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# ESS in a River Network with Two Branches*

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**Abstract** In a recent work by Jiang et al. [Bull. Math. Biol., 2020, Paper No. 131, 42pp], to discuss the impact of differing topology of river networks on the evolution of dispersal, the authors proposed three different models and found the winning of slower/faster diffuser or evolutionarily singular strategies. However, it is unknown whether there is an evolutionarily stable strategy (ESS, a central concept in evolution game theory) for these three models. In this paper, focusing on the Model (III) proposed by them (the most complicated one as they stated), we give a confirmed answer to this issue, that is, there does exist ESS.

**Keywords** Evolution of dispersal, evolutionarily stable strategy, advective patchy environment, selection gradient

**MSC(2010)** 34D20, 92D15, 92D40.

## 1. Introduction

The issue of the evolution of dispersal, a central topic in spatial ecology and evolutionary biology, has been extensively studied by both mathematicians and mathematical biologists in the past few decades. A well accepted result due to Hastings [11] (see also Dockery et al. [8]) says that in spatially heterogeneous and temporally constant environments, slower diffusion is selected for provided the populations take random diffusion only. This issue was later further explored in different biological situations, see, e.g., in temporally varying (time periodic) environments [12], in the situation where organisms take both random diffusion and some conditional dispersal like movement upward along the resource gradient [4–6, 9, 15, 16], in the advective environments such as rivers, streams where individuals are subject to passive downstream movement [7, 18, 22, 25, 26], and in the space-discrete environments with a finite number of patches located in a straight line [1–3, 10, 19, 21, 23]. To mention but a few.

Recently, considering river populations in a patchy environment, Jiang et al. [13] proposed a different angle to pursue further the above issue. Specifically, starting

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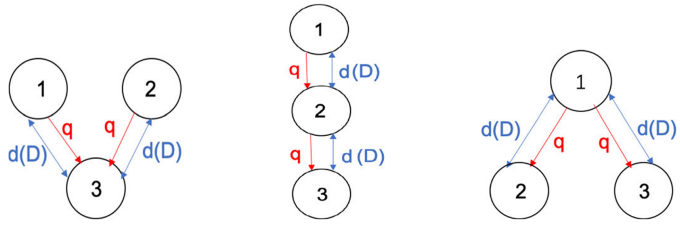
with the case of three patches, they considered three differing river network modules (not necessarily located in a line, see Fig. 1 below) and proposed three different models based on each module. Compared with the two-patch case [10,13,20,23], beside the phenomenon "the slower/faster diffuser wins", they also found the existence of evolutionarily singular strategies for the three-patch case.




**(a)** Model (I) **(b)** Model (II) **(c)** Model (III)

**Figure 1.** Three different river network modules proposed by Jiang et al. [13, Fig. 2]. Here, the two-way blue arrows reflect the random diffusion between connected patches and the one-way red arrows reflect the unidirectional drift.

Motivated by Jiang et al. [13], a natural question that deserves further investigation is whether there exists an evolutionarily stable strategy (abbreviated below as ESS), which is a core concept in evolutionary biology proposed by Maynard-Smith and Price [24]. Roughly speaking, a strategy is said to be an ESS (resp. EBP, i.e, evolutionarily branching point) if a resident population adopting it cannot (resp. can) be invaded by a mutant using a different strategy when rare; another related concept is the convergent stable strategy (CSS) and a strategy is called a CSS if the mutant can always invade the resident when the mutant strategy is closer to the CSS than the resident strategy, see the definitions in, e.g., [17]. Note that an evolutionarily singular strategy is not necessarily an ESS, but an ESS must be an evolutionarily singular strategy (see [17]).

For Model (I), a positive answer to the above question was recently given by Jin and Zhou [14]. As pointed out in Jiang et al. [13], Model (III) is the most complicated one and is still less understood. So, in the current paper, we aim to pursue further study on this model by employing some idea developed in [14]. To be more specific, we recall Model (III) as below

$$\begin{cases} u_{1t} = d(u_2 + u_3 - 2u_1) - 2qu_1 + u_1(1 - \frac{u_1+v_1}{K_1}), \\ u_{2t} = d(u_1 - u_2) + qu_1 + u_2(1 - \frac{u_2+v_2}{K_2}), \\ u_{3t} = d(u_1 - u_3) + qu_1 + u_3(1 - \frac{u_3+v_3}{K_3}), \\ v_{1t} = D(v_2 + v_3 - 2v_1) - 2qv_1 + v_1(1 - \frac{u_1+v_1}{K_1}), \\ v_{2t} = D(v_1 - v_2) + qv_1 + v_2(1 - \frac{u_2+v_2}{K_2}), \\ v_{3t} = D(v_1 - v_3) + qv_1 + v_3(1 - \frac{u_3+v_3}{K_3}), \\ u_i(0) = u_{i0} > 0, \quad v_i(0) = v_{i0} > 0, \quad i = 1,2,3, \end{cases} \tag{1.1}$$

where $u_i = u_i(t)$ (resp. $v_i = v_i(t)$), $i = 1,2,3$, denotes the population density of species $u$ (resp. $v$) in the patch $i$ with the carrying capacity $K_i > 0$, and the constants $d > 0$ and $D > 0$ are the diffusion rates and $q > 0$ is the advection rate.

To introduce the main result of system (1.1) in Jiang et al. [13], let $E_u =$

$(u_1^*, u_2^*, u_3^*, 0, 0, 0)$ be the semi-trivial equilibrium, which satisfies

$$\begin{cases} d(u_2^* + u_3^* - 2u_1^*) - 2qu_1^* + u_1^*(1 - \frac{u_1^*}{K_1}) = 0, \\ d(u_1^* - u_2^*) + qu_1^* + u_2^*(1 - \frac{u_2^*}{K_2}) = 0, \\ d(u_1^* - u_3^*) + qu_1^* + u_3^*(1 - \frac{u_3^*}{K_3}) = 0. \end{cases} \tag{1.2}$$

Linearizing system (1.1) at $E_u$, one gets the following eigenvalue problem

$$\mathbf{J}(\phi_1, \phi_2, \phi_3)^T + \Gamma(\phi_1, \phi_2, \phi_3)^T = (0, 0, 0)^T, \tag{1.3}$$

where

$$\mathbf{J} := \begin{pmatrix} -2D - 2q + 1 - \frac{u_1^*}{K_1} & D & D \\ D + q & -D + 1 - \frac{u_2^*}{K_2} & 0 \\ D + q & 0 & -D + 1 - \frac{u_3^*}{K_3} \end{pmatrix}. \tag{1.4}$$

By the Perron-Frobenius theorem, problem (1.2) has a principal eigenvalue denoted in the following by $\Gamma_1 = \Gamma_1(d, D, q)$ and the corresponding eigenvector denoted by $(\phi_1, \phi_2, \phi_3)^T$ satisfies $\phi_i > 0$. The so-called selection gradient is defined by (see [13])

$$\partial_D \Gamma_1(d, d, q). \tag{1.5}$$

The main result of system (1.1) in [13] can be summarized as follows.

**Theorem 1.1.** *Assume $K_1 > K_2 > K_3 > 0$ holds. Then the following statements hold true:*

*(i) If $2K_1K_3 - K_2(K_1 + K_3) > 0$ and $q < Q_1 := \frac{2K_1K_3 - K_2(K_1+K_3)}{K_1K_3 + K_2(K_1+K_3)}$, then $E_u$ is locally asymptotically stable if and only if $D > d$.*

*(ii) If $q > Q_2 := \max\{Q_2^1, Q_2^2\}$, then $E_u$ is locally asymptotically stable provided $d \ll 1$ and $d < D$, or $d \gg 1$ and $d > D$. Moreover, there exists $d_* = d_*(q)$ which is an evolutionarily singular strategy satisfying*

$$\operatorname{sgn}\big(\partial_D \Gamma_1(d, d, q)\big) = \begin{cases} 1, & d < d^*, d \text{ close to } d^*, \\ 0, & d = d^*, \\ -1, & d > d^*, d \text{ close to } d^*. \end{cases}$$

*Here,*

$$Q_2^1 := \frac{(K_2)^2 + (K_3)^2}{(K_2 - K_3)^2} \quad \text{and} \quad Q_2^2 := \frac{(K_3)^2(K_2 - u_\infty)^2 + (K_2)^2(K_3 - u_\infty)^2}{K_2K_3u_\infty(K_2 + K_3) - 2(K_2K_3)^2},$$

*with $u_\infty := \frac{3K_1K_2K_3}{K_1K_2 + K_1K_3 + K_2K_3}$.*

Recall that for given $K_i > 0$ $(i = 1, 2, 3)$ and $q > 0$, a dispersal strategy $d > 0$ is said to be an ESS if (see [17])

$$\partial_D \Gamma_1(d, d, q) = 0 \quad \text{and} \quad \partial_{DD}^2 \Gamma_1(d, d, q) > 0. \tag{1.6}$$

Clearly, the evolutionarily singular strategy found in Theorem 1.1 is not an ESS.

