带下游损失的分支河流网络中两类 Lotka–Volterra 竞争斑块模型的动力学

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摘要： 本文研究带下游损失的分支河流网络中两类 Lotka–Volterra 竞争斑块模型的动力学。首先分析系统的局部动力学，建立边界平衡点的稳定性判据。在此基础上，严格证明了正平衡点的不存在性，从而排除了两物种共存的可能性。结合单调动力系统理论，完整刻画了系统的全局渐近行为：当两物种具有相同的扩散速率时，对流速率较慢的物种胜出；当对流速率满足一定序关系时，扩散速率较快的物种获得竞争优势。

关键词： 应用数学；Lotka–Volterra 竞争；斑块模型；分支网络；下游损失；全局稳定性

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Dynamics of two classes of Lotka–Volterra competitive patch models in branched river networks with downstream loss

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Abstract: This paper investigates two classes of Lotka–Volterra competition patch models in branched river networks with downstream loss. We first analyze the local dynamics of the system and establish stability criteria for boundary equilibria. Based on these results, we provide a rigorous proof of the nonexistence of positive equilibria, thereby excluding the possibility of species coexistence. Combining these with the theory of monotone dynamical systems, we completely characterize the global asymptotic behavior: when the two species have the same diffusion rate, the species with the slower advection rate prevails; when advection rates satisfy a certain ordering, the species with the faster diffusion rate gains the competitive advantage.

Key words: Applied mathematics; Lotka–Volterra competition; Patch model; Branched network; Downstream loss; Global stability

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0 Introduction

Aquatic organisms inhabiting rivers, streams, and other flowing water bodies are subject not only to random dispersal but also to directed advective drift. More importantly, river systems often exhibit complex network structures—upstream bifurcations forming multiple tributaries and downstream confluences. Such spatial structures profoundly influence species survival, dispersal, and competition.

In recent years, reaction-diffusion-advection models have been extensively studied in river ecology. For instance, the pioneering work of Hastings[1] revealed a fundamental principle in spatially heterogeneous environments: for both continuous and discrete models, a mutant species can successfully invade if and only if it possesses a slower dispersal rate. Subsequently, Dockery et al.[2] further proved that in continuous models, the slower disperser not only invades but also excludes its faster counterpart. Analogous results for discrete models can be found in Chen et al.[3].

Building on these foundations, extensive research has been conducted on continuous reaction-diffusion-advection competition models [4, 5, 6, 7]. For discrete models, the two-patch case has been thoroughly investigated [8, 9, 10], while the influence of different network topologies in three-patch models has been carefully examined [11, 12, 13, 14]. Recent progress for the general n-patch case can be found in [15, 16, 17, 18].

However, most existing studies assume simple linear river structures (one-dimensional chains), with relatively few investigations into branched networks. Jiang et al.[12] proposed three types of competition patch models (distributary, confluent, and linear), but subsequent studies of these models have primarily focused on closed environments (without downstream loss) [12, 13, 14]. In reality, river systems often feature downstream loss (e.g., flow into the ocean). This motivates our study of three-patch competition models in open environments with two branches.

Our research is also inspired by the following spatial continuous competition model arising from river ecology [19, 20, 21], which describes the dynamics of two competing species in a river:

$$\begin{cases} u_t = d_1 u_{xx} - q_1 u_x + u[r - u - v], & 0 < x < L,\ t > 0, \\ v_t = d_2 v_{xx} - q_2 v_x + v[r - u - v], & 0 < x < L,\ t > 0, \\ d_1 u_x(0,t) - q_1 u(0,t) = d_2 v_x(0,t) - q_2 v(0,t) = 0, & t > 0, \\ d_1 u_x(L,t) - q_1 u(L,t) = -\beta q_1 u(L,t), & t > 0, \\ d_2 v_x(L,t) - q_2 v(L,t) = -\beta q_2 v(L,t), & t > 0, \\ u(x,0) = u_0(x) \geq, \not\equiv 0, \quad v(x,0) = v_0(x) \geq, \not\equiv 0, & 0 < x < L, \end{cases} \tag{1}$$

where $u(x,t)$ and $v(x,t)$ denote the densities of two competing species, $d_1, d_2 > 0$ are the

