsymbol{k}}\right) \leq 0\right\}$$

exists with $\tilde{d}^*(\theta) < d^*(\theta)$ *such that for any* (d_2, q_2) *with* $q_2 = d_2\theta$ *and* $\tilde{d}^*(\theta) < d_2 < d^*(\theta)$ *both semitrivial equilibria* $(\boldsymbol{u}^*, \boldsymbol{0})$ *and* $(\boldsymbol{0}, \boldsymbol{v}^*)$ *are unstable and model* (1.4) *admits a stable positive equilibrium.*

Moreover, $\tilde{d}^*(\theta)$ *satisfies*

$$\begin{cases} (\tilde{d}^*(\theta), \tilde{d}^*(\theta)\theta) \in G_{12} \ \ if \ \theta > \dfrac{q_1}{d_1}, \\ (\tilde{d}^*(\theta), \tilde{d}^*(\theta)\theta) \in G_{22} \ \ if \ 0 < \theta < \dfrac{q_1}{d_1}. \end{cases} \tag{3.15}$$

Proof. We prove (i), and (ii) can be proved similarly. Fix $\theta > 0$. Suppose $\tilde{\lambda}_1(\theta) < 0$. Let

$$A = \left\{d > 0: \ d > d^*(\theta) \ and \ \lambda_1\left(d_1, q_1, \boldsymbol{1} - \frac{\boldsymbol{v}^*\left(d, d\theta\right)}{\boldsymbol{k}}\right) \geq 0\right\}.$$

By Theorem 3.6 (ii), $(\boldsymbol{0}, \boldsymbol{v}^*)$ is unstable or neutrally stable if $(d_2, q_2) \in G_{11} \cup G_{13}$, which yields $A \neq \emptyset$. Since $\tilde{\lambda}_1(\theta) < 0$, there exists $\epsilon_0 > 0$ such that

$$\lambda_1\left(d_1, q_1, \boldsymbol{1} - \frac{\boldsymbol{v}^*\left(d^*(\theta) + \epsilon, \theta(d^*(\theta) + \epsilon)\right)}{\boldsymbol{k}}\right) < 0, \quad \text{for any } 0 < \epsilon < \epsilon_0.$$

Therefore, $\tilde{d}^*(\theta)$ exists with $d^*(\theta) < \tilde{d}^*(\theta)$.

If (d_2, q_2) satisfies $q_2 = d_2\theta$ and $\tilde{d}^*(\theta) < d_2 < d^*(\theta)$, by the definition of $\tilde{d}^*(\theta)$, we have

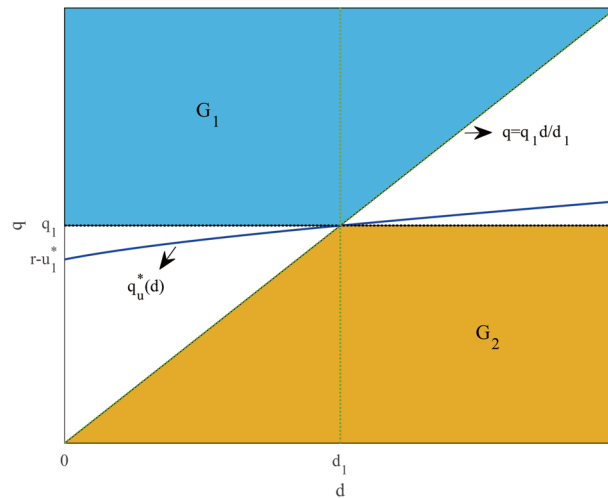$$\lambda_1\left(d_1, q_1, \boldsymbol{r} - \boldsymbol{v}^*(d_2, q_2)\right) < 0,$$

FIG. 6. Illustration of the main results for (1.4) with $k_1 = k_2 = k_3$ in [7]. The blue cure is the invasion curve, which always lies between the lines $q = q_1$ and $q = q_1 d/d_1$. Moreover, $(\boldsymbol{u}^*, \boldsymbol{0})$ is globally asymptotically stable if $(d_2, q_2) \in G_1$, and $(\boldsymbol{0}, \boldsymbol{v}^*)$ is globally asymptotically stable if $(d_2, q_2) \in G_2$

which means that $(\boldsymbol{0}, \boldsymbol{v}^*)$ is locally asymptotically stable. By Theorem 3.1, $(\boldsymbol{u}^*, \boldsymbol{0})$ is also locally asymptotically stable. By the monotone dynamical system theory [20,21,46], model (1.4) admits an unstable positive equilibrium. Finally, it is easy to see that (3.15) holds by Theorem 3.6.   □

4. Discussions and numerical simulations

In this section, we discuss the results of the paper and present some numerical simulations.

4.1. Impact of spatial heterogeneity

If the environment is homogeneous, i.e., assumption (**H**) is replaced by $k_1 = k_2 = k_3$, model (1.4) with n patches has been investigated in our recent paper [7]. The main results in [7] are summarized in Fig. 6. In particular, we prove that the invasion curve is between the lines $q = q_1$ and $q = q_1 d/d_1$, $(\boldsymbol{u}^*, \boldsymbol{0})$ is globally asymptotically stable in G_1, and $(\boldsymbol{0}, \boldsymbol{v}^*)$ is globally asymptotically stable in G_2. These results are independent of the magnitude of drift rate q_1 and are similar to the large drift rate case in this paper. Biologically, the downstream end is crowded due to the drift and thereby less friendly compared with the upstream end. If the environment perturbs from being uniformly distributed and the upstream locations become advantageous, e.g., assumption (**H**) holds, then a larger drift rate may compensate for it. This may explain why the homogeneous environment case is similar to the larger drift case in this paper.

4.2. Impact of drift rate

By Propositions 3.4 and 3.13, if the drift rate q_1 is small ($q_1 < \underline{q}$), the invasion curve $q = q_{\boldsymbol{u}}^*(d)$ is defined on a bounded interval and the species with a smaller random dispersal rate is advantageous; if q_1 is large ($q_1 > \overline{q}$), the invasion curve is unbounded with a slant asymptote $q = \theta d$ for some $\theta > 0$ and larger random dispersal rate is favored. The results for the small drift rate case align with the ones in the seminal works [15,19], which claim that the species with a smaller random dispersal rate will always out-compete the
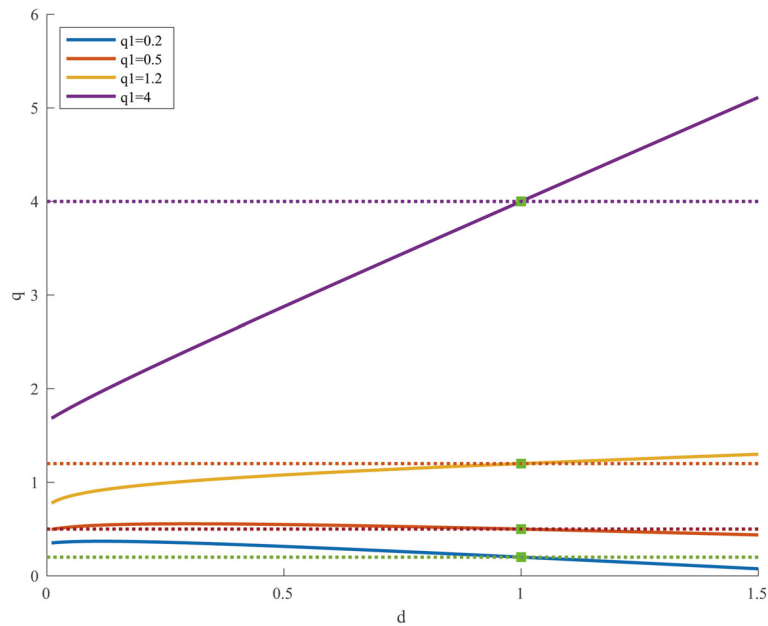
FIG. 7. The invasion curve for different values of q_1. Here, $\boldsymbol{k} = (5, 3, 1)$, $\boldsymbol{r} = (1, 2, 1)$, and $d_1 = 1$. The threshold values for the drift rates are $\underline{q} = 0.4$ and $\overline{q} = 2$

other one in a spatial heterogeneous environment, when both species randomly move in space and are different only by the movement rate. When the drift rate becomes large, the outcomes of the competition change dramatically, and the species with a larger dispersal rate may win the competition.

We numerically explore the impact of the drift rate q_1 on the shape of the invasion curve $q = q_{\boldsymbol{u}}^*(d)$. Fix $\boldsymbol{k} = (5, 3, 1)$, $\boldsymbol{r} = (1, 2, 1)$, and $d_1 = 1$. Then, we can compute the threshold values for the drift rates: $\underline{q} = 0.4$ and $\overline{q} = 2$. In Fig. 7, we plot the invasion curves for $q_1 = 0.2, 0.5, 1.2, 4$. If $q_1 = 0.2$ or 0.5, the invasion curves seem to be bounded with $\partial_d q_{\boldsymbol{u}}^*(d_1) < 0$, which indicates that a smaller random dispersal rate is favored when $q_1 = q_2$ and $d_1 \approx d_2$. In sharp contrast, if $d_1 = 1.2$ or 4, the invasion curves seem to be unbounded with $\partial_d q_{\boldsymbol{u}}^*(d_1) > 0$. This simulation also shows that the invasion curve can be bounded or unbounded for the intermediate drift case ($\underline{q} < q_1 < \overline{q}$).