As stated above, the main purpose of this paper is to establish the existence of ESS. Throughout this paper, we make the following hypothesis

$(H)$: $\quad K_1 > K_2$ and $0 < K_2 - K_3 < \delta_1 = \delta_1(K_1, K_2) := \min\{K_2 - \frac{K_2^3}{K_1^2}, \frac{\sqrt{17}-1}{8} K_2\}$.

Let us now state the main results of this paper. We first go to understand the local dynamics of system (1.1) around $E_u$.

**Theorem 1.2.** *Assume that $(H)$ holds. Then for each $d \in (0, 1]$, there are critical values $q_i(d)$ $(i = 1, 2, 3)$ with $q_1(d) > q_2(d) > q_3(d) > 0$ (given in Lemmas 4.2, 4.3 and 4.4 below) such that*

*(i) if $q \in (0, q_3(d)]$, $E_u$ is locally asymptotically stable if and only if $D > d$;*

*(ii) if $q \in [q_2(d), q_1(d)]$, $E_u$ is locally asymptotically stable if and only if $D < d$.*

If we define

$$q_1^* = \inf_{d \in (0,1]} q_1(d; K_i), \quad q_2^* = \sup_{d \in (0,1]} q_2(d; K_i) \quad \text{and} \quad q_3^* = \inf_{d \in (0,1]} q_3(d; K_i),$$

then we have the following consequence.

**Corollary 1.1.** *Assume that $(H)$ holds. Then we have*

*(i) For each $q \in (0, q_3^*)$, $E_u$ is locally asymptotically stable provided $d < D$ and $d \leq 1$;*

*(ii) For each $q \in (q_2^*, q_1^*)$, $E_u$ is locally asymptotically stable provided $D < d \leq 1$.*

The above result, biologically, suggests that if both of the two competitors adopt diffusion strategies in $(0, 1]$, then for suitably small advection, slower diffuser wins, which is in line with Theorem 1.1 $(i)$, while for intermediate advection, faster diffuser wins.

We now discuss the existence of ESS, which is obtained by a more careful examination of certain intermediate advection, see below. This result seems new.

**Theorem 1.3.** *Assume that $(H)$ holds. Then the following statements hold true:*

*(i) For each $d \in (0, 1]$ there exists at least one $q_*(d) \in (q_3(d), q_2(d))$ such that* (1.6) *holds.*

*(ii) There exists $\delta_2 = \delta_2(K_1, K_2) > 0$ such that for $0 < K_2 - K_3 < \delta_2$, $\mathcal{A}_1(d, q)$ defined in* (2.1) *below satisfies*

$$\partial_q \mathcal{A}_1(d, q_*(d)) < \frac{3K_1 K_2^2 (K_2 - K_1)}{2(2K_1 + K_2)^2} < 0, \quad \textit{for} \quad d \in (0, 1].$$

*Then for $0 < K_2 - K_3 < \delta_0 := \min\{\delta_1, \delta_2\}$, the above $q_*(d)$ is unique for each $d \in (0, 1]$ and is continuous for $d \in (0, 1]$. Moreover, if we define*

$$q_*^1 := \inf_{d \in (0,1]} q_*(d) \quad \textit{and} \quad q_*^2 := \sup_{d \in (0,1]} q_*(d),$$

*then for any $q \in (q_*^1, q_*^2)$, there exists at least one ESS.*

The remainder of this paper is organized as follows. In Sect. 2 below, we establish the property of the selection gradient. Then an auxiliary problem is discussed in Sect. 3 and a classification result is presented in Sect. 4. The main results are proved in Sect. 5 and some numerical simulations are exhibited in Sect. 6.

## 2. The selection gradient

In this section, we mainly discuss the property of the selection gradient defined in (1.5). The main result of this section is as the following.

**Theorem 2.1.** *Assume $K_1 > K_2 > K_3 > 0$. Then*

(*i*) $\mathrm{sgn}\big(\partial_D \Gamma_1(d,d,q)\big) = \mathrm{sgn}\big(\mathcal{A}_1(d,q)\big)$, *where*

$$\mathcal{A}_1(d,q) := u_2^*\Big(1-\frac{u_2^*}{K_2}\Big)(u_2^*-u_1^*) + u_3^*\Big(1-\frac{u_3^*}{K_3}\Big)(u_3^*-u_1^*); \tag{2.1}$$

(*ii*) *If $\partial_D\Gamma_1(d,d,q)=0$, then* $\mathrm{sgn}\big(\partial^2_{DD}\Gamma_1(d,d,q)\big) = \mathrm{sgn}\big(u_1^*-u_3^*\big)$.

**Proof.** Based on (1.3) and (1.4), one can directly compute

$$\begin{cases} \phi_1 = \prod_{i=2}^3 \big(D-1+\frac{u_i^*}{K_i}-\Gamma_1\big), \\ \phi_2 = (D+q)(D-1+\frac{u_2^*}{K_2}-\Gamma_1), \\ \phi_3 = (D+q)(D-1+\frac{u_3^*}{K_3}-\Gamma_1), \end{cases} \tag{2.2}$$

and

$$\begin{cases} \dot\phi_1 = (1-\dot\Gamma_1)(2D-2+\frac{u_2^*}{K_2}+\frac{u_3^*}{K_3}-2\Gamma_1), \\ \dot\phi_2 = (D-1+\frac{u_2^*}{K_2}-\Gamma_1)+(D+q)(1-\dot\Gamma_1), \\ \dot\phi_3 = (D-1+\frac{u_3^*}{K_3}-\Gamma_1)+(D+q)(1-\dot\Gamma_1), \end{cases} \tag{2.3}$$

where $\dot\phi_i := \partial_D\phi_i$ and $\dot\Gamma_1 := \partial_D\Gamma_1$. Differentiating (1.3) with respect to $D$, one sees

$$\dot{\mathbf{J}}(\phi_1,\phi_2,\phi_3)^T + \mathbf{J}(\dot\phi_1,\dot\phi_2,\dot\phi_3)^T + \dot\Gamma_1(\phi_1,\phi_2,\phi_3)^T + \Gamma_1(\dot\phi_1,\dot\phi_2,\dot\phi_3)^T = (0,0,0)^T, \tag{2.4}$$

and

$$\begin{aligned} &\ddot{\mathbf{J}}(\phi_1,\phi_2,\phi_3)^T + 2\dot{\mathbf{J}}(\dot\phi_1,\dot\phi_2,\dot\phi_3)^T + \mathbf{J}(\ddot\phi_1,\ddot\phi_2,\ddot\phi_3)^T \\ &+\ddot\Gamma_1(\phi_1,\phi_2,\phi_3)^T + 2\dot\Gamma_1(\dot\phi_1,\dot\phi_2,\dot\phi_3)^T + \Gamma_1(\ddot\phi_1,\ddot\phi_2,\ddot\phi_3)^T = (0,0,0)^T, \end{aligned} \tag{2.5}$$

where $\ddot\phi_i := \partial^2_{DD}\phi_i$, $\ddot\Gamma_1 := \partial^2_{DD}\Gamma_1$ and

$$\dot{\mathbf{J}} = \begin{pmatrix} -2 & 1 & 1 \\ 1 & -1 & 0 \\ 1 & 0 & -1 \end{pmatrix}, \quad \ddot{\mathbf{J}} = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}.$$

In order to solve (2.4) and (2.5), consider the conjugate problem of (1.3) as below

$$\mathbf{J}^T(\psi_1,\psi_2,\psi_3)^T + \Gamma_1(\psi_1,\psi_2,\psi_3)^T = (0,0,0)^T,$$

where

$$\begin{cases} \psi_1 = \prod_{i=2}^3 \big(D-1+\frac{u_i^*}{K_i}-\Gamma_1\big), \\ \psi_2 = D(D-1+\frac{u_2^*}{K_2}-\Gamma_1), \\ \psi_3 = D(D-1+\frac{u_3^*}{K_3}-\Gamma_1). \end{cases} \tag{2.6}$$

We now start to prove statement (*i*).