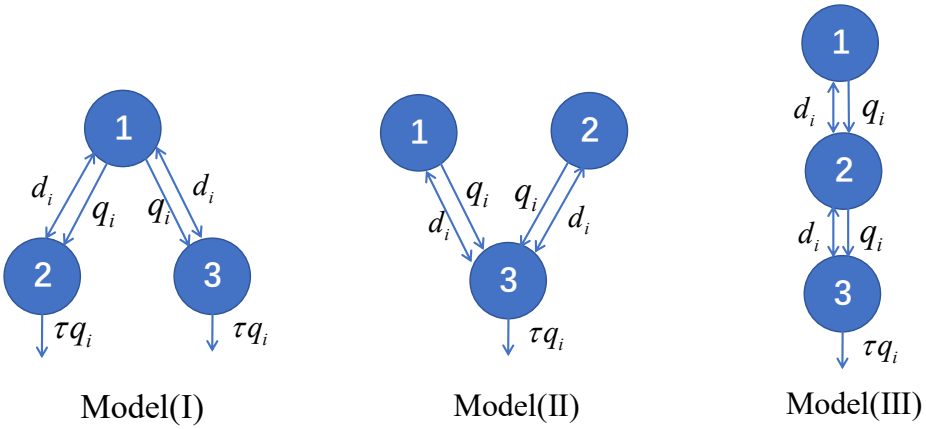


图 1: Three river network modules. Here d_i $(i = 1, 2)$ are the random dispersal rates of the two species and q_i $(i = 1, 2)$ are the drift rates of the two species. The parameter $\tau \geq 0$ measures the loss rate of individuals relative to flow at the downstream end.

random dispersal rates, $q_1, q_2 > 0$ are the directed drift rates, $r > 0$ is the intrinsic growth rate, and $\beta \geq 0$ represents the loss rate at the downstream end. For spatially homogeneous environments, studies [22, 23, 24] showed that to win the competition, a species should select a faster random dispersal rate to compensate for the net loss induced by directed movement. For spatially heterogeneous environments, the dynamics of model (1) are more complex, and multiple evolutionarily stable strategies may exist [25, 26].

We consider three river network modules as illustrated in Fig. 1 and the corresponding competition patch models are

$$\begin{cases} \dfrac{du_i}{dt} = \displaystyle\sum_{j=1}^{3} \left(d_1 D_{ij}^{(k)} + q_1 Q_{ij}^{(k)}\right) u_j + u_i(r_i - u_i - v_i), \quad i,k = 1,2,3, \\ \dfrac{dv_i}{dt} = \displaystyle\sum_{j=1}^{3} \left(d_2 D_{ij}^{(k)} + q_2 Q_{ij}^{(k)}\right) v_j + v_i(r_i - u_i - v_i), \quad i,k = 1,2,3, \\ u(0) = u_0 \geq \mathbf{0}, \not\equiv \mathbf{0}, \quad v(0) = v_0 \geq \mathbf{0}, \not\equiv \mathbf{0}, \end{cases} \tag{2}$$

for each $i = 1, 2, 3$, u_i and v_i denote the population densities of the two species in patch i, respectively. $r_i > 0$ represents the intrinsic growth rate in patch i. $d_1, d_2 > 0$ are the random dispersal rates of the two species and $q_1, q_2 > 0$ are the drift rates.

- Model (I) (distributary structure): a distributary stream with two branches at the down-

stream end.

$$k=1: \quad (D_{ij}^{(1)})=\begin{bmatrix}-2 & 1 & 1\\ 1 & -1 & 0\\ 1 & 0 & -1\end{bmatrix}, \qquad (Q_{ij}^{(1)})=\begin{bmatrix}-2 & 0 & 0\\ 1 & -\tau & 0\\ 1 & 0 & -\tau\end{bmatrix}. \tag{3}$$

- Model (II) (confluent structure): a tributary stream with two branches at the upstream end.

$$k=2: \qquad (D_{ij}^{(2)})=\begin{bmatrix}-1 & 0 & 1\\ 0 & -1 & 1\\ 1 & 1 & -2\end{bmatrix}, \qquad (Q_{ij}^{(2)})=\begin{bmatrix}-1 & 0 & 0\\ 0 & -1 & 0\\ 1 & 1 & -\tau\end{bmatrix}. \tag{4}$$

- Model (III) (linear structure): a straight stream.

$$k=3: \qquad (D_{ij}^{(3)})=\begin{bmatrix}-1 & 1 & 0\\ 1 & -2 & 1\\ 0 & 1 & -1\end{bmatrix}, \qquad (Q_{ij}^{(3)})=\begin{bmatrix}-1 & 0 & 0\\ 1 & -1 & 0\\ 0 & 1 & -\tau\end{bmatrix}. \tag{5}$$

Since Model (III) can be viewed as a special case of the n-patch linear structure, which has been studied in Li et al.[18], this paper focuses on the local and global dynamics of Models (I) and (II).