4.3. Bistability and coexistence phenomena

Let $d_1 = 1, q_1 = 1.5$, $\boldsymbol{r} = (3, 7, 3)$, and $\boldsymbol{k} = (5, 3, 1)$. We graph the invasion curve $(d^*(\theta), q^*(\theta))$ and $\tilde{\lambda}(\theta)$ in Fig. 8. The stability of $(\boldsymbol{0}, \boldsymbol{v}^*)$ when $(d_2, q_2) = (d^*(\theta), q^*(\theta))$ is determined by the sign of $\tilde{\lambda}(\theta)$. In Fig. 8, we can see that $\tilde{\lambda}(\theta)$ changes sign, which means that both bistability and coexistence are possible. Indeed, if we choose $(d_2, q_2) = (3.088, 1.239)$, which is slightly below the invasion curve, then both $(\boldsymbol{u}^*, \boldsymbol{0})$ and $(\boldsymbol{0}, \boldsymbol{v}^*)$ are locally asymptotically stable. As shown in Fig. 9, if the initial data are $(\boldsymbol{u}(0), \boldsymbol{v}(0)) = ((0.1, 0.1, 0.1), (5, 5, 5))$, then the solution of (1.4) converges to $(\boldsymbol{0}, \boldsymbol{v}^*)$; if the initial data are $(\boldsymbol{u}(0), \boldsymbol{v}(0)) = ((5, 5, 5), (0.1, 0.1, 0.1))$, then the solution converges to $(\boldsymbol{u}^*, \boldsymbol{0})$. Finally, we choose $(d_2, q_2) = (10.28, 0.03)$, which is slightly above the invasion curve ($(\boldsymbol{u}^*, \boldsymbol{0})$ is unstable). Since $\tilde{\lambda}$ is positive, $(\boldsymbol{0}, \boldsymbol{v}^*)$ is also unstable, and the model has at least one stable positive equilibrium. We graph the solution of (1.4) for initial data $(\boldsymbol{u}(0), \boldsymbol{v}(0)) = ((5, 5, 5), (5, 5, 5))$ and the solution seems to converge to a positive equilibrium, see Fig. 10.
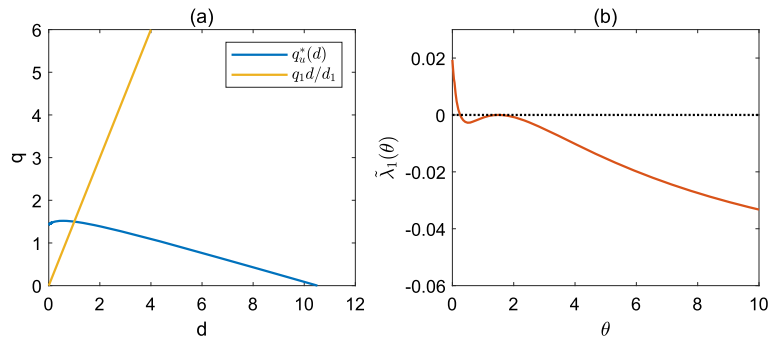
FIG. 8. **a** The invasion curve $(d^*(\theta), q^*(\theta))$ when $d_1 = 1$, $q_1 = 1.5$, $\boldsymbol{r} = (3, 7, 3)$, and $\boldsymbol{k} = (5, 3, 1)$. **b** The sign of the curve $\tilde{\lambda}_1(\theta)$ determines the stability of $(\boldsymbol{0}, \boldsymbol{v}^*)$ when $(d_2, q_2) = (d^*(\theta), q^*(\theta))$
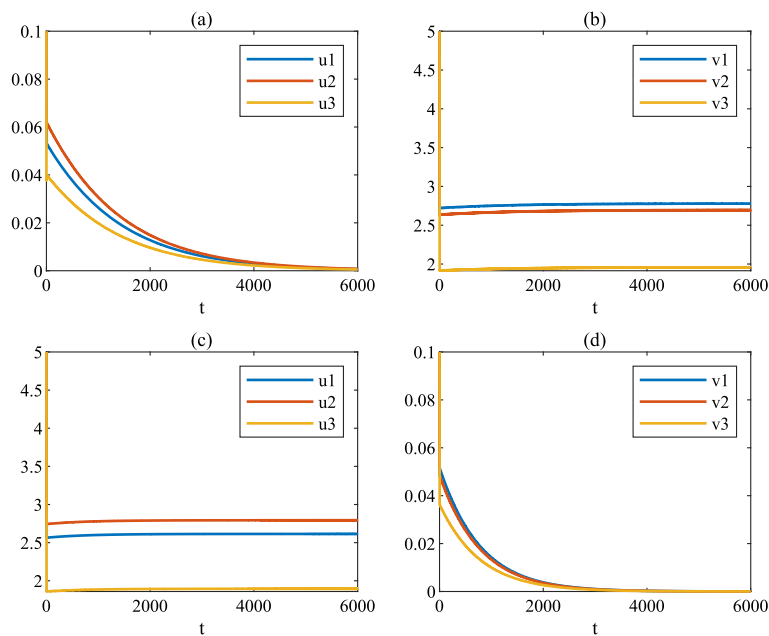

FIG. 9. Solutions of (1.4) with $d_1 = 1$, $q_1 = 1.5$, $d_2 = 3.088$, $q_2 = 1.239$, $\boldsymbol{r} = (3, 7, 3)$, $\boldsymbol{k} = (5, 3, 1)$. For **a**, **b**, the initial data are $\boldsymbol{u}(0) = (0.1, 0.1, 0.1)$ and $\boldsymbol{v}(0) = (5, 5, 5)$, and species $\boldsymbol{v}$ wins the competition; for **c**, **d**, the initial data are $\boldsymbol{u}(0) = (5, 5, 5)$ and $\boldsymbol{v}(0) = (0.1, 0.1, 0.1)$, and species $\boldsymbol{u}$ wins the competition

4.4. Evolutionarily singular strategies

We formulate a conjecture based on Corollary 3.13 about the existence of an evolutionarily stable strategy (ESS) for the diffusion rate, which may distinguish the 2-patch model from the 3-patch model.

We fix $q_2 = q_1 > 0$ and view the diffusion rate as an evolutionary strategy of the species. By Corollary 3.13 when $\underline{q} < \overline{q}$, we conjecture that there exists $\underline{q} \leq q_* < q^* \leq \overline{q}$ such that if $q < \underline{q}$, then the slower diffuser always wins the competition; if $q > q_*$, then the faster diffuser prevails; if $q_1 \in (q_*, q^*)$, there exists a unique $d^*(q_1) > 0$ such that $d_1 = d^*(q_1)$ is an evolutionarily singular strategy with the asymptotic
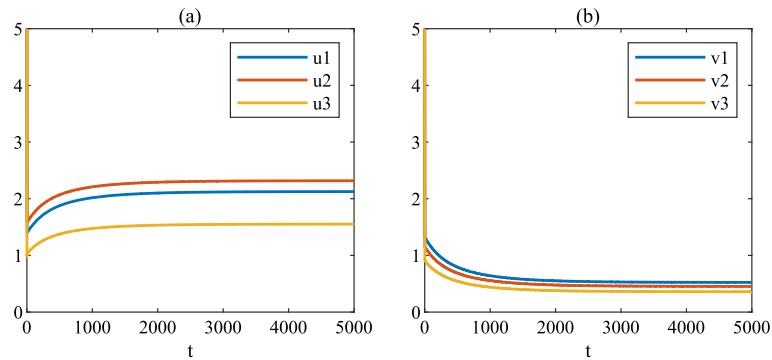
FIG. 10. Solution of (1.4) with $d_1 = 1$, $q_1 = 1.5$, $d_2 = 10.28$, $q_2 = 0.03$, $\boldsymbol{r} = (3, 7, 3)$, $\boldsymbol{k} = (5, 3, 1)$, and the initial data are $\boldsymbol{u}(0) = (5, 5, 5)$ and $\boldsymbol{v}(0) = (5, 5, 5)$. The two species seem to coexist

limits:

$$\lim_{q_1 \to q_*^+} d^*(q_1) = 0, \quad \lim_{q_1 \to q^{*-}} d^*(q_1) = +\infty;$$

or

$$\lim_{q_1 \to q_*^+} d^*(q_1) = +\infty, \quad \lim_{q_1 \to q^{*-}} d^*(q_1) = 0.$$

Moreover, we conjecture that the singular strategy is an ESS in the former case but not in the latter case (Fig. 11).

We provide some numerical evidence to support the conjecture below. Since

$$\lambda_1 (d_1, q_1, \boldsymbol{1} - \boldsymbol{u}^*/\boldsymbol{k}) = 0,$$

the sign of

$$\mathcal{S}(d_1, q_1) := \left. \frac{\partial \lambda_1 (d, q_1, \boldsymbol{1} - \boldsymbol{u}^*/\boldsymbol{k})}{\partial d} \right|_{d=d_1}$$

is crucial to determine which strategy is favored when $d_2 \approx d_1$: if $\mathcal{S}(d_1, q_1) < 0$ the slow diffuser is favored; if $\mathcal{S}(d_1, q_1) > 0$ the faster diffuser is favored. By Corollary 3.13, $\mathcal{S}(d_1, q_1)$ changes signs. In particular, if $q_1 < \underline{q}$, $\mathcal{S}(d_1, q_1) < 0$ and if $q_1 > \underline{q}$, $\mathcal{S}(d_1, q_1) > 0$. We numerically solve $\mathcal{S}(d_1, q_1) = 0$ and plot the solution in Fig. 11, which consists with a curve $d_1 = d^*(q_1)$, where $q_1 \in (q_*, q^*)$. In the left figure, the sign of $\mathcal{S}(d_1, q_1)$ changes from negative to positive when moving from above to below the curve. This suggests that the diffusion rate $d_1 = d^*$ may be an ESS for $q \in (q_*, q^*)$. In the right figure, opposite phenomenon appears when crossing the curve and we suspect that the singular strategy is not an ESS in this case.

We remark such an intermediate diffusion rate $d_1 = d^*$ as an ESS does not appear in the corresponding 2-patch model. For the 2-patch model, as proved in [18,45] (see [23, Theorem 1]), there exists a critical value q_* such that if $q_1 = q_2 < q_*$ then $d_1 = 0$ is an ESS; if $q_1 = q_2 > q_*$ then $d_1 = \infty$ is an ESS. We also note that if $\underline{q} = \overline{q}$ in the 3-patch model, then the curve $d_1 = d^*(q_1)$ is a vertical line and an intermediate ESS also does not exists (which is similar to the 2-patch case).