Define

$$\phi_i^* := \phi_i|_{D=d} \quad \text{and} \quad \psi_i^* := \psi_i|_{D=d}, \quad i = 1, 2, 3.$$

Multiplying (2.4) by $(\psi_1, \psi_2, \psi_3)$, restricting the resulting equation at $D = d$ and noting

$$\Gamma_1(d, d, q) = 0 \quad \text{and} \quad (\psi_1^*, \psi_2^*, \psi_3^*)\,\mathbf{J}|_{D=d} = (0, 0, 0),$$

one obtains

$$(\psi_1^*, \psi_2^*, \psi_3^*)\dot{\mathbf{J}}(\phi_1^*, \phi_2^*, \phi_3^*)^T + \partial_D\Gamma_1(d, d, q) \cdot (\psi_1^*, \psi_2^*, \psi_3^*)(\phi_1^*, \phi_2^*, \phi_3^*)^T = 0,$$

which, in view of (2.2), (2.3) and (2.6), implies

$$\begin{aligned}\partial_D\Gamma_1(d, d, q) &= -\frac{1}{\sum_{i=1}^3 \phi_i^*\psi_i^*}\big[(-2\psi_1^* + \psi_2^* + \psi_3^*)\phi_1^* + (\psi_1^* - \psi_2^*)\phi_2^* + (\psi_1^* - \psi_2^*)\phi_3^*\big] \\ &= -\frac{u_2^*(1 - \frac{u_2^*}{K_2})(u_1^* - u_2^*) + u_3^*(1 - \frac{u_3^*}{K_3})(u_1^* - u_3^*)}{(d+q)(u_1^*)^2 + d(u_2^*)^2 + d(u_3^*)^2},\end{aligned}$$

as desired.

To prove statement $(ii)$, define $\dot{\phi}_i^* := \partial_D\phi_i|_{D=d}$. Since $\Gamma_1(d, d, q) = 0$ and $\partial_D\Gamma_1(d, d, q) = 0$, one derives from (2.5) that

$$\begin{aligned}\partial_{DD}^2\Gamma_1(d, d, q) &= -\frac{2}{\sum_{i=1}^3 \phi_i^*\psi_i^*}\big[(-2\psi_1^* + \psi_2^* + \psi_3^*)\dot{\phi}_1^* + (\psi_1^* - \psi_2^*)\dot{\phi}_2^* + (\psi_1^* - \psi_2^*)\dot{\phi}_3^*\big] \\ &= \frac{2u_2^*u_3^*\big[(1 - \frac{u_2^*}{K_2})(u_2^* - u_1^*) + (1 - \frac{u_3^*}{K_3})(u_3^* - u_1^*)\big]}{(d+q)(u_1^*)^2 + d(u_2^*)^2 + d(u_3^*)^2}.\end{aligned}$$

This implies

$$\begin{aligned}\operatorname{sgn}\Big(\partial_{DD}^2\Gamma_1(d, d, q)\Big) &= \operatorname{sgn}\Big(u_2^*(1 - \frac{u_2^*}{K_2})(u_2^* - u_1^*) + u_2^*(1 - \frac{u_3^*}{K_3})(u_3^* - u_1^*)\Big) \\ &= \operatorname{sgn}\Big((1 - \frac{u_3^*}{K_3})(u_3^* - u_1^*)(u_2^* - u_3^*)\Big) \\ &= \operatorname{sgn}\Big(u_1^* - u_3^*\Big),\end{aligned}$$

where the second equality used $\partial_D\Gamma_1(d, d, q) = 0$ and statement $(i)$ and the last equality used the following estimate (see [13])

$$u_3^* > K_3 \quad \text{and} \quad u_2^* > u_3^*. \tag{2.7}$$

□

## 3. An auxiliary problem

To establish the existence of ESS, for some technical reason we need to assume that $K_3$ is close to $K_2$. So, in this section, we consider the following auxiliary problem (i.e., system (1.1) with $K_3 = K_2$)

$$\begin{cases} w_{1t} = d(w_2 + w_3 - 2w_1) - 2qw_1 + w_1(1 - \frac{w_1+v_1}{K_1}), \\ w_{2t} = d(w_1 - w_2) + qw_1 + w_2(1 - \frac{w_2+v_2}{K_2}), \\ w_{3t} = d(w_1 - w_3) + qw_1 + w_3(1 - \frac{w_3+v_3}{K_2}), \\ v_{1t} = D(v_2 + v_3 - 2v_1) - 2qv_1 + v_1(1 - \frac{w_1+v_1}{K_1}), \\ v_{2t} = D(v_1 - v_2) + qv_1 + v_2(1 - \frac{w_2+v_2}{K_2}), \\ v_{3t} = D(v_1 - v_3) + qv_1 + v_3(1 - \frac{w_3+v_3}{K_2}), \\ u_i(0) = u_{i0} > 0, \quad v_i(0) = v_{i0} > 0, \quad i = 1, 2, 3. \end{cases} \tag{3.1}$$

Clearly, the system (3.1) also admits a semi-trivial equilibrium $E_w = (w_1^*, w_2^*, w_3^*, 0, 0, 0)$, where $w_i^* > 0$, $i = 1, 2, 3$. If $K_1 > K_2$, then it is not difficult to verify

$$w_1^* < K_1 \quad \text{and} \quad w_2^* = w_3^* > K_2, \tag{3.2}$$

by slightly modifying the proof of [13, Lemmas 13, 16].

Recall $\mathcal{A}_1(d, q)$ defined in Lemma 2.1 $(i)$. Then,

$$\lim_{K_3 \nearrow K_2} \mathcal{A}_1(d, q) = 2\mathcal{B}(d, q),$$

where

$$\mathcal{B}(d, q) := w_2^*\Big(1 - \frac{w_2^*}{K_2}\Big)\Big(w_2^* - w_1^*\Big), \quad (d, q) \in (0, 1] \times (0, \infty). \tag{3.3}$$

We now establish a useful property of $\mathcal{B}(d, q)$. See below.

**Lemma 3.1.** *If $K_1 > K_2$, then there exists a unique $q_{**} := \frac{K_1 - K_2}{2K_1 + K_2}$ such that $\mathcal{B}(d, q_{**}) = 0$ and*

$$\partial_q \mathcal{B}(d, q_{**}) < \mathcal{B}_*(K_1, K_2) := \frac{3K_1K_2^2(K_2 - K_1)}{2(2K_1 + K_2)^2} < 0 \quad \textit{for all} \quad d \in (0, 1]. \tag{3.4}$$

**Proof.** We first calculate $q_{**}$. In view of (3.2),

$$\mathcal{B}(d, q_{**}) = 0 \quad \Longleftrightarrow \quad w_1^*(d, q_{**}) = w_2^*(d, q_{**}),$$

which, together with (1.2), implies $q_{**} = \frac{K_1 - K_2}{2K_1 + K_2}$ and $w_i^*(d, q_{**}) = \frac{3K_1K_2}{2K_1 + K_2}$, $i = 1, 2, 3$.