The remainder of this paper is organized as follows. In Section 1, we present some preliminary results. Section 2 is devoted to the local dynamics of boundary equilibria for system (2). In Section 3, we establish the nonexistence of positive equilibria. Section 4 investigates the global dynamics of system (2). Finally, numerical simulations are presented in Section 5, followed by conclusions and discussion in Section 6.

1 Some preliminaries

Now we give some preliminaries which are useful in the following sections. Let $\mathbf{x}=(x_1,x_2,\ldots,x_n)^T\in\mathbb{R}^n$ be a real vector. We write $\mathbf{x}\gg\mathbf{0}$ (or $\mathbf{x}\geq\mathbf{0}$) if $x_i>0$ (or $x_i\geq 0$) for all $1\leq i\leq n$, and $\mathbf{x}>\mathbf{0}$ if $\mathbf{x}\geq\mathbf{0}$ and $\mathbf{x}\neq\mathbf{0}$.

For an $n\times n$ real matrix $A=(a_{ij})$, let $\sigma(A)$ denote the set of all its eigenvalues. The spectral bound of A is defined as

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

The matrix A is called reducible if there exists a nonempty proper subset $E\subset\{1,2,\ldots,n\}$ such that $a_{ij}=0$ for all $i\in E$ and $j\notin E$; otherwise, A is called irreducible. If all off-diagonal entries of A are nonnegative, i.e., $a_{ij}\geq 0$ for $i\neq j$, then A is called an essentially nonnegative matrix.

For irreducible essentially nonnegative matrices, the Perron–Frobenius theorem [27] provides the following important property.

Theorem 1. *Let A be an irreducible essentially nonnegative matrix. Then its spectral bound $s(A)$ is an eigenvalue of A, called the principal eigenvalue, and there exists a unique (up to scalar multiples) positive eigenvector $\boldsymbol{\xi} \gg \mathbf{0}$ associated with it. Moreover, apart from $s(A)$, A has no other eigenvalue with a positive eigenvector.*

In this case, $s(A)$ is referred to as the principal eigenvalue of A, and the corresponding eigenvector is called the principal eigenvector.

We will employ the theory of monotone dynamical systems [28, 29, 30, 31] to study the global dynamics of system (2). For competitive systems, the dynamical behavior can be characterized by the stability of boundary equilibria [18].

Theorem 2. *Assume that system (2) admits two boundary equilibria $(\mathbf{u}^*, \mathbf{0})$ and $(\mathbf{0}, \mathbf{v}^*)$. If $(\mathbf{u}^*, \mathbf{0})$ is linearly unstable and the system has no positive equilibrium, then $(\mathbf{0}, \mathbf{v}^*)$ is globally asymptotically stable. Similarly, if $(\mathbf{0}, \mathbf{v}^*)$ is linearly unstable and the system has no positive equilibrium, then $(\mathbf{u}^*, \mathbf{0})$ is globally asymptotically stable. If both boundary equilibria are linearly unstable, then the system possesses at least one positive equilibrium.*

2 Local dynamics of system (2)

In this section, we study the local stability of the semi-trivial equilibria $(\mathbf{u}^*, \mathbf{0})$ and $(\mathbf{0}, \mathbf{v}^*)$. We denote $\mathbf{u}^* = (u_1^*, u_2^*, u_3^*)^T \gg \mathbf{0}$ and $\mathbf{v}^* = (v_1^*, v_2^*, v_3^*)^T \gg \mathbf{0}$, satisfying

$$\sum_{j=1}^{3}(d_1 D_{ij} + q_1 Q_{ij})u_j^* + u_i^*(r_i - u_i^*) = 0, \quad i = 1, 2, 3, \tag{6}$$

$$\sum_{j=1}^{3}(d_2 D_{ij} + q_2 Q_{ij})v_j^* + v_i^*(r_i - v_i^*) = 0, \quad i = 1, 2, 3. \tag{7}$$

We first present a useful identity for the principal eigenvalues.