Finally, we conjecture that the results in this paper hold for the N-patch model. Our results for 3-patch model are based on the monotonicity of the semitrivial equilibrium (see Lemma 5.1 (iii)–(iv)), which we cannot prove for the N-patch model. Similarly, if the movement rates among patches are not homogeneous (i.e., the off-diagonal entries of D and Q are not 1s), it is also not trivial to show how the movement rates affect the monotonicity of the semitrivial equilibrium.
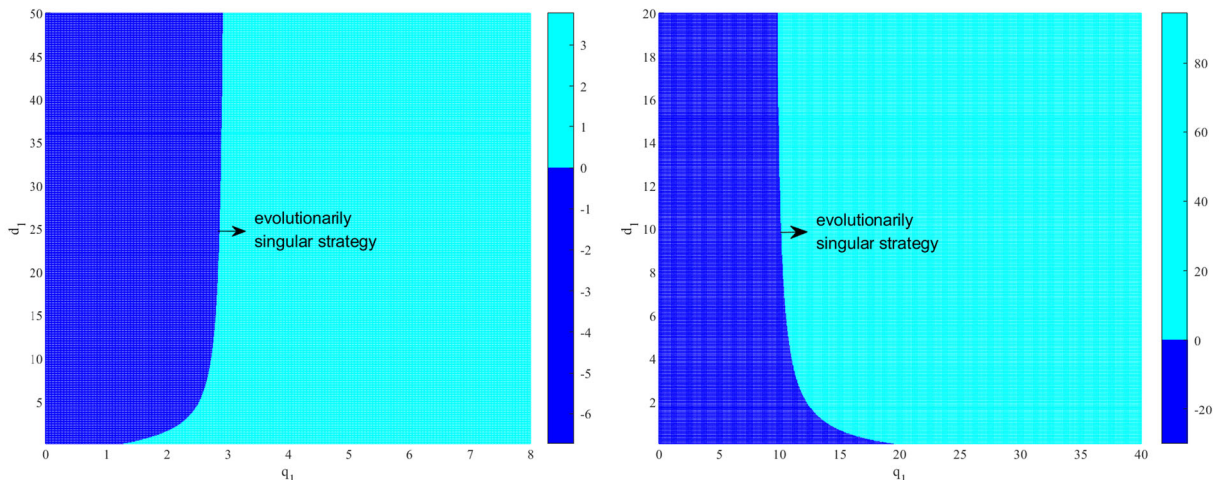
FIG. 11. The sign of $\mathcal{S}(d_1, q_1)$, where $\mathcal{S}(d_1, q_1) < 0$ in the dark blue region and $\mathcal{S}(d_1, q_1) > 0$ in the light blue region. Left figure: $\boldsymbol{r} = (3, 7, 3)$, $\boldsymbol{k} = (5, 3, 1)$; right F $\boldsymbol{r} = (50, 3, 3)$, $\boldsymbol{k} = (5, 3, 1)$

5. Proofs for the invasion curve

In this section, we present the proofs of the results on the invasion curve $q_{\boldsymbol{u}}^*(d)$. We begin with an analysis on $\boldsymbol{u}^*$. A similar result of the following lemma when $r_1 = r_2 = r_3$ except for the sign of $\sum_{i=1}^3 r_i \left(1 - u_i^*/k_i\right)$ can be found in [23].

Lemma 5.1. *Suppose that* (**H**) *holds,* $\boldsymbol{r} \gg \boldsymbol{0}$, $d_1 > 0$, *and* $q_1 \geq 0$. *Then, the following statements on* $\boldsymbol{u}^*$ *hold:*

(i) $d_1 u_{i+1}^* - (d_1 + q_1)u_i^* < 0$ *for* $i = 1, 2$;

(ii) $u_1^* < k_1$ *and* $u_3^* > k_3$;

(iii) *If* $q_1 > \bar{q}$, *then* $u_1^* < u_2^* < u_3^*$ *and* $\sum_{i=1}^3 r_i \left(1 - \frac{u_i^*}{k_i}\right) > 0$;

(iv) *If* $q_1 < \underline{q}$, *then* $u_1^* > u_2^* > u_3^*$ *and* $\sum_{i=1}^3 r_i \left(1 - \frac{u_i^*}{k_i}\right) < 0$.

Proof. By (1.4), we have

$$\begin{cases} d_1 u_2^* - (d_1 + q_1)u_1^* = -r_1 u_1^* \left(1 - \dfrac{u_1^*}{k_1}\right), \\ (d_1 u_3^* - (d_1 + q_1)u_2^*) - (d_1 u_2^* - (d_1 + q_1)u_1^*) = -r_2 u_2^* \left(1 - \dfrac{u_2^*}{k_2}\right), \\ d_1 u_3^* - (d_1 + q_1)u_2^* = r_3 u_3^* \left(1 - \dfrac{u_3^*}{k_3}\right). \end{cases} \tag{5.1}$$

Suppose to the contrary that $d_1 u_2^* - (d_1 + q_1)u_1^* \geq 0$. Then, by the first equation of (5.1), we have $u_2^* \geq u_1^* \geq k_1$. This, together with assumption (**H**) and the second equation of (5.1), implies that $d_1 u_3^* - (d_1 + q_1)u_2^* > 0$ and $u_3^* > k_3$, which contradicts the third equation of (5.1). Therefore, we have $d_1 u_2^* - (d_1 + q_1)u_1^* < 0$. Similarly, we can prove $d_1 u_3^* - (d_1 + q_1)u_2^* < 0$. This proves (i). By (i) and the first and third equations of (5.1), we can easily obtain (ii).

The proof of (iv) is similar to that of (iii), so we only prove (iii) here. Suppose $q_1 > \bar{q}$. We rewrite (5.1) as follows:

$$\begin{cases} d_1(u_2^* - u_1^*) = -r_1 u_1^* \left(1 - \dfrac{q_1}{r_1} - \dfrac{u_1^*}{k_1} \right), \\ d_1(u_3^* - u_2^*) - (d_1 + q_1)(u_2^* - u_1^*) = -r_2 u_2^* \left(1 - \dfrac{u_2^*}{k_2} \right), \\ -(d_1 + q_1)(u_3^* - u_2^*) = -r_3 u_3^* \left(1 + \dfrac{q_1}{r_3} - \dfrac{u_3^*}{k_3} \right). \end{cases} \tag{5.2}$$

Suppose to the contrary that $u_1^* \geq u_2^*$. Then, by the first equation of (5.2), we have $k_1 - \dfrac{q_1 k_1}{r_1} - u_1^* \geq 0$. Since $q_1 > \dfrac{r_1}{k_1}(k_1 - k_2)$, we obtain

$$k_2 > k_1 - \dfrac{q_1 k_1}{r_1} \geq u_1^* \geq u_2^*.$$

Then, by the second equation of (5.2), we get $u_2^* > u_3^*$. This, combined with $q_1 > \dfrac{r_3}{k_3}(k_2 - k_3)$, yields

$$k_3 \left(1 + \dfrac{q_1}{r_3} \right) > k_2 > u_2^* > u_3^*,$$

which contradicts the last equation of (5.2). This proves $u_1^* < u_2^*$.

Suppose to the contrary that $u_2^* \geq u_3^*$. Then, by the last equation of (5.2), we have $u_3^* \geq k_3 \left(1 + \dfrac{q_1}{r_3} \right)$. By $q_1 > \bar{q}$, we obtain

$$u_2^* \geq u_3^* \geq k_3 \left(1 + \dfrac{q_1}{r_3} \right) > k_2 > k_1 - \dfrac{q_1 k_1}{r_1}.$$

Then, by the second equation of (5.2), we have $u_1^* > u_2^*$. By the first equation of (5.2), we get

$$0 > d_1(u_2^* - u_1^*) = -r_1 u_1^* \left(1 - \dfrac{q_1}{r_1} - \dfrac{u_1^*}{k_1} \right) > 0,$$

which is a contradiction. This proves $u_2^* < u_3^*$.

Dividing the ith equation of (5.2) by u_i^*, we have

$$\begin{cases} -(d_1 + q_1) + d_1 \dfrac{u_2^*}{u_1^*} + r_1 \left(1 - \dfrac{u_1^*}{k_1} \right) = 0, \\ (d_1 + q_1) \left(\dfrac{u_1^*}{u_2^*} - 1 \right) - d_1 \left(1 - \dfrac{u_3^*}{u_2^*} \right) + r_2 \left(1 - \dfrac{u_2^*}{k_2} \right) = 0, \\ (d_1 + q_1) \dfrac{u_2^*}{u_3^*} - d_1 + r_3 \left(1 - \dfrac{u_3^*}{k_3} \right) = 0. \end{cases} \tag{5.3}$$

Adding up the equations in (5.3), we obtain

$$\sum_{i=2}^{3} \left((d_1 + q_1) \left(\dfrac{u_{i-1}^*}{u_i^*} - 1 \right) + d_1 \left(\dfrac{u_i^*}{u_{i-1}^*} - 1 \right) \right) + \sum_{i=1}^{3} r_i \left(1 - \dfrac{u_i^*}{k_i} \right)$$

$$= \sum_{i=2}^{3} \dfrac{(u_{i-1}^* - u_i^*)((d_1 + q_1)u_{i-1}^* - d_1 u_i^*)}{u_{i-1}^* u_i^*} + \sum_{i=1}^{3} r_i \left(1 - \dfrac{u_i^*}{k_i} \right) = 0. \tag{5.4}$$

Then, by (i) and $u_1^* < u_2^* < u_3^*$, we have $\sum_{i=1}^{3} r_i \left(1 - \dfrac{u_i^*}{k_i} \right) > 0$. This proves (iii). $\qquad \square$

5.1. Proof of Theorem 3.1

We prove the existence of the invasion curve $q = q_{\boldsymbol{u}}^*(d)$ in this subsection.

Lemma 5.2. *Suppose that* (**H**) *holds*, $\boldsymbol{r} \gg \boldsymbol{0}$, *and* $d_1, q_1 > 0$. *Then, the following statements hold about the semitrivial equilibrium* $(\boldsymbol{u}^*, \boldsymbol{0})$ *of* (1.4):

(i) *If* $\sum_{i=1}^3 r_i \left(1 - u_i^*/k_i\right) \geq 0$, *then for any* $d > 0$ *there exists* $q_{\boldsymbol{u}}^*(d) > 0$ *such that* $\lambda_1 \left(d, q_{\boldsymbol{u}}^*(d), \boldsymbol{1} - \boldsymbol{u}^*/\boldsymbol{k}\right) = 0$, $\lambda_1 \left(d, q, \boldsymbol{1} - \boldsymbol{u}^*/\boldsymbol{k}\right) < 0$ *for all* $q > q_{\boldsymbol{u}}^*(d)$, *and* $\lambda_1 \left(d, q, \boldsymbol{1} - \boldsymbol{u}^*/\boldsymbol{k}\right) > 0$ *for all* $q < q_{\boldsymbol{u}}^*(d)$;

(ii) *If* $\sum_{i=1}^3 r_i \left(1 - u_i^*/k_i\right) < 0$, *then there exists* $d_0 > 0$ *such that* $\lambda_1(d_0, 0, \boldsymbol{1} - \boldsymbol{u}^*/\boldsymbol{k}) = 0$, $\lambda_1(d, 0, \boldsymbol{1} - \boldsymbol{u}^*/\boldsymbol{k}) < 0$ *for all* $d > d_0$, *and* $\lambda_1(d, 0, \boldsymbol{1} - \boldsymbol{u}^*/\boldsymbol{k}) > 0$ *for all* $d < d_0$. *Moreover, the following results hold:*

(ii$_1$) *For any* $d \in (0, d_0)$, *there exists* $q_{\boldsymbol{u}}^*(d) > 0$ *such that the statement in* (i) *holds*;

(ii$_2$) *For any* $d \in [d_0, \infty)$, *we have* $\lambda_1(d, q, \boldsymbol{1} - \boldsymbol{u}^*/\boldsymbol{k}) < 0$ *for all* $q > 0$.