We next prove (3.4). By direct computations,

$$\partial_q \mathcal{B}(d, q_{**}) = w_2^*(d, q_{**})\Big(1 - \frac{w_2^*(d, q_{**})}{K_2}\Big)\Big(\partial_q w_2^*(d, q_{**}) - \partial_q w_1^*(d, q_{**})\Big),$$

where $\partial_q w_i^*(d, q_{**})$, $i = 1, 2$, is uniquely determined by

$$\begin{cases} 2d\partial_q w_2^* - \big[\frac{2dw_2^*}{w_1^*} + \frac{w_1^*}{K_1}\big]\partial_q w_1^* = 2w_1^*, \\ (d+q)\partial_q w_1^* - \big[\frac{(d+q)w_1^*}{w_2^*} + \frac{w_2^*}{K_2}\big]\partial_q w_2^* = -w_1^*. \end{cases}$$

Based on the above equations, one can further derive

$$\partial_q w_1^* = \frac{\rho_1}{\rho_2} < 0 \quad \text{and} \quad \partial_q w_2^* = \frac{K_2 w_2^*\big[(d+q)\partial_q w_1^* + w_1^*\big]}{(d+q)K_2 w_1^* + (w_1^*)^2},$$

where

$$\rho_1 := -\frac{w_1^*}{K_1} - \frac{2d(w_2^*)^3}{w_1^*\{(d+q)K_2w_1^* + (w_1^*)^2\}} < 0,$$

and

$$\rho_2 := \frac{2w_1^*w_2^*(2w_2^* - K_2)}{(d+q)K_2w_1^* + (w_1^*)^2} > 0.$$

Hence,

$$\begin{aligned}\partial_q w_2^*(d,q_{**}) - \partial_q w_1^*(d,q_{**}) &= \frac{-\big[w_1^*(d,q_{**})\big]^2\partial_q w_1^*(d,q_{**}) + K_2 w_1^*(d,q_{**})w_2^*(d,q_{**})}{(d+q_{**})K_2w_1^*(d,q_{**}) + \big[w_1^*(d,q_{**})\big]^2} \\ &> \frac{K_2\big[w_1^*(d,q_{**})\big]^2}{(1+q_{**})K_2w_1^*(d,q_{**}) + \big[w_1^*(d,q_{**})\big]^2} \\ &= \frac{K_2}{2},\end{aligned}$$

where the inequality used $0 < d \le 1$ and $\partial_q w_1^* < 0$. Substituting the above estimate and the expression of $w_i^*(d,q_{**})$ into $\partial_q \mathcal{B}(d,q_{**})$, one gets the desired result. $\square$

## 4. Classification in parameters

To determine the sign of the selection gradient, by Theorem 2.1 $(i)$, one needs to figure out

$$\operatorname{sgn}(u_2^* - K_2), \quad \operatorname{sgn}(u_1^* - u_2^*), \quad \operatorname{sgn}(u_3^* - K_3) \quad \text{and} \quad \operatorname{sgn}(u_1^* - u_3^*).$$

In what follows, we address this issue by regarding $d$ and $q$ as bifurcation parameters. Recall the estimate in (2.7). We now restrict ourselves to the case $(d,q) \in \Omega := (0,1] \times (0,\infty)$ and define the following sets:

$$\begin{aligned}\mathcal{R}_1^j &:= \big\{(d,q) \in \Omega : u_1^* < u_3^* < u_2^*,\ u_2^* \sim_j K_2\big\},\\ \mathcal{R}_2^j &:= \big\{(d,q) \in \Omega : u_1^* = u_3^* < u_2^*,\ u_2^* \sim_j K_2\big\},\\ \mathcal{R}_3^j &:= \big\{(d,q) \in \Omega : u_3^* < u_1^* < u_2^*,\ u_2^* \sim_j K_2\big\},\\ \mathcal{R}_4^j &:= \big\{(d,q) \in \Omega : u_3^* < u_1^* = u_2^*,\ u_2^* \sim_j K_2\big\},\\ \mathcal{R}_5^j &:= \big\{(d,q) \in \Omega : u_3^* < u_2^* < u_1^*,\ u_2^* \sim_j K_2\big\},\end{aligned}$$

where the notation

$$\sim_j \ \text{ means } \begin{cases} <, & \text{if } \ j = 1,\\ =, & \text{if } \ j = 2,\\ >, & \text{if } \ j = 3.\end{cases}$$

The main result of this section is as the following, which plays an important role in later analysis.

**Theorem 4.1.** *Assume that* $(H)$ *holds. Then*

$$\mathcal{R}_i^j = \emptyset, \quad \text{for} \quad i = 1, \cdots, 4 \quad \text{and} \quad j = 1, 2,$$

*and*

$$\mathcal{R}_1^1 = \big\{(d,q) : 0 < d \le 1,\ q > q_1(d)\big\}, \quad \mathcal{R}_1^2 = \big\{(d,q) : 0 < d \le 1,\ q = q_1(d)\big\},$$
$$\mathcal{R}_1^3 = \big\{(d,q) : 0 < d \le 1,\ q_2(d) < q < q_1(d)\big\}, \quad \mathcal{R}_2^3 = \big\{(d,q) : 0 < d \le 1,\ q = q_2(d)\big\},$$
$$\mathcal{R}_3^3 = \big\{(d,q) : 0 < d \le 1,\ q_3(d) < q < q_2(d)\big\}, \quad \mathcal{R}_4^3 = \big\{(d,q) : 0 < d \le 1,\ q = q_3(d)\big\},$$
$$\mathcal{R}_5^3 = \big\{(d,q) : 0 < d \le 1,\ q < q_3(d)\big\}.$$

*Note that* $q_i(d)$, $i = 1, 2, 3$ *is, respectively, given in Lemmas 4.2, 4.3 and 4.4 below.*

We include below a characterization of $E_u$. The proof is elementary. It can be derived from the equations (1.2) and the facts $\mathcal{P}(0) \ge 0$, $\mathcal{P}(+\infty) = -\infty$ and $\mathcal{P}''(x) < 0$.

**Lemma 4.1.** *For* $E_u$*, we have*

$$u_i^* = \frac{1}{2}\left[K_i(1-d) + \sqrt{K_i^2(1-d)^2 + 4K_i(d+q)u_1^*}\right], \quad i = 2, 3,$$

*and* $u_1^*$ *is the unique positive root of* $\mathcal{P}(x) = 0$ *where*

$$\mathcal{P}(x) := \frac{d(1-d)}{2}(K_2+K_3) + \frac{d}{2}\sum_{i=2}^{3}\sqrt{K_i^2(1-d)^2 + 4K_i(d+q)x} + [1-2(d+q)]x - \frac{x^2}{K_1}.$$

*Moreover,* $\mathcal{P}'(u_1^*) < 0$.

## 4.1. $\mathrm{sgn}(u_2^* - K_2)$

We first determine $\mathrm{sgn}(u_2^* - K_2)$. See below.

**Lemma 4.2.** *Assume that* $(H)$ *holds. Then for each* $d \in (0, 1]$,

- $(i)$ $\mathrm{sgn}(u_2^* - K_2) = 1$ *if and only if* $q < q_1(d)$;
- $(ii)$ $\mathrm{sgn}(u_2^* - K_2) = -1$ *if and only if* $q > q_1(d)$;

*where* $q_1(d)$ *is the unique positive root of*

$$K_1 = \mathcal{F}_1(d, q; K_2, K_3) := \frac{dK_2^2}{(d+q)^2 \mathcal{G}_1(d, q; K_2, K_3)},$$

*with*

$$\mathcal{G}_1(d, q; K_2, K_3) := K_2(-1 + \frac{1}{d+q}) + \frac{(1-d)}{2}K_3 + \frac{1}{2}\sqrt{K_3^2(1-d)^2 + 4dK_2K_3}.$$

**Proof.** By the second equation of (1.2) and Lemma 4.1,

$$\begin{aligned} u_2^* > K_2 \quad &\Longleftrightarrow \quad u_1^* > \frac{dK_2}{d+q} \quad \Longleftrightarrow \quad \mathcal{P}\Big(\frac{dK_2}{d+q}\Big) > 0, \\ u_2^* < K_2 \quad &\Longleftrightarrow \quad u_1^* < \frac{dK_2}{d+q} \quad \Longleftrightarrow \quad \mathcal{P}\Big(\frac{dK_2}{d+q}\Big) < 0, \end{aligned} \tag{4.1}$$

where

$$\mathcal{P}\Big(\frac{dK_2}{d+q}\Big) = -\frac{1}{K_1}\Big(\frac{dK_2}{d+q}\Big)^2 + d\mathcal{G}_1(d,q;K_2,K_3). \tag{4.2}$$

We next discuss the sign of $\mathcal{P}(\frac{dK_2}{d+q})$ through several claims.