Lemma 1. *For Model (I), assume $d_1, d_2 > 0$, $q_1, q_2 > 0$. Then*

$$\begin{aligned}(\lambda_1^2 - \lambda_1^1)\sum_{i=1}^{3}\phi_i^1\phi_i^2\beta_i &= (\beta_1\phi_1^1 - \beta_3\phi_3^1)\big[(d_2-d_1)(\phi_3^2-\phi_1^2) - (q_2-q_1)\phi_1^2\big] \\ &\quad + (\beta_1\phi_1^1 - \beta_2\phi_2^1)\big[(d_2-d_1)(\phi_2^2-\phi_1^2) - (q_2-q_1)\phi_1^2\big] \\ &\quad - \tau(q_2-q_1)\phi_2^1\phi_2^2\beta_2 - \tau(q_2-q_1)\phi_3^1\phi_3^2\beta_3, \end{aligned} \tag{8}$$

$$\begin{aligned}(\lambda_1^1 - \lambda_1^2)\sum_{i=1}^{3}\phi_i^1\phi_i^2\omega_i &= (\omega_1\phi_1^2 - \omega_3\phi_3^2)\big[(d_1-d_2)(\phi_3^1-\phi_1^1) - (q_1-q_2)\phi_1^1\big] \\ &\quad + (\omega_1\phi_1^1 - \omega_2\phi_2^2)\big[(d_1-d_2)(\phi_2^1-\phi_1^1) - (q_1-q_2)\phi_1^1\big] \\ &\quad - \tau(q_1-q_2)\phi_2^1\phi_2^2\omega_2 - \tau(q_1-q_2)\phi_3^1\phi_3^2\omega_3, \end{aligned} \tag{9}$$

where

$$(\beta_1,\beta_2,\beta_3) = \left(\frac{d_1}{d_1+q_1}, \left(\frac{d_1}{d_1+q_1}\right)^2, \left(\frac{d_1}{d_1+q_1}\right)^2\right),$$
$$(\omega_1,\omega_2,\omega_3) = \left(\frac{d_2}{d_2+q_2}, \left(\frac{d_2}{d_2+q_2}\right)^2, \left(\frac{d_2}{d_2+q_2}\right)^2\right).$$

Proof. We only prove (8), the proof of (9) is similar. The eigen-pairs (λ_1^1, ϕ_i^1) and (λ_1^2, ϕ_i^2) satisfy

$$\begin{cases}\sum_{j=1}^{3}(d_1D_{ij} + q_1Q_{ij})\phi_j^1 + r_i\phi_i^1 = \lambda_1^1\phi_i^1, \\ \sum_{j=1}^{3}(d_2D_{ij} + q_2Q_{ij})\phi_j^2 + r_i\phi_i^2 = \lambda_1^2\phi_i^2. \end{cases}$$

These can be rewritten as

$$\begin{cases}\sum_{j=1}^{3}(d_1D_{ij} + q_1Q_{ij})\phi_j^1 + r_i\phi_i^1 - \lambda_1^1\phi_i^1 = 0, \\ \sum_{j=1}^{3}(d_2D_{ij} + q_2Q_{ij})\phi_j^2 + r_i\phi_i^2 - \lambda_1^2\phi_i^2 = -\sum_{j=1}^{3}[(d_2-d_1)D_{ij} + (q_2-q_1)Q_{ij}]\phi_j^2. \end{cases} \tag{10}$$

Multiplying the first equation of (10) by $\beta_i\phi_i^2$ and summing over i, and similarly multiplying the second equation of (10) by $\beta_i\phi_i^1$ and summing over i. Subtracting the resulting equations yields (8) after simplification, where β_i are defined in Lemma 1. □

Lemma 2. *For Model (II), assume $d_1, d_2 > 0$, $q_1, q_2 > 0$. Then*

$$\begin{aligned}(\lambda_1^2 - \lambda_1^1)\sum_{i=1}^{3}\phi_i^1\phi_i^2\beta_i' &= (\beta_1'\phi_1^1 - \beta_3'\phi_3^1)\big[(d_2-d_1)(\phi_3^2-\phi_1^2) - (q_2-q_1)\phi_1^2\big]\\ &\quad + (\beta_3'\phi_3^1 - \beta_2'\phi_2^1)\big[(d_2-d_1)(\phi_2^2-\phi_3^2) + (q_2-q_1)\phi_2^2\big]\\ &\quad - \tau(q_2-q_1)\phi_3^1\phi_3^2\beta_3', \end{aligned} \tag{11}$$