Proof. For simplicity, we denote $\lambda_1(d, q) := \lambda_1 \left(d, q, \boldsymbol{1} - \boldsymbol{u}^*/\boldsymbol{k}\right)$. An essential step of the proof is to show the following claim.

Claim 1: Fixing $d > 0$, equation $\lambda_1(d, q) = 0$ has at most one root for $q \in [0, \infty)$.

Proof of Claim: Let $\boldsymbol{\psi}$ be the positive eigenvector corresponding to $\lambda_1(d, q)$ with $\sum_{i=1}^3 \psi_i = 1$. Then, we have

$$\lambda_1(d, q)\psi_i = d \sum_{j=1}^3 D_{ij}\psi_j + q \sum_{j=1}^3 Q_{ij}\psi_j + r_i \left(1 - \frac{u_i^*}{k_i}\right)\psi_i, \quad i = 1, 2, 3. \tag{5.5}$$

Differentiating (5.5) with respect to q and denoting $' = \partial/\partial q$, we obtain

$$\lambda_1'\psi_i + \lambda_1\psi_i' = d \sum_{j=1}^3 D_{ij}\psi_j' + \sum_{j=1}^3 Q_{ij}\psi_j + q \sum_{j=1}^3 Q_{ij}\psi_j' + r_i \left(1 - \frac{u_i^*}{k_i}\right)\psi_i', \quad i = 1, 2, 3. \tag{5.6}$$

Multiplying (5.5) by ψ_i' and (5.6) by ψ_i and taking the difference of them, we have

$$\lambda_1'\psi_i^2 = \sum_{j=1}^3 (dD_{ij} + qQ_{ij})(\psi_i\psi_j' - \psi_i'\psi_j) + \sum_{j=1}^3 Q_{ij}\psi_i\psi_j, \quad i = 1, 2, 3. \tag{5.7}$$

Motivated by [7, Eq. (3.7)], we introduce $(\beta_1, \beta_2, \beta_3) = \left(1, d/(d+q), d^2/(d+q)^2\right)$. Multiplying (5.7) by β_i and summing up in i, we obtain

$$\lambda_1' \sum_{i=1}^3 \beta_i\psi_i^2 = \sum_{i=1}^2 \left(\frac{d}{d+q}\right)^{i-1} \left(-\psi_i + \frac{d}{d+q}\psi_{i+1}\right)\psi_i. \tag{5.8}$$

Suppose $\lambda_1(d, \tilde{q}) = 0$ for some $\tilde{q} \geq 0$. By Lemma 5.1 (ii), we see that

$$d\psi_2 - (d + \tilde{q})\psi_1 = -\psi_1 r_1 \left(1 - \frac{u_1^*}{k_1}\right) < 0,$$

$$d\psi_3 - (d + \tilde{q})\psi_2 = \psi_3 r_1 \left(1 - \frac{u_3^*}{k_3}\right) < 0.$$

Therefore, by (5.8), we have $\lambda'(d, \tilde{q}) < 0$. This proves the claim.

According to the claim, whether the equation $\lambda_1(d, q) = 0$ has a root in q is determined by the sign of $\lambda_1(d, 0)$ and $\lim_{q \to \infty} \lambda_1(d, q)$.

Claim 2: $\lim_{q \to \infty} \lambda_1(d, q) < 0$.

Proof of claim: Adding up all the equations of (5.5), we have

$$\lambda_1(d, q) = \sum_{i=1}^3 r_i \left(1 - \frac{u_i^*}{k_i}\right)\psi_i, \tag{5.9}$$

which implies that $\lambda_1(d, q)$ is bounded for $d, q > 0$. So up to a subsequence, we may assume $\lim_{q\to\infty} \psi = \tilde{\psi}$. Dividing (5.5) by q and taking $q \to \infty$, we obtain

$$\sum_{i=1}^{3} Q_{ij}\tilde{\psi}_j = 0, \quad i = 1, 2, 3,$$

which yields $\tilde{\psi} = (0, 0, 1)^T$. Then, taking $q \to \infty$ in (5.9), we have

$$\lim_{q\to\infty} \lambda_1(d, q) = r_3 \left(1 - \frac{u_3^*}{k_3}\right) < 0,$$

where we have used Lemma 5.1 (ii) in the last step. This proves the claim.

By Lemma 2.1, $\lambda_1(d, 0)$ is strictly decreasing in d with

$$\lim_{d\to 0} \lambda(d, 0) = \max_{1\le i\le 3} r_i \left(1 - \frac{u_i^*}{k_i}\right) > 0 \quad \text{and} \quad \lim_{d\to\infty} \lambda(d, 0) = \frac{1}{3} \sum_{i=1}^{3} r_i \left(1 - \frac{u_i^*}{k_i}\right),$$

where we have used Lemma 5.1 (ii) again to see that $1 - u_1^*/k_1 > 0$. Now, the desired results follow from this and Claims 1 and 2. $\qquad\square$

We are ready to prove Theorem 3.1.

Proof of Theorem 3.1. Let d_0 be defined in Lemma 5.2, d^* be defined by (3.2), and $q = q_{\boldsymbol{u}}^*(d) : (0, d^*) \to \mathbb{R}_+$ be defined in Lemma 5.2. Then, Theorem 3.1 (i)–(ii) follows from Lemmas 5.1–5.2 and the fact that the stability/instability of $(\boldsymbol{u}^*, \boldsymbol{0})$ is determined by the sign of $\lambda_1(d, q, \boldsymbol{1} - \boldsymbol{u}^*/\boldsymbol{k})$. The continuity of $q = q_{\boldsymbol{u}}^*(d)$ follows from $\partial_q \lambda_1(d, q_{\boldsymbol{u}}^*(d), \boldsymbol{1} - \boldsymbol{u}^*/\boldsymbol{k}) < 0$ (Claim 1 of Lemma 5.2) and the implicit function theorem. $\qquad\square$

5.2. Proof of Propositions 3.3 and 3.4

First, we prove the following useful result:

Lemma 5.3. *Suppose that* (**H**) *holds,* $\boldsymbol{r} \gg \boldsymbol{0}$, *and* $d_1, q_1 > 0$. *Then, we have*

$$\lambda_1 \left(d_2, q_2, \boldsymbol{1} - \frac{\boldsymbol{u}^*}{\boldsymbol{k}}\right) \neq 0,$$

if one of the following conditions holds:

(i) $(d_2, q_2) \in G_{11} \cup G_{21}$;
(ii) $q_1 > \bar{q}$ *and* $(d_2, q_2) \in G_{12} \cup G_{22}$;
(iii) $q_1 < \underline{q}$ *and* $(d_2, q_2) \in G_{13} \cup G_{23}$.

Proof. Suppose to the contrary that $\lambda_1(d_2, q_2, \boldsymbol{1} - \boldsymbol{u}^*/\boldsymbol{k}) = 0$, and let $\phi \gg 0$ be a corresponding eigenvector. Note that $\lambda_1(d_1, q_1, \boldsymbol{1} - \boldsymbol{u}^*/\boldsymbol{k}) = 0$ with a corresponding eigenvector $\boldsymbol{u}^*$. Let

$$\tilde{f}_0 = \tilde{f}_3 = 0, \quad \tilde{g}_0 = \tilde{g}_3 = 0,$$

and

$$\tilde{f}_j = d_1 u_{j+1}^* - (d_1 + q_1)u_j^*, \quad \tilde{g}_j = d_2\phi_{j+1} - (d_2 + q_2)\phi_j, \quad j = 1, 2. \tag{5.10}$$

Then, we have

$$\tilde{f}_j - \tilde{f}_{j-1} = -r_j u_j^* \left(1 - \frac{u_j^*}{k_j}\right), \quad j = 1, 2, 3, \tag{5.11a}$$

$$\tilde{g}_j - \tilde{g}_{j-1} = -r_j \phi_j \left(1 - \frac{u_j^*}{k_j}\right), \quad j = 1, 2, 3. \tag{5.11b}$$

Using similar arguments as in [7, Lemma 5.7], we can show

$$\sum_{j=1}^{2} \left[(d_1 - d_2)(\phi_{j+1} - \phi_j) - (q_1 - q_2)\phi_j \right] \tilde{f}_j \frac{d_1^j}{(d_1 + q_1)^{j+1}} = 0, \tag{5.12}$$

and

$$\sum_{k=1}^{2} \left[(d_2 - d_1)(u_{j+1}^* - u_j^*) - (q_2 - q_1)u_j^* \right] \tilde{g}_j \frac{d_2^j}{(d_2 + q_2)^{j+1}} = 0. \tag{5.13}$$

Indeed, multiplying (5.11a) by $\left(\frac{d_1}{d_1 + q_1} \right)^j \phi_j$, and summing up from $j = 1$ to $j = 3$, we have

$$-\sum_{j=1}^{3} r_j u_j^* \phi_j \left(1 - \frac{u_j^*}{k_j} \right) \left(\frac{d_1}{d_1 + q_1} \right)^j$$

$$= \sum_{j=1}^{3} \left(\tilde{f}_j - \tilde{f}_{j-1} \right) \phi_j \left(\frac{d_1}{d_1 + q_1} \right)^j$$

$$= \tilde{f}_3 \phi_3 \left(\frac{d_1}{d_1 + q_1} \right)^3 - \tilde{f}_0 \phi_1 \left(\frac{d_1}{d_1 + q_1} \right) + \sum_{j=1}^{2} \tilde{f}_j \left(\frac{d_1}{d_1 + q_1} \right)^j \left(\phi_j - \frac{d_1}{d_1 + q_1} \phi_{j+1} \right) \tag{5.14}$$

$$= -\sum_{j=1}^{2} (d_1 \phi_{j+1} - (d_1 + q_1)\phi_j) \tilde{f}_j \frac{d_1^j}{(d_1 + q_1)^{j+1}},$$

where we have used $\tilde{f}_3 = \tilde{f}_0 = 0$ in the last step. Similarly, multiplying (5.11b) by $\left(\frac{d_1}{d_1 + q_1} \right)^j u_j^*$ and summing up from $j = 1$ to $j = 3$, we obtain

$$-\sum_{j=1}^{3} r_j u_j^* \phi_j \left(1 - \frac{u_j^*}{k_j} \right) \left(\frac{d_1}{d_1 + q_1} \right)^j = -\sum_{j=1}^{2} \tilde{g}_j \tilde{f}_j \frac{d_1^j}{(d_1 + q_1)^{j+1}}. \tag{5.15}$$

Taking the difference of (5.14) and (5.15), we obtain (5.12). Similarly, we can prove (5.13).