**Claim A.1:** For any $d \in (0,1]$, there exists $\bar{q}_1(d) \in (0,\infty)$ such that

$$\mathcal{G}_1(d,q;K_2,K_3) > 0 \ \text{ if } \ q < \bar{q}_1(d), \qquad \mathcal{G}_1(d,q;K_2,K_3) < 0 \ \text{ if } \ q > \bar{q}_1(d).$$

In particular, if $q \geqslant \bar{q}_1(d)$, $\mathcal{P}(\frac{dK_2}{d+q}) < 0$.

It is easy to see $\frac{\partial}{\partial q}\mathcal{G}_1(d,q;K_2,K_3) < 0$ and

$$\mathcal{G}_1(d,0;K_2,K_3) = K_2(\frac{1}{d}-1) + \frac{(1-d)}{2}K_3 + \frac{1}{2}\sqrt{K_3^2(1-d)^2 + 4dK_2K_3} > 0.$$

So Claim A.1 follows if one can prove $\mathcal{G}_1(d,\infty;K_2,K_3) < 0$. Indeed,

$$\mathcal{G}_1(d,\infty;K_2,K_3) = -K_2 + \frac{(1-d)}{2}K_3 + \frac{1}{2}\sqrt{K_3^2(1-d)^2 + 4dK_2K_3}.$$

By computations, for $d \in (0,1]$,

$$\frac{\partial}{\partial d}\mathcal{G}_1(d,\infty;K_2,K_3) = \frac{K_3}{2}\Big(-1 + \frac{2K_2 - K_3(1-d)}{\sqrt{K_3^2(1-d)^2 + 4dK_2K_3}}\Big) > 0,$$

so

$$\mathcal{G}_1(d,\infty;K_2,K_3) \le \mathcal{G}_1(1,\infty;K_2,K_3) = -K_2 + \sqrt{K_2K_3} < 0,$$

as desired.

Based on Claim A.1, we only need to consider the case $q \in (0,\bar{q}_1(d))$, for which,

$$\mathcal{G}_1(d,q;K_2,K_3) > 0.$$

Moreover, it is easy to check

$$\mathcal{P}\Big(\frac{dK_2}{d+q}\Big) > \ (\text{or } \ <) \ 0 \iff K_1 > \ (\text{or } \ <) \ \mathcal{F}_1(d,q;K_2,K_3).$$

To compare $K_1$ and $\mathcal{F}_1(d,q;K_2,K_3)$, we need the following two claims.

**Claim A.2:** $K_2 < \mathcal{F}_1(d,0;K_2,K_3) < K_1$ and $\lim_{q\nearrow\bar{q}_1(d)}\mathcal{F}_1(d,q;K_2,K_3) = +\infty$.

The limit in the above claim is trivial. By direct computations,

$$\mathcal{F}_1(d,0;K_2,K_3) = \frac{K_2^2}{K_3\mathcal{S}_1(d,\alpha)},$$

where

$$\mathcal{S}_1(d,\alpha) := (1-d)\alpha + \frac{d(1-d)}{2} + \frac{d}{2}\sqrt{(1-d)^2 + 4d\alpha}, \quad \alpha := \frac{K_2}{K_3} \in (1,2).$$

Since $-2d+1-2\alpha < 0$ and

$$\begin{aligned}&(-2d+1-2\alpha)^2[(1-d)^2+4\alpha d] - [2d^2+3(2\alpha-1)d+1]^2\\ &= 4\alpha[2\alpha(2\alpha-1)(\alpha-1)d+\alpha-1] > 0,\end{aligned}$$

one sees

$$\frac{\partial}{\partial d}\mathcal{S}_1(d,\alpha) = \frac{[2d^2+3(2\alpha-1)d+1]+(-2d+1-2\alpha)\sqrt{(1-d)^2+4\alpha d}}{2\sqrt{(1-d)^2+4\alpha d}} < 0,$$

which implies

$$\frac{K_2^2}{K_3\mathcal{S}_1(d,\alpha)} > \frac{K_2^2}{K_3\mathcal{S}_1(0,\alpha)} = K_2 \quad \text{and} \quad \frac{K_2^2}{K_3\mathcal{S}_1(d,\alpha)} \le \frac{K_2^2}{K_3\mathcal{S}_1(1,\alpha)} = \frac{K_2^2}{\sqrt{K_2K_3}} < K_1,$$

where the last inequality used the definition of $\delta_1$ in $(H)$. Hence, Claim A.2 is finished.

**Claim A.3:** For any $d \in (0,1]$, there exists $\tilde{q}_1(d) \in (0, \bar{q}_1(d))$ such that

$$\frac{\partial}{\partial q}\mathcal{F}_1(d,q;K_2,K_3) < 0 \quad \text{for} \quad q \in (0,\tilde{q}_1(d)),$$
$$\frac{\partial}{\partial q}\mathcal{F}_1(d,q;K_2,K_3) > 0 \quad \text{for} \quad q \in (\tilde{q}_1(d),\bar{q}_1(d)).$$

Indeed, $\tilde{q}_1(d) = -d + \frac{2K_2-(1-d)K_3+\sqrt{K_3^2(1-d)^2+4dK_2K_3}}{4(K_2-K_3)}$.

By computations,

$$\frac{\partial}{\partial q}\mathcal{F}_1(d,q;K_2,K_3) = -\frac{dK_2^2\mathcal{H}_1(d,q;K_2,K_3)}{(d+q)^3\mathcal{G}_1^2(d,q;K_2,K_3)},$$

where

$$\begin{aligned}\mathcal{H}_1(d,q;K_2,K_3) :=& 2\mathcal{G}_1(d,q;K_2,K_3) + (d+q)\frac{\partial}{\partial q}\mathcal{G}_1(d,q;K_2,K_3)\\ =& \frac{K_2}{(d+q)} - 2K_2 + (1-d)K_3 + \sqrt{K_3^2(1-d)^2+4dK_2K_3}.\end{aligned}$$

We turn to check the sign of $\mathcal{H}_1(d,q;K_2,K_3)$. Clearly, $\frac{\partial}{\partial q}\mathcal{H}_1(d,q;K_2,K_3) < 0$.

We first prove $\mathcal{H}_1(d,0;K_2,K_3) > 0$. Indeed, $\mathcal{H}_1(d,0;K_2,K_3) = K_3\mathcal{S}_2(d,\alpha)$, where

$$\mathcal{S}_2(d,\alpha) := (\frac{1}{d}-2)\alpha + (1-d) + \sqrt{(1-d)^2+4d\alpha}.$$

Recall $\alpha := \frac{K_2}{K_3} \in (1,2)$. Since

$$\mathcal{S}_2(d,\alpha) \ge \tilde{\mathcal{S}}_2(d,\alpha) := -\alpha + (1-d) + \sqrt{(1-d)^2+4d\alpha},$$

and since

$$\frac{\partial}{\partial \alpha}\tilde{\mathcal{S}}_2(d,\alpha) = -1 + \frac{2d}{\sqrt{(1-d)^2+4\alpha d}} < 0,$$

$\tilde{\mathcal{S}}_2(d,\alpha) > \tilde{\mathcal{S}}_2(d,2) = -(1+d) + \sqrt{(1-d)^2+8d} > 0$, and so $\mathcal{H}_1(d,0;K_2,K_3) > 0$.

We then prove $\mathcal{H}_1(d,\infty;K_2,K_3) < 0$. In fact, $\mathcal{H}_1(d,\infty;K_2,K_3) = K_3\mathcal{S}_3(d,\alpha)$, where

$$\mathcal{S}_3(d,\alpha) := -2\alpha + (1-d) + \sqrt{(1-d)^2+4d\alpha}.$$

Since

$$\frac{\partial}{\partial \alpha}\mathcal{S}_3(d,\alpha) = 2\Big(-1 + \frac{d}{\sqrt{(1-d)^2+4\alpha d}}\Big) < 2\Big(-1 + \frac{d}{1+d}\Big) < 0,$$

$\mathcal{S}_3(d,\alpha) < \mathcal{S}_3(d,1) = 0$. Hence, $\mathcal{H}_1(d,\infty;K_2,K_3) < 0$.