$$\begin{aligned}(\lambda_1^1 - \lambda_1^2)\sum_{i=1}^{3}\phi_i^1\phi_i^2\omega_i' &= (\omega_1'\phi_1^2 - \omega_3'\phi_3^2)\big[(d_1-d_2)(\phi_3^1-\phi_1^1) - (q_1-q_2)\phi_1^1\big]\\ &\quad + (\omega_3'\phi_3^2 - \omega_2'\phi_2^2)\big[(d_1-d_2)(\phi_2^1-\phi_3^1) + (q_1-q_2)\phi_2^1\big]\\ &\quad - \tau(q_1-q_2)\phi_3^1\phi_3^2\omega_3', \end{aligned} \tag{12}$$

where

$$(\beta_1', \beta_2', \beta_3') = \left(\frac{d_1}{d_1+q_1}, \frac{d_1}{d_1+q_1}, \left(\frac{d_1}{d_1+q_1}\right)^2\right),$$
$$(\omega_1', \omega_2', \omega_3') = \left(\frac{d_2}{d_2+q_2}, \frac{d_2}{d_2+q_2}, \left(\frac{d_2}{d_2+q_2}\right)^2\right).$$

Proof. The proof is analogous to that of Lemma 1. □

Now we present the local stability results for the semi-trivial equilibria.

Theorem 3. *For Model (I), assume $d_1 = d_2 = d > 0$, $q_1 > q_2 > 0$, $r_1 \geq \max\{r_2, r_3\}$, $\tau \in [0, +\infty)$. Then*

(i) If $(u^*, 0)$ exists, it is linearly unstable.

(ii) If $(0, v^*)$ exists, it is linearly stable.

Proof. We first prove (i). Linearizing system (2) at $(u^*, 0)$, we find that the stability of $(u^*, 0)$ is determined by the sign of $\lambda_1(d_2, q_2, r - u^*)$. If $\lambda_1(d_2, q_2, r - u^*) < 0$, it is stable; if $\lambda_1(d_2, q_2, r - u^*) > 0$, it is unstable.

From (6) we know $\lambda_1(d_1, q_1, r - u^*) = 0$ with eigenvector u^*. Combining $(\lambda_1(d_2, q_2, r - u^*), \psi)$, substituting into (9) yields

$$\begin{aligned}&\lambda_1(d_2, q_2, r-u^*)\sum_{i=1}^{n} u_i^*\psi_i\beta_i\\ &= (\beta_1 u_1^* - \beta_3 u_3^*)(q_1-q_2)\psi_1 + (\beta_1 u_1^* - \beta_2 u_2^*)(q_1-q_2)\psi_1 - \tau(q_2-q_1)u_2^*\psi_2\beta_2\\ &\quad - \tau(q_2-q_1)u_3^*\psi_3\beta_3\\ &= (q_1-q_2)\psi_1\big(2\beta_1 u_1^* - \beta_2 u_2^* - \beta_3 u_3^*\big) - \tau(q_2-q_1)u_2^*\psi_2\beta_2\\ &\quad - \tau(q_2-q_1)u_3^*\psi_3\beta_3\\ &= \psi_1\frac{d_1(q_1-q_2)}{(d_1+q_1)^2}\big(2(d_1+q_1)u_1^* - d_1u_2^* - d_1u_3^*\big) - \tau(q_2-q_1)u_2^*\psi_2\beta_2\\ &\quad - \tau(q_2-q_1)u_3^*\psi_3\beta_3,\end{aligned}$$

where we have used the notation β_i as defined in Lemma 1. To determine the sign of $\lambda_1(d_2, q_2, r_2 - u^*)$, it suffices to examine the sign of $2(d_1+q_1)u_1^* - d_1u_2^* - d_1u_3^*$.

System (6) can be rewritten as

$$\begin{cases} -2(d_1+q_1)u_1^* + d_1u_2^* + d_1u_3^* + (r_1 - u_1^*)u_1^* = 0, \\ (d_1+q_1)u_1^* + (-d_1 - \tau q_1)u_2^* + (r_2 - u_2^*)u_2^* = 0, \\ (d_1+q_1)u_1^* + (-d_1 - \tau q_1)u_3^* + (r_3 - u_3^*)u_3^* = 0. \end{cases} \tag{13}$$