By Lemma 5.1 (i)–(ii) and (5.11b), we have $\tilde{f}_j, \tilde{g}_j < 0$ for $j = 1, 2$. Now we obtain a contradiction for each of (i)–(iii).

(i) We only consider the case $(d_2, q_2) \in G_{21}$, since the case $(d_2, q_2) \in G_{11}$ can be studied similarly. Suppose $(d_2, q_2) \in G_{21}$. Then, we have $d_2 \leq d_1, q_2 \leq q_1 d_2 / d_1$, and $(d_1, q_1) \neq (d_2, q_2)$. If $d_1 \neq d_2$, then it is easy to check that

$$\frac{q_1 - q_2}{d_1 - d_2} \geq \frac{q_2}{d_2}.$$

(This inequality can be found in [53, Lemma 2.4].) This, together with $\tilde{g}_1, \tilde{g}_2 < 0$, yields

$$(d_1 - d_2)(\phi_{j+1} - \phi_j) - (q_1 - q_2)\phi_j < 0, \quad j = 1, 2. \tag{5.16}$$

If $d_1 = d_2$, then $q_1 > q_2$ and (5.16) also holds. Then, by $\tilde{f}_1, \tilde{f}_2 < 0$ and (5.12), we have

$$0 < \sum_{j=1}^{2} \left[(d_1 - d_2)(\phi_{j+1} - \phi_j) - (q_1 - q_2)\phi_j \right] \tilde{f}_j \frac{d_1^j}{(d_1 + q_1)^{j+1}} = 0,$$

which is a contradiction.

(ii) We only need to obtain a contradiction for the case $(d_2, q_2) \in G_{22}$, since the case $(d_2, q_2) \in G_{12}$ can be studied similarly. Suppose $(d_2, q_2) \in G_{22}$. Then, we have $d_2 > d_1$ and $q_2 \leq q_1$. By Lemma 5.1 (i), we have $u_1^* < u_2^* < u_3^*$, which implies that

$$(d_2 - d_1)(u_{j+1}^* - u_j^*) - (q_2 - q_1)u_j^* > 0, \quad j = 1, 2.$$

This, combined with $\tilde{g}_1, \tilde{g}_2 < 0$ and (5.13), gives a contradiction.

(iii) We only obtain a contradiction for the case $(d_2, q_2) \in G_{23}$, since the case $(d_2, q_2) \in G_{13}$ can be studied similarly. Suppose $(d_2, q_2) \in G_{23}$. Then, we have $d_2 \leq d_1$, $q_2 \leq q_1$, and $(d_1, q_1) \neq (d_2, q_2)$. By Lemma 5.1 (ii), we have $u_1^* > u_2^* > u_3^*$, which implies that

$$(d_2 - d_1)(u_{j+1}^* - u_j^*) - (q_2 - q_1)u_j^* > 0, \quad j = 1, 2.$$

This combined with $\tilde{g}_1, \tilde{g}_2 < 0$ and (5.13) gives a contradiction. $\qquad\square$

We are ready to prove Propositions 3.3 and 3.4.

Proof of Proposition 3.3. (i) We only prove the case $G_{21} \subset S_2$, (i.e., $(\boldsymbol{u}^*, \boldsymbol{0})$ is unstable for $(d_2, q_2) \in G_{21}$), since the case $G_{11} \subset S_1$ can be proved similarly. To avoid confusion, we denote $\boldsymbol{u}^*$ by $\boldsymbol{u}_{\boldsymbol{k}}^*$. It is easy to see that $\boldsymbol{u}_{\boldsymbol{k}}^*$ depends continuously on $\boldsymbol{k}$.

Suppose $(d_2, q_2) \in G_{21}$. We need to prove that $\lambda_1(d_2, q_2, \boldsymbol{1} - \boldsymbol{u}_{\boldsymbol{k}}^*/\boldsymbol{k}) > 0$. Suppose to the contrary that $\lambda_1(d_2, q_2, \boldsymbol{1} - \boldsymbol{u}_{\boldsymbol{k}}^*/\boldsymbol{k}) \leq 0$. By Lemma 5.3, we must have $\lambda_1(d_2, q_2, \boldsymbol{1} - \boldsymbol{u}_{\boldsymbol{k}}^*/\boldsymbol{k}) < 0$. By [7, Theorem 4.2], we have $\lambda_1(d_2, q_2, \boldsymbol{1} - \boldsymbol{u}_{\boldsymbol{k}'}^*/\boldsymbol{k}') > 0$, where $\boldsymbol{k}' = (k_3, k_3, k_3)$.

Let $\Lambda(s) := \lambda_1\left(d_2, q_2, \boldsymbol{1} - \boldsymbol{u}_{\boldsymbol{k}_1(s)}^*/\boldsymbol{k}_1(s)\right)$, where $\boldsymbol{k}_1(s) = s\boldsymbol{k} + (1-s)\boldsymbol{k}'$ satisfies (**H**) for any $s \in [0, 1]$. Since

$$\Lambda(1) = \lambda_1\left(d_2, q_2, \boldsymbol{1} - \frac{\boldsymbol{u}_{\boldsymbol{k}}^*}{\boldsymbol{k}}\right) < 0 \quad \text{and} \quad \Lambda(0) = \lambda_1\left(d_2, q_2, \boldsymbol{1} - \frac{\boldsymbol{u}_{\boldsymbol{k}'}^*}{\boldsymbol{k}'}\right) > 0,$$

there exists $s_0 \in (0, 1)$ such that $\Lambda(s_0) = 0$, which contradicts Lemma 5.3.

(ii) By [7, Theorem 4.2], if $(d_2, q_2) \in G_{22}$, then $\lambda_1\left(d_2, q_2, \boldsymbol{1} - \boldsymbol{u}_{\boldsymbol{k}'}^*/\boldsymbol{k}'\right) > 0$; and if $(d_2, q_2) \in G_{12}$, then $\lambda_1\left(d_2, q_2, \boldsymbol{1} - \boldsymbol{u}_{\boldsymbol{k}'}^*/\boldsymbol{k}'\right) < 0$, where $\boldsymbol{k}' = (k_3, k_3, k_3)$. Then, using similar arguments as (i), we can prove (ii).

(iii) Let $\boldsymbol{\psi}$ be the positive eigenvector corresponding to $\lambda_1 := \lambda_1(d_2, q_1, \boldsymbol{1} - \boldsymbol{u}^*/\boldsymbol{k})$ with $\sum_{i=1}^3 \psi_i = 1$. Then, we have

$$\lambda_1 \psi_i = d_2 \sum_{j=1}^3 D_{ij} \psi_j + q_1 \sum_{j=1}^3 Q_{ij} \psi_j + r_i \left(1 - \frac{u_i^*}{k_i}\right) \psi_i, \quad i = 1, 2, 3. \tag{5.17}$$

Differentiating (5.5) with respect to d_2 and denoting $' = \partial/\partial d_2$, we obtain

$$\lambda_1' \psi_i + \lambda_1 \psi_i' = d_2 \sum_{j=1}^3 D_{ij} \psi_j' + \sum_{j=1}^3 D_{ij} \psi_j + q_1 \sum_{j=1}^3 Q_{ij} \psi_j' + r_i \left(1 - \frac{u_i^*}{k_i}\right) \psi_i', \quad i = 1, 2, 3. \tag{5.18}$$

Multiplying (5.17) by ψ_i' and (5.18) by ψ_i and taking the difference of them, we have

$$\lambda_1' \psi_i^2 = \sum_{j=1}^3 (d_2 D_{ij} + q_1 Q_{ij})(\psi_i \psi_j' - \psi_i' \psi_j) + \sum_{j=1}^3 D_{ij} \psi_i \psi_j, \quad i = 1, 2, 3. \tag{5.19}$$

Similar to the proof of Lemma 5.2, let $(\beta_1, \beta_2, \beta_3) = \left(1, d_2/(d_2 + q_1), d_2^2/(d_2 + q_1)^2\right)$. Multiplying (5.19) by β_i and adding up them in i, we obtain

$$\lambda_1' \sum_{i=1}^3 \beta_i \psi_i^2 = \sum_{i=1}^2 \left(\frac{d_2}{d_2 + q_1}\right)^{i-1} \left(-\psi_i + \frac{d_2}{d_2 + q_1} \psi_{i+1}\right)(\psi_i - \psi_{i+1}). \tag{5.20}$$

Note that $\lambda_1 (d_1, q_1, \mathbf{1} - \mathbf{u}^*/\mathbf{k}) = 0$ with a corresponding eigenvector $(u_1^*, u_2^*, u_3^*)^T$. Moreover, by Lemma 5.1, we have $d_1 u_{i+1}^* - (d_1 + q_1) u_i^* < 0$ for $i = 1, 2$ and $u_1^* > u_2^* > u_3^*$. Then, it follows from (5.20) that

$$\left. \frac{\partial \lambda_1 (d_2, q_1, \mathbf{1} - \mathbf{u}^*/\mathbf{k})}{\partial d_2} \right|_{d_2 = d_1} < 0. \tag{5.21}$$

This implies that $\lambda_1 (d_2, q_1, \mathbf{1} - \mathbf{u}^*/\mathbf{k}) > 0$ if $0 < d_1 - d_2 \ll 1$ and $\lambda_1 \left(d_2, q_1, \mathbf{1} - \frac{\mathbf{u}^*}{\mathbf{k}} \right) < 0$ if $0 < d_2 - d_1 \ll 1$. Then, by Lemma 5.3, we have $G_{13} \subset S_1$ and $G_{23} \subset S_2$. $\qquad\square$

Remark 5.4. A similar inequality of (5.21) is proved in [23], and we include the proof for completeness here.