The above analysis guarantees that for any $d \in (0,1]$, there is a unique $\tilde{q}_1(d) \in (0,\infty)$ such that

$$\mathcal{H}_1(d,q;K_2,K_3) > 0 \text{ if } q \in (0,\tilde{q}_1(d)), \quad \mathcal{H}_1(d,q;K_2,K_3) < 0 \text{ if } q \in (\tilde{q}_1(d),\infty).$$

To finish Claim A.3, it suffices to show $\tilde{q}_1(d) \in (0,\bar{q}_1(d))$, which is implied by Claim A.2.

Based on Claims A.2 and A.3, one can conclude (see Fig. 2 below for an illustration) that for any $d \in (0,1]$, there exists $q_1(d) \in (0,\bar{q}_1(d))$ such that

$$K_1 > \mathcal{F}_1(d,q;K_2,K_3) \text{ if } q \in (0,q_1(d)), \quad K_1 < \mathcal{F}_1(d,q;K_2,K_3) \text{ if } q \in (q_1(d),\bar{q}_1(d)).$$

This, together with (4.2), implies

$$\mathcal{P}\Big(\frac{dK_2}{d+q}\Big) > 0 \text{ if } q \in (0,q_1(d)), \quad \mathcal{P}\Big(\frac{dK_2}{d+q}\Big) < 0 \text{ if } q \in (q_1(d),\bar{q}_1(d)).$$

Finally, combining Claim A.1 and (4.1), one gets the desired result. □

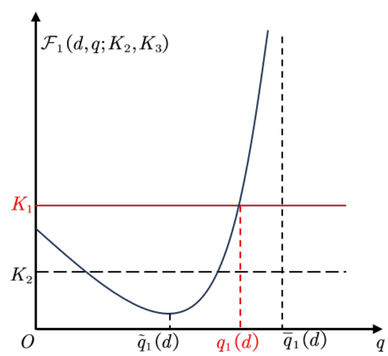



**Figure 2.** Illustration of the existence of $q_1(d)$.

## 4.2. $\mathrm{sgn}(u_1^* - u_2^*)$ and $\mathrm{sgn}(u_1^* - u_3^*)$

We now discuss $\mathrm{sgn}(u_1^* - u_3^*)$ and $\mathrm{sgn}(u_1^* - u_2^*)$, see the following Lemmas 4.3 and 4.4.

**Lemma 4.3.** *Assume that $(H)$ holds. Then for each $d \in (0,1]$,*

*(i) $\mathrm{sgn}(u_1^* - u_3^*) = 1$ if and only if $q < q_2(d)$;*

*(ii) $\mathrm{sgn}(u_1^* - u_3^*) = -1$ if and only if $q > q_2(d)$;*

*where $q_2(d)$ is the unique positive root of*

$$K_1 = \mathcal{F}_2(d,q;K_2,K_3) := \frac{K_3^2(1+q)^2}{\mathcal{G}_2(d,q;K_2,K_3)},$$

*with*

$$\begin{aligned}\mathcal{G}_2(d,q;K_2,K_3) :=& K_3(1+q)[1-2(d+q)] + \frac{dK_3}{2}(1+d+2q) + \frac{d(1-d)}{2}(K_2+K_3)\\ &+ \frac{d}{2}\sqrt{K_2^2(1-d)^2 + 4K_2K_3(d+q)(1+q)}.\end{aligned}$$

**Proof.** By the third equation of (1.2) and Lemma 4.1,

$$u_1^* > u_3^* \iff u_1^* > K_3(1+q) \iff \mathcal{P}(K_3(1+q)) > 0,$$
$$u_1^* < u_3^* \iff u_1^* < K_3(1+q) \iff \mathcal{P}(K_3(1+q)) < 0,$$

where

$$\mathcal{P}(K_3(1+q)) = -\frac{K_3^2(1+q)^2}{K_1} + \mathcal{G}_2(d,q;K_2,K_3). \tag{4.3}$$

We next discuss the sign of $\mathcal{P}(K_3(1+q))$ through several claims.

**Claim B.1:** For any $d \in (0,1]$, there exists $\bar{q}_2(d) \in (0,\infty)$ such that

$$\mathcal{G}_2(d,q;K_2,K_3) > 0 \ \text{ if } \ q < \bar{q}_2(d), \qquad \mathcal{G}_2(d,q;K_2,K_3) < 0 \ \text{ if } \ q > \bar{q}_2(d).$$

In particular, if $q \geqslant \bar{q}_2(d)$, $\mathcal{P}(K_3(1+q)) < 0$.

Clearly, $\mathcal{G}_2(d,q;K_2,K_3) = K_2\mathcal{T}_1(d,q,\beta)$, where $\beta := \frac{K_3}{K_2}$ and

$$\mathcal{T}_1(d,q,\beta) := (1+q)(1-d-2q)\beta + \frac{d(1-d)}{2} + \frac{d}{2}\sqrt{(1-d)^2 + 4(d+q)(1+q)\beta}.$$

This claim follows directly from the following facts:

$$\mathcal{T}_1(d,0,\beta) = (1-d)\beta + \frac{d(1-d)}{2} + \frac{d}{2}\sqrt{(1-d)^2+4\beta d} > 0, \qquad \mathcal{T}_1(d,\infty,\beta) < 0$$

and

$$\frac{\partial}{\partial q}\mathcal{T}_1(d,q,\beta) = -2q\beta + (2q+d+1)\beta\Big(-1 + \frac{d}{\sqrt{(1-d)^2+4(d+q)(1+q)\beta}}\Big) < 0.$$

Based on Claim B.1, we only need to consider $q \in (0,\bar{q}_2(d))$, for which, $\mathcal{G}_2(d,q;K_2,K_3) > 0$. Moreover,

$$\mathcal{P}(K_3(1+q)) > \ (\text{or } \ <) \ 0 \iff K_1 > \ (\text{or } \ <) \ \mathcal{F}_2(d,q;K_2,K_3).$$

To compare $K_1$ and $\mathcal{F}_2(d,q;K_2,K_3)$, we need the following claim.

**Claim B.2:** For $q \in (0,\bar{q}_2(d))$, it holds that

$$\frac{\partial}{\partial q}\mathcal{F}_2(d,q;K_2,K_3) > 0, \quad \mathcal{F}_2(d,0;K_2,K_3) < K_2, \quad \lim_{q\nearrow\bar{q}_2}\mathcal{F}_2(d,q;K_2,K_3) = +\infty.$$

By Claim B.1, it is easy to see

$$\begin{aligned}&\frac{\partial}{\partial q}\mathcal{F}_2(d,q;K_2,K_3)\\ =&\frac{K_3^2(1+q)}{\mathcal{G}_2^2(d,q;K_2,K_3)}\Big[2\mathcal{G}_2(d,q;K_2,K_3) - (1+q)\frac{\partial}{\partial q}\mathcal{G}_2(d,q;K_2,K_3)\Big]\\ >&0.\end{aligned}$$

The limit in the above claim is trivial. Moreover, by direct computations,

$$\mathcal{F}_2(d,0;K_2,K_3) - K_2 = \frac{K_3(K_3-K_2) + K_2^2\mathcal{T}_2(d,\beta)}{\mathcal{G}_2(d,0;K_2,K_3)},$$

where

$$\mathcal{T}_2(d,\beta) := d\beta - \frac{d(1-d)}{2} - \frac{d}{2}\sqrt{(1-d)^2 + 4d\beta}.$$

Since

$$\frac{\partial \mathcal{T}_2}{\partial \beta} = d\Big(1 - \frac{d}{\sqrt{(1-d)^2 + 4d\beta}}\Big) > 0,$$

we have $\mathcal{T}_2(d, \frac{K_3}{K_2}) < \mathcal{T}_2(d,1) = 0$ and so $\mathcal{F}_2(d,0;K_2,K_3) - K_2 < 0$.