We claim that $2(d_1+q_1)u_1^* - d_1u_2^* - d_1u_3^* > 0$. From (13) we can write

$$h_1 + h_2 = -(r_1 - u_1^*)u_1^*,$$

$$h_1 = (r_2 - u_2^* - \tau q_1)u_2^*,$$

$$h_2 = (r_3 - u_3^* - \tau q_1)u_3^*,$$

where $h_1 = d_1u_2^* - (d_1+q_1)u_1^*$, $h_2 = d_1u_3^* - (d_1+q_1)u_1^*$. If $h_1 + h_2 \geq 0$, then $r_1 \leq u_1^*$. Assume $h_1 \geq 0$, then $u_2^* \geq u_1^*$. So $r_2 \leq r_1 \leq u_1^* < u_2^*$, implying $r_2 - u_2^* - \tau q_1 < 0$. Hence $h_1 < 0$, a contradiction. Thus $h_1 + h_2 < 0$, which gives $2(d_1+q_1)u_1^* - d_1u_2^* - d_1u_3^* > 0$. Consequently $\lambda_1(d_2, q_2, r - u^*) > 0$, i.e., $(u^*, 0)$ is linearly unstable. The proof of (ii) is analogous and is omitted. □

Theorem 4. *For Model (I), assume $d_1 > d_2 > 0$, $q_2 \geq q_1 > 0$, $r_1 \geq r_2 = r_3 > 0$, $\tau \in [0, 1]$. Then*

(i) If $(u^*, 0)$ exists, it is linearly stable.

(ii) If $(0, v^*)$ exists, it is linearly unstable.

Proof. We prove (i) and (ii) is similar. Denote $(\bar{\lambda}_1, \psi) = (\lambda_1(d_2, q_2, r - u^*), \psi)$. By (9) we obtain

$$\begin{aligned} -\bar{\lambda}_1 \sum_{i=1}^{3} u_i^* \psi_i \omega_i = {} & (\omega_1\psi_1 - \omega_3\psi_3)\big[(d_1 - d_2)(u_3^* - u_1^*) - (q_1 - q_2)u_1^*\big] \\ & + (\omega_1\psi_1 - \omega_2\psi_2)\big[(d_1 - d_2)(u_2^* - u_1^*) - (q_1 - q_2)u_1^*\big] \\ & - \tau(q_1 - q_2)u_2^*\psi_2\omega_2 - \tau(q_1 - q_2)u_3^*\psi_3\omega_3. \end{aligned} \tag{14}$$

Since $r_2 = r_3$, by (13) we have $u_2^* = u_3^*$. System (13) can be rewritten as

$$\begin{cases} d_1(u_2^* - u_1^*) + d_1(u_3^* - u_1^*) - 2q_1u_1^* = -u_1^*(r_1 - u_1^*), \\ (d_1+q_1)(u_1^* - u_2^*) + (1-\tau)q_1u_2^* = -u_2^*(r_2 - u_2^*), \\ (d_1+q_1)(u_1^* - u_3^*) + (1-\tau)q_1u_3^* = -u_3^*(r_3 - u_3^*). \end{cases} \tag{15}$$

We claim that $u_2^* > u_1^*$. Suppose to the contrary that $u_2^* \le u_1^*$. Combining $\tau \in [0,1]$ and (15) we obtain $r_1 \le r_2 \le u_2^* \le u_1^*$. We have

$$0 > d_1(u_2^* - u_1^*) + d_1(u_3^* - u_1^*) - 2q_1u_1^* = -u_1^*(r_1 - u_1^*) \ge 0,$$

a contradiction. Hence $u_2^* > u_1^*$ and $u_3^* > u_1^*$.

Now (14) can be simplified as

$$\begin{aligned}
-\bar{\lambda}_1 \sum_{i=1}^{3} u_i^* \psi_i \omega_i &= \big(2\omega_1\psi_1 - \omega_2\psi_2 - \omega_3\psi_3\big)\big[(d_1 - d_2)(u_3^* - u_1^*) - (q_1 - q_2)u_1^*\big] \\
&\quad - \tau(q_1 - q_2)u_2^*\psi_2\omega_2 - \tau(q_1 - q_2)u_3^*\psi_3\omega_3 \\
&= \frac{d_2}{(d_2 + q_2)^2}\big(2(d_2 + q_2)\psi_1 - d_2\psi_2 - d_2\psi_3\big)\big[(d_1 - d_2)(u_3^* - u_1^*) - (q_1 - q_2)u_1^*\big] \\
&\quad - \tau(q_1 - q_2)u_2^*\psi_2\omega_2 - \tau(q_1 - q_2)u_3^*\psi_3\omega_3.
\end{aligned}$$