Proof of Proposition 3.4. For any $0 < d < d^*$, let $\boldsymbol{\psi}$ be the eigenvector corresponding to $\lambda_1 (d, q_{\mathbf{u}}^*(d), \mathbf{1} - \mathbf{u}^*/\mathbf{k}) = 0$ with $\boldsymbol{\psi} \gg 0$ and $\sum_{i=1}^3 \psi_i = 1$. Then,

$$d \sum_{j=1}^3 D_{ij} \psi_j + q_{\mathbf{u}}^*(d) \sum_{j=1}^3 Q_{ij} \psi_j + r_i \left(1 - \frac{u_i^*}{k_i} \right) \psi_i = 0, \quad i = 1, 2, 3. \tag{5.22}$$

(i) Up to a subsequence, we may assume $\lim_{d \to 0} \boldsymbol{\psi} = \tilde{\boldsymbol{\psi}}$ for some $\tilde{\boldsymbol{\psi}} \geq \mathbf{0}$ and $\sum_{i=1}^3 \tilde{\psi}_i = 1$. We first claim that $q_{\mathbf{u}}^*(d)$ is bounded for $d \in (0, \delta)$ with $\delta \ll 1$. If it is not true, then dividing (5.22) by $q_{\mathbf{u}}^*(d)$ and taking $d \to 0$, we have

$$\sum_{j=1}^3 Q_{ij} \tilde{\psi}_j = 0, \quad i = 1, 2, 3, \tag{5.23}$$

which yields $\tilde{\boldsymbol{\psi}} = (0, 0, 1)^T$. Adding up all the equations of (5.22) and taking $d \to 0$ in (5.24), we have

$$\sum_{i=1}^3 r_i \left(1 - \frac{u_i^*}{k_i} \right) \tilde{\psi}_i = 0, \tag{5.24}$$

and consequently, $k_3 - u_3^* = 0$, which contradicts Lemma 5.1 (ii). This proves the claim. By the claim, up to a subsequence, we may assume $\lim_{d \to 0} q^*(\theta) = \tilde{q}_0 \in [0, \infty)$. Consequently, for sufficiently small $\epsilon > 0$, there exists $\bar{d} > 0$ such that $q_{\mathbf{u}}^*(d) < \tilde{q}_0 + \epsilon$ for all $0 < d < \bar{d}$. It follows from Lemma 5.2 that

$$\lambda_1 \left(d, \tilde{q}_0 + \epsilon, \mathbf{1} - \frac{\mathbf{u}^*}{\mathbf{k}} \right) < 0 \tag{5.25}$$

for all $0 < d < \bar{d}$. Hence,

$$\lim_{d \to 0} \lambda_1 \left(d, \tilde{q}_0 + \epsilon, \mathbf{1} - \frac{\mathbf{u}^*}{\mathbf{k}} \right)$$
$$= \max \left\{ r_1 \left(1 - \frac{u_1^*}{k_1} \right) - (\tilde{q}_0 + \epsilon), r_2 \left(1 - \frac{u_2^*}{k_2} \right) - (\tilde{q}_0 + \epsilon), r_3 \left(1 - \frac{u_3^*}{k_3} \right) \right\} \leq 0.$$

Since $k_3 - u_3^* = 0$ and $\epsilon > 0$ was arbitrary,

$$\max \left\{ r_1 \left(1 - \frac{u_1^*}{k_1} \right) - \tilde{q}_0, r_2 \left(1 - \frac{u_2^*}{k_2} \right) - \tilde{q}_0 \right\} \leq 0. \tag{5.26}$$

Therefore, we have $\tilde{q}_0 \geq q_0 > 0$. Similarly, we can prove $\tilde{q}_0 \leq q_0$. This proves (i).

Now we prove (ii)–(iv). If we show that (3.7) holds when $\sum_{i=1}^3 r_i (1 - u_i^*/k_i) < 0$, (3.8) holds with $\theta \in (0, q_1/d_1)$ when $\sum_{i=1}^3 r_i (1 - u_i^*/k_i) > 0$, and (3.8) holds with $\theta = 0$ when $\sum_{i=1}^3 r_i (1 - u_i^*/k_i) = 0$. Then, (iv) holds and (ii)–(iii) follow from Theorem 5.1 (iii)–(iv).

By Lemma 5.2 (i), the function $q = q_{\boldsymbol{u}}^*(d)$ is defined for $d \in (0, \infty)$ when $\sum_{i=1}^3 r_i (1 - u_i^*/k_i) \geq 0$. We claim that $q_{\boldsymbol{u}}^*(d)/d$ is bounded for $d \in (\delta, \infty)$ for any fixed $\delta > 1$. If it is not true, up to a subsequence, we may assume

$$\lim_{d \to \infty} \frac{q_{\boldsymbol{u}}^*(d)}{d} = \infty \text{ and } \lim_{d \to \infty} \boldsymbol{\psi} = \hat{\boldsymbol{\psi}}$$

for some $\hat{\boldsymbol{\psi}} \geq \boldsymbol{0}$ and $\sum_{i=1}^3 \hat{\psi}_i = 1$. Then, dividing (5.22) by $q_{\boldsymbol{u}}^*(d)$ and taking $d \to \infty$, we can obtain a contradiction using similar arguments as in the proof of (i). Therefore, $q_{\boldsymbol{u}}^*(d)/d$ is bounded for $d \in (\delta, \infty)$. Then, using similar arguments as in the proof of [7, Proposition 4.4], we can show that (3.8) holds with $\theta \in (0, q_1/d_1)$ when $\sum_{i=1}^3 r_i (1 - u_i^*/k_i) > 0$, and (3.8) holds with $\theta = 0$ when $\sum_{i=1}^3 r_i (1 - u_i^*/k_i) = 0$.

By Lemma 5.2 (ii), the function $q = q_{\boldsymbol{u}}^*(d)$ is defined for $d \in (0, d_0)$ when $\sum_{i=1}^3 r_i (1 - u_i^*/k_i) < 0$. Using similar arguments as in (i), we can show that $q_{\boldsymbol{u}}^*(d)$ is bounded for $d \in (d_0 - \delta, d_0)$ for some $\delta \ll 1$. Then, up to a subsequence, we may assume

$$\lim_{d \to d_0} q_{\boldsymbol{u}}^*(d) = \eta \text{ and } \lim_{d \to d_0} \boldsymbol{\psi} = \boldsymbol{\psi}^*$$

for some $\boldsymbol{\psi}^* \geq \boldsymbol{0}$ and $\sum_{i=1}^3 \psi_i^* = 1$. Taking $d \to d_0$ in (5.22), we see that

$$d_0 \sum_{j=1}^3 D_{ij} \psi_j^* + \eta \sum_{j=1}^3 Q_{ij} \psi_j^* + r_i \left(1 - \frac{u_i^*}{k_i} \right) \psi_i^* = 0, \quad i = 1, 2, 3, \tag{5.27}$$

which yields $\lambda_1 (d_0, \eta, \boldsymbol{1} - \boldsymbol{u}^*/\boldsymbol{k}) = 0$. By the proof of Lemma 5.2, $\lambda_1 (d_0, q, \boldsymbol{1} - \boldsymbol{u}^*/\boldsymbol{k}) = 0$ has at most one root for $q \in [0, \infty)$. Since $\lambda_1 (d_0, 0, \boldsymbol{1} - \boldsymbol{u}^*/\boldsymbol{k}) = 0$, we must have $\eta = 0$. This proves (3.7). □

6. Proofs for the competitive exclusion results

Let $(\boldsymbol{u}, \boldsymbol{v})$ be a positive equilibrium of model (1.4). Define

$$\begin{aligned} &f_0 = f_3 = 0, \quad g_0 = g_3 = 0, \\ &f_j = d_1 u_{j+1} - (d_1 + q_1)u_j, \quad g_j = d_2 v_{j+1} - (d_2 + q_2)v_j, \quad j = 1, 2. \end{aligned} \tag{6.1}$$

Clearly, we have

$$f_j - f_{j-1} = -r_j u_j \left(1 - \frac{u_j + v_j}{k_j} \right), \quad j = 1, 2, 3, \tag{6.2}$$

and

$$g_j - g_{j-1} = -r_j v_j \left(1 - \frac{u_j + v_j}{k_j} \right), \quad j = 1, 2, 3. \tag{6.3}$$

Then, we have the following result about the sign of $f_j, g_j, j = 1, 2$.

Lemma 6.1. *Suppose that* (**H**) *holds,* $\boldsymbol{r} \gg \boldsymbol{0}$, *and* $d_1, q_1, d_2, q_2 > 0$. *If* $(\boldsymbol{u}, \boldsymbol{v})$ *is a positive equilibrium of model* (1.4), *then we have* $f_1, g_1, f_2, g_2 < 0$.

Proof. First we prove $f_1 < 0$. Suppose to the contrary that $f_1 \geq 0$. By (6.2) and (6.3), we have $k_1 - u_1 - v_1 \leq 0$ and $g_1 \geq 0$. Since $f_1, g_1 \geq 0$, we have $u_2 > u_1$ and $v_2 > v_1$. This combined with (**H**) implies that $k_2 - u_2 - v_2 < 0$. Then, by (6.2) and (6.3) again, we obtain that $f_2, g_2 > 0$ and $k_3 - u_3 - v_3 < 0$, which contradicts (6.2) with $j = 3$. Therefore, we have $f_1 < 0$. Consequently, by (6.2) and (6.3) with $j = 1$, we have $g_1 < 0$. Using similar arguments, we can prove $f_2, g_2 < 0$. □

The following result is similar to [7, Lemma 5.7] with $j = 1$ and $j = n = 3$ (see also the proof of Lemma 5.3). Thus, we omit the proof.

Lemma 6.2. *Suppose that* (**H**) *holds,* $r \gg 0$*, and* $d_1, q_1, d_2, q_2 > 0$*. If* $(\boldsymbol{u}, \boldsymbol{v})$ *is a positive equilibrium of model* (1.4)*, then the following equations hold:*

$$\sum_{j=1}^{2} \left[(d_1 - d_2)(v_{j+1} - v_j) - (q_1 - q_2)v_j\right] f_j \frac{d_1^j}{(d_1 + q_1)^{j+1}} = 0, \tag{6.4}$$

and

$$\sum_{j=1}^{2} \left[(d_2 - d_1)(u_{j+1} - u_j) - (q_2 - q_1)u_j\right] g_k \frac{d_2^j}{(d_2 + q_2)^{j+1}} = 0. \tag{6.5}$$

An essential step to prove the competitive exclusion results for model (1.4) is to show the nonexistence of positive equilibrium:

Lemma 6.3. *Suppose that* (**H**) *holds,* $r \gg 0$*, and* $d_1, q_1 > 0$*. Let* G_{12}^* *and* G_{23}^* *be defined by* (3.9) *and* (3.10)*, respectively. Then, model* (1.4) *admits no positive equilibrium, if one of the following conditions holds:*

(i) $(d_2, q_2) \in G_{11} \cup G_{21}$*;*
(ii) $q_1 > \bar{q}$ *and* $(d_2, q_2) \in G_{12} \cup G_{22} \cup G_{23}^*$*;*
(iii) $q_1 < \underline{q}$ *and* $(d_2, q_2) \in G_{13} \cup G_{23} \cup G_{12}^*$*.*
(iv) $\underline{q} \le q_1 \le \bar{q}$ *and* $(d_2, q_2) \in G_{12}^* \cup G_{23}^*$*;*

Proof. Suppose to the contrary that model (1.4) admits a positive equilibrium $(\boldsymbol{u}, \boldsymbol{v})$. Then, we will obtain a contradiction for each of the cases (i)–(iv).