Based on Claim B.2, one can conclude that for each $d \in (0,1]$, there exists $q_2(d) \in (0, \bar{q}_2(d))$ such that (see Fig. 3 below for an illustration)

$$K_1 > \mathcal{F}_2(d,q;K_2,K_3) \text{ if } q \in (0, q_2(d)),\ \ K_1 < \mathcal{F}_2(d,q;K_2,K_3) \text{ if } q \in (q_2(d), \bar{q}_2(d)).$$

Combining this with (4.3), one sees

$$\mathcal{P}(K_3(1+q)) > 0 \text{ if } q \in (0, q_2(d)), \quad \mathcal{P}(K_3(1+q)) < 0 \text{ if } q \in (q_2(d), \bar{q}_2(d)),$$

which, together with Claim B.1, implies the desired result. $\square$

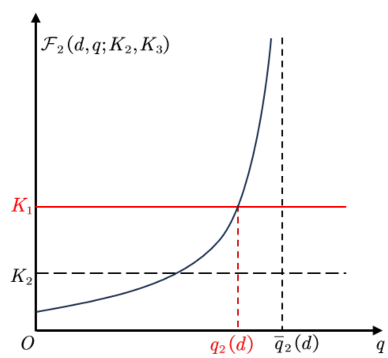



**Figure 3.** Illustration of the existence of $q_2(d)$.

**Lemma 4.4.** *Assume that* $(H)$ *holds. Then for each* $d \in (0,1]$,

(*i*) $\operatorname{sgn}(u_1^* - u_2^*) = 1$ *if and only if* $q < q_3(d)$;

(*ii*) $\operatorname{sgn}(u_1^* - u_2^*) = -1$ *if and only if* $q > q_3(d)$;

*where* $q_3(d)$ *is the unique positive root of*

$$K_1 = \mathcal{F}_3(d,q;K_2,K_3) := \frac{K_2^2(1+q)^2}{\mathcal{G}_3(d,q;K_2,K_3)},$$

*with*

$$\begin{aligned}\mathcal{G}_3(d,q;K_2,K_3) :=& K_2(1+q)[1-2(d+q)] + \frac{dK_2}{2}(1+d+2q) + \frac{d(1-d)}{2}(K_2+K_3)\\ &+ \frac{d}{2}\sqrt{K_3^2(1-d)^2 + 4K_2K_3(d+q)(1+q)}.\end{aligned}$$

**Proof.** By an easy inspection, one finds that $\mathcal{F}_2(d,q;K_2,K_3)$ becomes $\mathcal{F}_3(d,q;K_2,K_3)$ if interchanging the role of $K_2$ and $K_3$. So this lemma can be proved by the same argument as in Lemma 4.3. In particular, one can establish two similar results to Claims B.1 and B.2. We omit the details here. $\square$

## 4.3. Proof of Theorem 4.1

We now are in a position to prove Theorem 4.1.

**Proof.** [Proof of Theorem 4.1] In view of Lemmas 4.2, 4.3 and 4.4, it suffices to show

$$q_1(d) > q_2(d) > q_3(d) \quad \text{for each} \quad d \in (0, 1].$$

We first prove $q_2(d) > q_3(d)$ for any given $d \in (0, 1]$. Recall that $q_i(d)$, $i = 2, 3$, satisfies

$$K_1 = \mathcal{F}_i(d, q_i(d); K_2, K_3).$$

From the proof of Lemmas 4.3 and 4.4, one has

$$\frac{\partial}{\partial q}\mathcal{F}_i(d, q; K_2, K_3) > 0, \quad i = 2, 3, \tag{4.4}$$

and

$$\mathcal{F}_2(d, 0; K_2, K_3) < K_2 < \mathcal{F}_3(d, 0; K_2, K_3). \tag{4.5}$$

Moreover, we should have $\bar{q}_3(d) \leqslant \bar{q}_2(d)$ and

$$\mathcal{F}_2(d, q; K_2, K_3) < \mathcal{F}_3(d, q; K_2, K_3) \quad \text{for any} \quad q \in (0, \bar{q}_3(d)). \tag{4.6}$$

Indeed, if $\bar{q}_3(d) > \bar{q}_2(d)$, then $\mathcal{F}_i(d, q_i(d); K_2, K_3)$, $i = 2, 3$, as a function of $q$, should intersect somewhere, say at $q = q_0 \in (0, \bar{q}_2(d))$. If choosing $q = q_0$ and $K_1 = \mathcal{F}_2(d, q_0; K_2, K_3)$, it follows from Lemmas 4.3 and 4.4 that $u_1^* = u_2^* = u_3^*$, contradicting the estimate (2.7). Following the same spirit, one can prove (4.6). The desired result would then follow from (4.4), (4.5) and (4.6). See also Fig. 4 ($a$) below for an illustration.

We now verify $q_1(d) > q_2(d)$ for any given $d \in (0, 1]$. By direct computations, the two curves $K_1 = \mathcal{F}_i(d, q; K_2, K_3)$, $i = 1, 2$ only intersect at the point $(q_c, K_1^c)$, where

$$q_c = q_c(d; K_2, K_3) := \frac{1}{2K_3}\left[-(1+d)K_3 + \sqrt{K_3^2(1-d)^2 + 4dK_2K_3}\right],$$

and

$$K_1^c := \mathcal{F}_1(d, q_c; K_2, K_3).$$

Since $-K_3(1-d) + 2K_2 > 0$ and

$$[-K_3(1-d) + 2K_2]^2 - [K_3^2(1-d)^2 + 4dK_2K_3] = 4K_2(K_2 - K_3) > 0,$$

we have

$$\frac{\partial q_c}{\partial d} = \frac{1}{2}\Big[-1 + \frac{-K_3(1-d) + 2K_2}{\sqrt{K_3^2(1-d)^2 + 4dK_2K_3}}\Big] > 0,$$

which implies

$$q_c(d; K_2, K_3) \leq q_c(1; K_2, K_3) = \frac{\sqrt{K_2K_3} - K_3}{K_3}.$$

Recall $\tilde{q}_1(d)$ given in Claim A.3, which satisfies

$$\tilde{q}_1(d) = -d + \frac{2K_2 - (1-d)K_3 + \sqrt{K_3^2(1-d)^2 + 4dK_2K_3}}{4(K_2 - K_3)} > \frac{2K_3 - K_2}{2(K_2 - K_3)}.$$

By the definition of $\delta_1$ in $(H)$,

$$q_c(d) \leq \frac{\sqrt{K_2K_3} - K_3}{K_3} < \frac{2K_3 - K_2}{2(K_2 - K_3)} < \tilde{q}_1(d),$$

which, together with Claims A.2 and A.3 in Lemma 4.2 as well as Claim B.2 in Lemma 4.3, implies

$$\mathcal{F}_2(d, q; K_2, K_3) > \mathcal{F}_1(d, q; K_2, K_3), \quad \text{if} \quad q > q_c(d).$$

Since $q_i(d)$ satisfies $K_1 = \mathcal{F}_i(d, q; K_2, K_3)$, $i = 1, 2$, the desired result follows. See also Fig. 4 $(b)$ below for an illustration. □

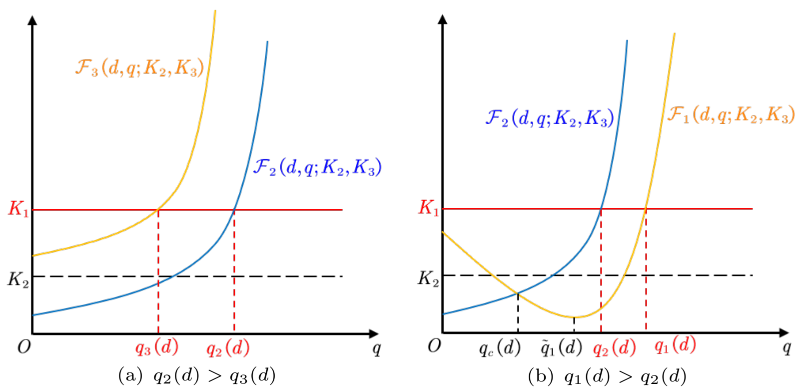



**Figure 4.** Illustrations of the proof of Theorem 4.1.

## 5. Proof of main results

This section is devoted to the proof of the main results.

We first prove Theorem 1.2.