To determine the sign of $2(d_2 + q_2)\psi_1 - d_2\psi_2 - d_2\psi_3$, we consider the eigenvalue problem for $(\bar{\lambda}_1, \psi)$:

$$\begin{cases}
(-2d_2 - 2q_2)\psi_1 + d_2\psi_2 + d_2\psi_3 + (r_1 - u_1^*)\psi_1 = \bar{\lambda}_1\psi_1, \\
(d_2 + q_2)\psi_1 + (-d_2 - \tau q_2)\psi_2 + (r_2 - u_2^*)\psi_2 = \bar{\lambda}_1\psi_2, \\
(d_2 + q_2)\psi_1 + (-d_2 - \tau q_2)\psi_3 + (r_3 - u_3^*)\psi_3 = \bar{\lambda}_1\psi_3.
\end{cases} \tag{16}$$

Set $m_1 = d_2\psi_2 - (d_2 + q_2)\psi_1$ and $m_2 = d_2\psi_3 - (d_2 + q_2)\psi_1$. Then (16) can be rewritten as

$$\begin{cases}
-(m_1 + m_2) = (r_1 - u_1^* - \bar{\lambda}_1)\psi_1, \\
m_1 = (r_2 - u_2^* - \bar{\lambda}_1 - \tau q_2)\psi_2, \\
m_2 = (r_3 - u_3^* - \bar{\lambda}_1 - \tau q_2)\psi_3.
\end{cases} \tag{17}$$

We claim that $m_1 + m_2 < 0$. Assume to the contrary that $m_1 + m_2 \ge 0$, and so $r_1 \le u_1^* + \bar{\lambda}_1$. Without loss of generality, suppose $m_1 \ge 0$. Using (17) one deduce

$$r_2 \ge u_2^* + \bar{\lambda}_1 + \tau q_2 \ge u_2^* + \bar{\lambda}_1 > u_1^* + \bar{\lambda}_1 \ge r_1,$$

which contradicts $r_2 \le r_1$. Hence, $m_1 + m_2 < 0$ which implies $\bar{\lambda}_1 < 0$, i.e., $(u^*, 0)$ is linearly stable. □

Theorem 5. *For Model (II), assume $d_1 = d_2 = d > 0$, $q_1 > q_2 > 0$, $r_1 = r_2 \ge r_3$, $\tau \in [0, +\infty)$. Then we have*

(i) If $(u^*, 0)$ exists, it is linearly unstable.

(ii) If $(0, v^*)$ exists, it is linearly stable.

Proof. We prove (ii) and (i) is analogous. Linearizing system (2) at $(0, v^*)$, the stability is determined by $\lambda_1(d_1, q_1, r - v^*)$. By (7), $\lambda_1(d_2, q_2, r - v^*) = 0$ with eigenvector v^*, combining $(\lambda_1(d_1, q_1, r - v^*), \varphi)$, substituting into (12) yields

$$\begin{aligned}\lambda_1(d_1, q_1, r - v^*) \sum_{i=1}^{3} v_i^* \varphi_i \omega_i' = & \frac{d_2}{(d_2 + q_2)^2}(d_2 v_3^* - (d_2 + q_2)v_1^*)(q_1 - q_2)\varphi_1 \\ & + \frac{d_2}{(d_2 + q_2)^2}(d_2 v_3^* - (d_2 + q_2)v_2^*)(q_1 - q_2)\varphi_2 \\ & - (q_1 - q_2)\omega_3' v_3^* \varphi_3.\end{aligned}$$

By (7) we can write $h_1' = d_2 v_3^* - (d_2 + q_2)v_1^*$, $h_2' = d_2 v_3^* - (d_2 + q_2)v_2^*$, with

$$\begin{cases} h_1' = -(r_1 - v_1^*)v_1^*, \\ h_2' = -(r_2 - v_2^*)v_2^*, \\ h_1' + h_2' = (r_3 - v_3^* - \tau q_2)v_3^*. \end{cases} \tag{18}$$

We now prove $h_1' + h_2' < 0$. Suppose to the contrary that $h_1' + h_2' \geq 0$, then $r_3 \geq v_3^* + \tau q_2$. Without loss of generality, assume $h_1' \geq 0$, by the definition of h_1' we have $v_3^* > v_1^*$. Consequently,

$$r_1 \geq r_3 \geq v_3^* + \tau q_2 > v_1^*.$$

Thus $r_1 - v_1^* > 0$, which implies $h_1' < 0$, a contradiction. Hence, $h_1' + h_2' < 0$.