(i) We only consider the case $(d_2, q_2) \in G_{21}$. Since the nonlinear terms of (1.4) are symmetric, the case $(d_2, q_2) \in G_{11}$ can be proved similarly. Suppose $(d_2, q_2) \in G_{21}$. Then, we have $d_2 \le d_1, q_2 \le q_1 d_2 / d_1$ and $(d_1, q_1) \ne (d_2, q_2)$. First, we claim that

$$(d_1 - d_2)(v_{j+1} - v_j) - (q_1 - q_2)v_j < 0 \quad \text{for} \ \ j = 1, 2. \tag{6.6}$$

Indeed if $d_1 = d_2$, then $q_1 > q_2$ and (6.6) holds. If $d_1 > d_2$, then it is easy to check that

$$\frac{q_1 - q_2}{d_1 - d_2} \ge \frac{q_2}{d_2}.$$

(This inequality is in [53, Lemma 2.4]). This, combined with $g_1, g_2 < 0$, proves (6.6). Then, by $f_1, f_2 < 0$ and (6.4), we have

$$0 < \sum_{j=1}^{2} \left[(d_1 - d_2)(v_{j+1} - v_j) - (q_1 - q_2)v_j\right] f_j \frac{d_1^j}{(d_1 + q_1)^{j+1}} = 0,$$

which is a contradiction.

(ii) We first consider the case $(d_2, q_2) \in G_{22}$. Since the nonlinear terms of (1.4) are symmetric, the case $(d_2, q_2) \in G_{12}$ can be proved similarly. Suppose $(d_2, q_2) \in G_{22}$. Then, $d_2 > d_1$ and $q_2 \le q_1$. By (1.4),

we have

$$d_1(u_2 - u_1) = -r_1 u_1 \left(1 - \frac{q_1}{r_1} - \frac{u_1 + v_1}{k_1} \right), \tag{6.7a}$$

$$d_2(v_2 - v_1) = -r_1 v_1 \left(1 - \frac{q_2}{r_1} - \frac{u_1 + v_1}{k_1} \right), \tag{6.7b}$$

$$(d_1 + q_1)(u_1 - u_2) - d_1(u_2 - u_3) = -r_2 u_2 \left(1 - \frac{u_2 + v_2}{k_2} \right), \tag{6.7c}$$

$$(d_2 + q_2)(v_1 - v_2) - d_2(v_2 - v_3) = -r_2 v_2 \left(1 - \frac{u_2 + v_2}{k_2} \right), \tag{6.7d}$$

$$(d_1 + q_1)(u_2 - u_3) = -r_3 u_3 \left(1 + \frac{q_1}{r_3} - \frac{u_3 + v_3}{k_3} \right), \tag{6.7e}$$

$$(d_2 + q_2)(v_2 - v_3) = -r_3 u_3 \left(1 + \frac{q_2}{r_3} - \frac{u_3 + v_3}{k_3} \right). \tag{6.7f}$$

Then, we show that $u_1 < u_2 < u_3$. Suppose to the contrary that $u_1 \geq u_2$. Then, by (6.7a), we see that

$$u_1 + v_1 \leq k_1 - \frac{q_1 k_1}{r_1} \leq k_1 - \frac{q_2 k_1}{r_1},$$

where we have used $q_2 \leq q_1$ in the last inequality. This, combined with (6.7b), implies that $v_1 \geq v_2$. Noticing that

$$q_1 > \bar{q} \geq \frac{r_1}{k_1}(k_1 - k_2),$$

we have

$$u_2 + v_2 \leq u_1 + v_1 \leq k_1 - \frac{q_1 k_1}{r_1} < k_2,$$

and consequently $u_3 < u_2$ and $v_3 < v_2$ by (6.7c) and (6.7d). This, combined with $q_1 > \bar{q}$, implies that

$$u_3 + v_3 < u_2 + v_2 < k_2 < k_3 + \frac{k_3 q_1}{r_3},$$

which contradicts (6.7e). Similarly, we can show that $u_2 < u_3$. So, $u_1 < u_2 < u_3$, which leads to

$$(d_2 - d_1)(u_{j+1} - u_j) - (q_2 - q_1)u_j > 0, \quad j = 1, 2.$$

Then, by Lemma 6.1 and (6.5), we have

$$0 > \sum_{j=1}^{2} [(d_2 - d_1)(u_{j+1} - u_j) - (q_2 - q_1)u_j] g_j \frac{d_2^j}{(d_2 + q_2)^{j+1}} = 0,$$

which is a contradiction.

Now suppose that $(d_2, q_2) \in G_{23}^*$. Then, $q_2 < \underline{q}$ and $(d_1, q_1) \in \hat{G}_{13}$, where

$$\hat{G}_{13} := \{(d, q) : d \geq d_2, q_2 \leq q < \frac{q_2}{d_2}d, (d, q) \neq (d_2, q_2)\}. \tag{6.8}$$

Since the nonlinear terms of (1.4) are symmetric, this case can be proved similarly as the case $(d_2, q_2) \in G_{13}$ (the proof is immediately below).

(iii) Suppose that $(d_2, q_2) \in G_{13}$. Then, we have $d_2 \geq d_1$, $q_1 \leq q_2 \leq q_1 d_2/d_1$, and $(d_1, q_1) \neq (d_2, q_2)$. We show that $u_1 > u_2 > u_3$. Suppose to the contrary that $u_1 \leq u_2$. Then, by (6.7a) and $q_2 \geq q_1$, we have

$$u_1 + v_1 \geq k_1 - \frac{q_1 k_1}{r_1} > k_1 - \frac{q_2 k_1}{r_1}.$$

This, combined with (6.7b), yields $v_1 \le v_2$. Noting that

$$q_1 < \underline{q} < \frac{r_1}{k_1}(k_1 - k_2),$$

we have

$$k_2 < k_1 - \frac{q_1 k_1}{r_1} \le u_1 + v_1 \le u_2 + v_2.$$

Then, by (6.7c) and (6.7d), we have $u_3 > u_2$ and $v_3 > v_2$. Since $q_1 < \underline{q}$, we have

$$k_3 + \frac{k_3 q_1}{r_3} < k_2 < u_2 + v_2 < u_3 + v_3,$$

which contradicts (6.7e). Similarly, we can show $u_2 > u_3$. Therefore, we have $u_1 > u_2 > u_3$ and

$$(d_2 - d_1)(u_{j+1} - u_j) - (q_2 - q_1)u_j < 0, \quad j = 1, 2.$$

Then, it follows from Lemma 6.1 and (6.5) that

$$0 < \sum_{j=1}^{2} [(d_2 - d_1)(u_{j+1} - u_j) - (q_2 - q_1)u_j] \, g_j \frac{d_2^j}{(d_2 + q_2)^{j+1}} = 0,$$

which is a contradiction.

For the case $(d_2, q_2) \in G_{23}$, using similar arguments as above, we can obtain $v_1 > v_2 > v_3$, which leads to

$$(d_1 - d_2)(v_{j+1} - v_j) - (q_1 - q_2)v_j < 0, \quad j = 1, 2.$$

This, combined with Lemma 6.1 and (6.4), implies that

$$0 < \sum_{j=1}^{2} [(d_1 - d_2)(v_{j+1} - v_j) - (q_1 - q_2)v_j] \, f_j \frac{d_1^j}{(d_1 + q_1)^{j+1}} = 0,$$

which is a contradiction.

Next suppose that $(d_2, q_2) \in G_{12}^*$. Then, $q_2 > \bar{q}$ and $(d_1, q_1) \in \hat{G}_{22}$, where

$$\hat{G}_{22} := \{(d, q) : \; d > d_2, 0 < q \le q_2\}.$$

Since the nonlinear terms of (1.4) are symmetric, this case can be proved similarly the case $(d_2, q_2) \in G_{22}$ in (ii).

(iv) If $(d_2, q_2) \in G_{23}^*$, the proof is similar to the corresponding case in (ii). If $(d_2, q_2) \in G_{12}^*$, the proof is similar to the corresponding case in (iii). $\qquad\square$

We are ready to prove Theorems 3.6, 3.8 and 3.10.

Proof of Theorem 3.6. (i) Suppose that $q_1 < \underline{q}$ and $(d_2, q_2) \in G_{21} \cup G_{23}$. By Lemma 6.3 (i) and (iii), model (1.4) admits no positive equilibrium. By Theorem 3.3 (i) and (iii), $(\boldsymbol{u}^*, \boldsymbol{0})$ is unstable. Then, it follows from the monotone dynamical system theory [20,21,29,46] that $(\boldsymbol{u}^*, \boldsymbol{0})$ is globally asymptotically stable.

(ii) Suppose that $q_1 < \underline{q}$ and $(d_2, q_2) \in G_{11} \cup G_{12}^*$. By Lemma 6.3 (i) and (iii), model (1.4) admits no positive equilibrium. By the monotone dynamical system theory [20,21,29,46], it suffices to show that $(\boldsymbol{0}, \boldsymbol{v}^*)$ is unstable. If $(d_1, q_1) \in G_{12}^*$, then $q_2 > \bar{q}$ and $(d_1, q_1) \in \tilde{G}_{22} := \{(d, q) : d > d_2, 0 < q \le q_2\}$. Since the nonlinear terms of model (1.4) are symmetric, it follows from Proposition 3.3 (ii) that $(\boldsymbol{0}, \boldsymbol{v}^*)$ is unstable. If $(d_2, q_2) \in G_{11}$, then $(d_1, q_1) \in \tilde{G}_{21}$, where

$$\tilde{G}_{21} := \left\{(d, q) : 0 < d \le d_2, 0 < q \le \frac{q_2}{d_2}d, (d, q) \ne (d_2, q_2)\right\}.$$

Similarly, it follows from Proposition 3.3 (i) that $(\boldsymbol{0}, \boldsymbol{v}^*)$ is unstable.