**Proof.** [Proof of Theorem 1.2] We only prove statement $(i)$ since $(ii)$ can be treated similarly.

For any $(d, q) \in \mathcal{R}_5^3 \cup \mathcal{R}_4^3$, we claim that $\Gamma_1(d, D, q) \neq 0$ for each $D \neq d$. Indeed, if not, then by [13, Proposition 6],

$$D = \frac{(-2q + 1 - \frac{u_1^*}{K_1})(1 - \frac{u_2^*}{K_2})(1 - \frac{u_3^*}{K_3})}{d \sum_{i=1}^{3}(1 - \frac{u_i^*}{K_i})},$$

which, in view of [13, Corollary 4] and the definition of $\mathcal{R}_5^3 \cup \mathcal{R}_4^3$, implies $D \leq 0$, a contradiction.

Moreover, by the definition of $\mathcal{R}_5^3 \cup \mathcal{R}_4^3$ and Theorem 2.1 $(i)$, $\frac{\partial \Gamma_1}{\partial D}\big|_{D=d} > 0$. This, together with the above claim, implies the desired result. □

We now prove Theorem 1.3.

**Proof.** [Proof of Theorem 1.3] In view of (1.6) and Theorem 2.1, for given $K_i > 0$ $(i = 1, 2, 3)$ and $q > 0$, the strategy $d = d_*(q)$ is a local ESS if and only if $(d, q)$

satisfies

$$\begin{cases} \mathcal{A}_1(d,q) := u_2^*(1-\frac{u_2^*}{K_2})(u_2^*-u_1^*) + u_3^*(1-\frac{u_3^*}{K_3})(u_3^*-u_1^*) = 0, \\ u_1^* - u_3^* > 0. \end{cases} \tag{5.1}$$

We first prove statement $(i)$.

For each $d \in (0,1]$, by the definition of $\mathcal{R}_3^3$ and $q_3(d)$ and $q_2(d)$,

$$\mathcal{A}_1(d, q_3(d)) > 0 \quad \text{and} \quad \mathcal{A}_1(d, q_2(d)) < 0.$$

By the continuity, there exists $q_* := q_*(d)$ such that $\mathcal{A}_1(d, q_*) = 0$.

Then, we prove statement $(ii)$ by the perturbation argument.

Recall $\lim_{K_3 \nearrow K_2} \mathcal{A}_1(d,q) = 2\mathcal{B}(d,q)$, where $\mathcal{B}_2(d,q)$ is defined in (3.3). By Lemma 3.1,

$$\lim_{K_3 \nearrow K_2} q_*(d) = q_{**} = \frac{K_1 - K_2}{2K_1 + K_2},$$

and

$$\begin{aligned} &\lim_{K_3 \nearrow K_2} \partial_q \mathcal{A}_1(d, q_*(d)) \\ &= \lim_{K_3 \nearrow K_2} \left( \sum_{i=2}^{3} u_2^*(1 - \frac{u_i^*}{K_i})(\partial_q u_i^* - \partial_q u_1^*) + \partial_q u_i^*(1 - \frac{2u_i^*}{K_i})(u_i^* - u_1^*) \right) \Bigg|_{(d, q_*(d))} \\ &= 2\partial_q \mathcal{B}(d, q_{**}) < 2\mathcal{B}_*(K_1, K_2) < 0. \end{aligned}$$

Hence, there exists $\delta_2 = \delta_2(K_1, K_2) > 0$ such that for $0 < K_2 - K_3 < \delta_2$,

$$\partial_q \mathcal{A}_1(d, q_*(d)) < \mathcal{B}_*(K_1, K_2) < 0, \quad \text{for all} \quad d \in (0,1].$$

In summary, for $K_3$ satisfying $0 < K_2 - K_3 < \delta_0 := \min\{\delta_1, \delta_2\}$, it follows from the implicit function theorem that $q_*(d)$ above is unique for each $d \in (0,1]$ and thus is continuous in $d \in (0,1]$. Moreover, for such $(d, q_*(d))$, the inequality in (5.1) holds by the definition of $\mathcal{R}_3^3$. The desired result would then follow from the mean value theorem. □

# 6. Numerical simulation

In this section, we mainly study system (1.1) via the numerical approach. Throughout this section, let us fix

$$K_1 = 3 \quad \text{and} \quad K_2 = 2.$$

Then, by computations, $\delta_1(K_1, K_2) = 0.7808$. To fulfill the assumption $(H)$, we choose $K_3 = 1.75$. By Theorem 1.2 and Corollary 1.1,

$$q_1^* = 8.0063, \quad q_2^* = 0.1880, \quad q_3^* = 0.1008.$$

Note that $Q_1$ defined in Theorem 1.1 $(i)$ is 0.0678. Moreover, by Theorem 1.3 and the equation (5.1), one can compute

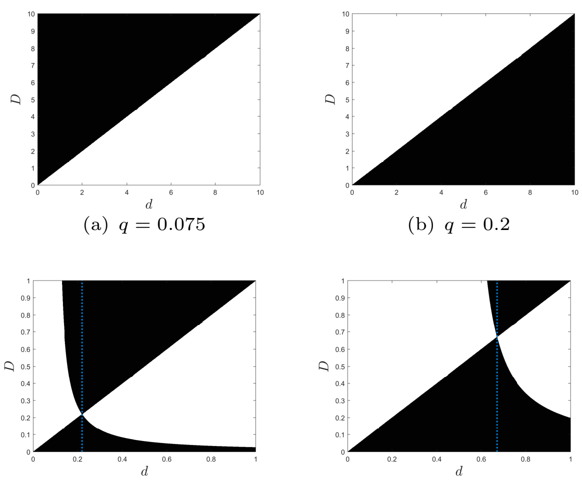
$$q_*^1 = 0.1429 \quad \text{and} \quad q_*^2 = 0.1533.$$

In what follows, we numerically compute the pairwise invasibility plots (PIPs), which reflects the sign of the invasion fitness function $\Gamma_1$ as the dispersal strategies $d$ and $D$ vary.

For $q = 0.075 \in (Q_1, q_3^*)$, Fig. 5 $(a)$ below shows that the slower diffuser wins the competition, while for $q = 0.2 \in (q_2^*, q_1^*)$, as shown in Fig. 5 $(b)$ below, the faster diffuser has more competitive advantages. There simulation results are in line with those theoretical ones in Corollary 1.1. Moreover, our choice of $q = 0.075 \in (Q_1, q_3^*)$, to some extent, indicates that $Q_1$ obtained by Jiang et al. [13] (see Theorem 1.1) is not the optimal one to guarantee the winner of slower diffuser.

In Fig. 5$(c)$ and $(d)$ below, we select, respectively, $q = 0.145$ and $q = 0.15$, both lying in $(q_*^1, q_*^2) = (0.1429, 0.1533)$, and there appears an ESS at $d = 0.2202$ and $d = 0.6702$, respectively. This consists with the theoretical finding Theorem 1.3.

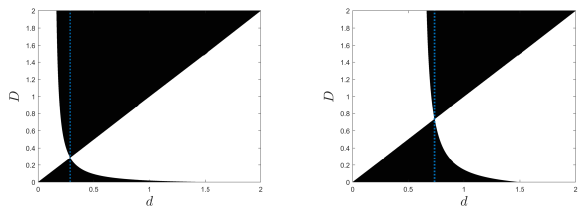
Both the above theoretical and numerical results are obtained under the assumption $(H)$. To further understand system (1.1) especially when $(H)$ fails, we choose $K_3 = 1$. Then it seems that ESS could also exist, see the following Fig. 6, where for $q = 0.25$ and $q = 0.35$, there exists an ESS at $d = 0.2877$ and $d = 0.7344$, respectively. We note here that this is a numerical observation and mathematically it deserves further investigation.




(a) $q = 0.075$ (b) $q = 0.2$

(c) $q = 0.145$ (d) $q = 0.15$

**Figure 5.** PIPs when the assumption $(H)$ holds. Note that $E_u$ is locally asymptotically stable (resp. unstable) when $d$ and $D$ lie in the black (resp. white) regions.




(a) $q = 0.25$ (b) $q = 0.35$

**Figure 6.** PIPs when the assumption $(H)$ fails. Note that $E_u$ is locally asymptotically stable (resp. unstable) when $d$ and $D$ lie in the black (resp. white) regions.

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