Finally, suppose that $q_1 < \underline{q}$ and $(d_2, q_2) \in G_{13}$. By Proposition 3.3 (iii), $(\boldsymbol{u}^*, \boldsymbol{0})$ is locally asymptotically stable. By Lemma 6.3 (iv), model (1.4) admits no positive equilibrium. If $(\boldsymbol{0}, \boldsymbol{v}^*)$ is locally asymptotically stable, then model (1.4) admits one unstable positive steady state, which is a contradiction. If $(\boldsymbol{0}, \boldsymbol{v}^*)$ is unstable, then the monotone dynamical system theory [20, 21, 29, 46] implies that $(\boldsymbol{u}^*, \boldsymbol{0})$ is globally asymptotically stable. If $(\boldsymbol{0}, \boldsymbol{v}^*)$ is neutrally stable, by [29, Theorem 1.4], $(\boldsymbol{u}^*, \boldsymbol{0})$ is globally asymptotically stable. This proves (ii). □

Proof of Theorems 3.8 and 3.10. We only need to prove the case $(d_2, q_2) \in G_{23}^*$, since the other cases can be proved using similar arguments in the proof of Theorem 3.6. If $(d_2, q_2) \in G_{23}^*$, then $q_2 < \underline{q}$ and $(d_1, q_1) \in \hat{G}_{13}$, where

$$\hat{G}_{13} := \{(d, q) : \ d \geq d_2, q_2 \leq q < \frac{q_2}{d_2} d, (d, q) \neq (d_2, q_2)\}.$$

Since the nonlinear terms of model (1.4) are symmetric, it follows from Theorem 3.6 (ii) that $(\boldsymbol{0}, \boldsymbol{v}^*)$ is globally asymptotically stable. □

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Appendix

In the Appendix, we study the relations of $\overline{q}$, $\underline{q}$ and q_0. For convenience, we recall the definition of $\overline{q}$, $\underline{q}$ and q_0:

$$\overline{q} = \max\left\{\frac{r_1}{k_1}(k_1 - k_2), \frac{r_3}{k_3}(k_2 - k_3)\right\}, \tag{6.9a}$$

$$\underline{q} = \min\left\{\frac{r_1}{k_1}(k_1 - k_2), \frac{r_3}{k_3}(k_2 - k_3)\right\}, \tag{6.9b}$$

$$q_0 = \max\left\{r_1\left(1 - \frac{u_1^*}{k_1}\right), r_2\left(1 - \frac{u_2^*}{k_2}\right)\right\}. \tag{6.9c}$$

Lemma 6.4. *Suppose that* (**H**) *holds,* $\boldsymbol{r} \gg \boldsymbol{0}$, *and* $d_1, q_1 > 0$. *Then, the following statements hold:*

(i) *If* $q_1 < \underline{q}$, *then* $q_0 > q_1$;
(ii) *If* $q_1 > \overline{q}$, *then* $q_0 < q_1$;
(iii) *If* $q_1 > \underline{q}$, *then* $q_0 > \underline{q}$;
(iv) *If* $q_1 < \overline{q}$, *then* $q_0 < \overline{q}$.

Proof. By (5.10) and (5.11) and Lemma 5.1 (i), we have

$$\tilde{f}_1 = d_1 u_2^* - (d_1 + q_1)u_1^* = -r_1 u_1^*\left(1 - \frac{u_1^*}{k_1}\right) < 0, \tag{6.10a}$$

$$\tilde{f}_2 = d_1 u_3^* - (d_2 + q_2)u_2^* = r_3\left(1 - \frac{u_3^*}{k_3}\right) < 0, \tag{6.10b}$$

$$\tilde{f}_2 - \tilde{f}_1 = -r_2 u_2^*\left(1 - \frac{u_2^*}{k_2}\right), \tag{6.10c}$$

which will be used in the proof below.

(i) By Lemma 5.1 (iv), we have $u_1^* > u_2^* > u_3^*$. This, together with (6.9c) and (6.10a), implies that

$$q_0 \geq r_1 \left(1 - \frac{u_1^*}{k_1} \right) = \frac{(d_1 + q_1)u_1^* - d_1 u_2^*}{u_1^*} = d_1 \left(1 - \frac{u_2^*}{u_1^*} \right) + q_1 > q_1. \tag{6.11}$$

(ii) By Lemma 5.1 (iii), we have $u_1^* < u_2^* < u_3^*$. Then, by (6.10a) again, we obtain

$$r_1 \left(1 - \frac{u_1^*}{k_1} \right) = d_1 \left(1 - \frac{u_2^*}{u_1^*} \right) + q_1 < q_1. \tag{6.12}$$

By (6.10c), we obtain that

$$\begin{aligned}
r_2 \left(1 - \frac{u_2^*}{k_2} \right) &= \frac{((d_1 + q_1)u_2^* - d_1 u_3^*) + \tilde{f}_1}{u_2^*} \\
&= d_1 \left(1 - \frac{u_3^*}{u_2^*} \right) + \frac{\tilde{f}_1}{u_2^*} + q_1 < q_1,
\end{aligned} \tag{6.13}$$

where we have used (6.10c) and $u_2^* < u_3^*$ in the last step. It follows from (6.9c), (6.12) and (6.13) that $q_0 < q_1$.

(iii) We divide the proof into three cases:

$$\text{(A1)} \ \ u_1^* < k_2, \ \ \text{(A2)} \ \ u_1^* \geq u_2^*, \ \ \text{(A3)} \ \ k_2 \leq u_1^* < u_2^*.$$

For case (A1), we see from (6.9b) and (6.9c) that

$$q_0 \geq r_1 \left(1 - \frac{u_1^*}{k_1} \right) > \frac{r_1}{k_1} (k_1 - k_2) \geq \underline{q}.$$

For case (A2), we see from (6.9c) and (6.10a) that

$$q_0 \geq r_1 \left(1 - \frac{u_1^*}{k_1} \right) = d_1 \left(1 - \frac{u_2^*}{u_1^*} \right) + q_1 \geq q_1 > \underline{q}.$$

Now we consider (A3). Suppose to the contrary that $q_0 \leq \underline{q}$. This, combined with (6.9b) and (6.9c), yields

$$r_1 \left(1 - \frac{u_1^*}{k_1} \right) \leq q_0 \leq \underline{q} \leq \frac{r_3}{k_3} (k_2 - k_3). \tag{6.14}$$

Noticing that $u_2^* > k_2$, we see from (6.10c) that

$$\tilde{f}_2 - \tilde{f}_1 = d_1(u_3^* - u_2^*) - (d_1 + q_1)(u_2^* - u_1^*) = -r_2 u_2^* \left(1 - \frac{u_2^*}{k_2} \right) > 0. \tag{6.15}$$

Since $u_1^* < u_2^*$, we see from (6.15) that $u_2^* < u_3^*$. Then, we have

$$0 > \tilde{f}_2 > \tilde{f}_1 \ \text{ and } \ k_2 \leq u_1^* < u_2^* < u_3^*, \tag{6.16}$$

which yields

$$-\frac{\tilde{f}_2}{u_3^*} < -\frac{\tilde{f}_1}{u_1^*}. \tag{6.17}$$

This, together with (6.16), (6.10a) and (6.10b), implies that

$$r_1 \left(1 - \frac{u_1^*}{k_1} \right) = -\frac{\tilde{f}_1}{u_1^*} > -\frac{\tilde{f}_2}{u_3^*} = \frac{r_3}{k_3} (u_3^* - k_3) > \frac{r_3}{k_3} (k_2 - k_3),$$

which contradicts (6.14). Therefore, $q_0 > \underline{q}$ for case (A3).

(iv) We first show that

$$r_1 \left(1 - \frac{u_1^*}{k_1} \right) < \overline{q}, \tag{6.18}$$

and the proof is divided into three cases:

$$\text{(B1)} \ \ u_1^* > k_2, \ \ \text{(B2)} \ \ u_1^* \le u_2^*, \ \ \text{(B3)} \ \ k_2 \ge u_1^* > u_2^*.$$

For case (B1), we have

$$r_1 \left(1 - \frac{u_1^*}{k_1} \right) < \frac{r_1}{k_1} (k_1 - k_2) \le \overline{q}.$$

For case (B2), we see from (6.10a) that

$$r_1 \left(1 - \frac{u_1^*}{k_1} \right) = d_1 \left(1 - \frac{u_2^*}{u_1^*} \right) + q_1 \le q_1 < \overline{q}. \tag{6.19}$$

For case (B3), using similar arguments as the above case (A3), we have

$$0 > \tilde{f}_1 > \tilde{f}_2 \ \ \text{and} \ \ k_2 \ge u_1^* > u_2^* > u_3^*.$$

This, combined with (6.10a) and (6.10b), implies that

$$r_1 \left(1 - \frac{u_1^*}{k_1} \right) = -\frac{\tilde{f}_1}{u_1^*} < -\frac{\tilde{f}_2}{u_1^*} < -\frac{\tilde{f}_2}{u_3^*} = r_3 \left(\frac{u_3^*}{k_3} - 1 \right) < \frac{r_3}{k_3} (k_2 - k_3) \le \overline{q}.$$

Then, we show that

$$r_2 \left(1 - \frac{u_2^*}{k_2} \right) < \overline{q}, \tag{6.20}$$

and the proof is also divided into three cases:

$$\text{(C1)} \ \ u_2^* \le u_3^*, \ \ \text{(C2)} \ \ u_2^* > u_3^* \ge k_2, \ \ \text{(C3)} \ \ u_2^* > u_3^* \ \text{and} \ k_2 > u_3^*.$$

For case (C1), we see from (6.13) that

$$r_2 \left(1 - \frac{u_2^*}{k_2} \right) < q_1 < \overline{q}.$$

For case (C2), we have

$$r_2 \left(1 - \frac{u_2^*}{k_2} \right) < 0 < \overline{q}.$$

For case (C3), we see from (6.10) that

$$r_2 \left(1 - \frac{u_2^*}{k_2} \right) = \frac{\tilde{f}_1 - \tilde{f}_2}{u_2^*} < -\frac{\tilde{f}_2}{u_2^*} < -\frac{\tilde{f}_2}{u_3^*} = \frac{r_3}{k_3} (u_3^* - k_3) < \frac{r_3}{k_3} (k_2 - k_3) \le \overline{q}.$$

By (6.18) and (6.20), we see that (iv) holds. $\qquad \square$

Remark 6.5. By $\underline{q} \le \overline{q}$ and Lemma 6.4, we see that if $q_1 < \underline{q}$, then $q_1 < q_0 < \overline{q}$; if $q_1 > \overline{q}$, then $\underline{q} < q_0 < q_1$; and if $\underline{q} < q_1 < \overline{q}$, then $\underline{q} < q_0 < \overline{q}$.

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