Next we prove $h_1' < 0$. Suppose to the contrary that $h_1' \geq 0$. Since $h_1' + h_2' < 0$ we obtain $h_2' < 0$, and thus $r_1 \leq v_1^*$. Moreover,

$$(d_2 + q_2)v_1^* \leq d_2 v_3^* < (d_2 + q_2)v_2^*,$$

which yields $v_1^* < v_2^*$. Therefore $r_2 = r_1 \leq v_1^* < v_2^*$, leading to a contradiction with $h_2' > 0$. A similar argument shows $h_2' < 0$. Consequently, $\lambda_1(d_1, q_1, r_1) < 0$, i.e., $(0, v_1^*)$ is linearly stable. □

Theorem 6. *For Model (II), assume $d_1 > d_2 > 0$, $q_2 \geq q_1 > 0$, $r_1 = r_2 = r_3 = r > 0$, $\tau \in [0, 2]$. Then we have*

(i) If $(u^*, 0)$ exists, it is linearly stable.

(ii) If $(0, v^*)$ exists, it is linearly unstable.

Proof. We only need to prove (i), since the proof of (ii) is similar. Denote $(\tilde{\lambda}_1, \varphi) = (\lambda_1(d_2, q_2, r-$

$u^*), \varphi)$. Combining with (12) we obtain

$$\begin{aligned}-\tilde{\lambda}_1 \sum_{i=1}^{3} u_i^* \varphi_i \omega_i' = & \frac{d_2}{(d_2+q_2)^2}\left[d_2\varphi_3 - (d_2+q_2)\varphi_1\right]\left[(d_1-d_2)(u_1^*-u_3^*) + (q_1-q_2)u_1^*\right] \\ & + \frac{d_2}{(d_2+q_2)^2}\left[d_2\varphi_3 - (d_2+q_2)\varphi_2\right]\left[(d_1-d_2)(u_2^*-u_3^*) + (q_1-q_2)u_2^*\right] \\ & - \tau(q_1-q_2)u_3^*\varphi_3\omega_3'. \end{aligned} \tag{19}$$

Since $r_1 = r_2$, from (6) we easily obtain $u_1^* = u_2^*$. Moreover, (6) can be rewritten as

$$\begin{cases} d_1(u_3^* - u_1^*) = -(r_1 - u_1^* - q_1)u_1^*, \\ d_1(u_3^* - u_2^*) = -(r_2 - u_2^* - q_1)u_2^*, \\ (d_1+q_1)(u_1^* + u_2^* - u_3^*) + (2-\tau)q_1u_3^* = -(r_3 - u_3^*)u_3^*. \end{cases} \tag{20}$$

We claim that $u_3^* > u_1^*$. Suppose to the contrary that $u_3^* \le u_1^*$. By (20) we obtain $r_3 \ge r_1 \ge u_1^* + q_1 > u_3^*$. Then

$$0 \le (d_1+q_1)(u_1^* + u_2^* - 2u_3^*) + (2-\tau)q_1u_3^* = -(r_3 - u_3^*)u_3^* < 0,$$

a contradiction. Hence $u_3^* > u_1^*$ and $u_3^* > u_2^*$.

Now (19) can be simplified as

$$\begin{aligned}-\tilde{\lambda}_1 \sum_{i=1}^{3} u_i^* \varphi_i \omega_i' = & \frac{d_2}{(d_2+q_2)^2}\left[2d_2\varphi_3 - (d_2+q_2)\varphi_1 - (d_2+q_2)\varphi_2\right] \\ & \times \left[(d_1-d_2)(u_1^*-u_3^*) + (q_1-q_2)u_1^*\right] \\ & - \tau(q_1-q_2)u_3^*\varphi_3\omega_3'. \end{aligned}$$

Indeed, we only need to determine the sign of $2d_2\varphi_3 - (d_2+q_2)\varphi_1 - (d_2+q_2)\varphi_2$. Let $m_1' = d_2\varphi_3 - (d_2+q_2)\varphi_1$, $m_2' = d_2\varphi_3 - (d_2+q_2)\varphi_2$. The eigenvalue problem for $(\tilde{\lambda}_1, \varphi)$ gives

$$\begin{cases} m_1' = -(r - u_1^* - \tilde{\lambda}_1)\varphi_1, \\ m_2' = -(r - u_2^* - \tilde{\lambda}_1)\varphi_2, \\ m_1' + m_2' = (r - u_3^* - \tilde{\lambda}_1 - \tau q_2)\varphi_3. \end{cases} \tag{21}$$

We claim that $m_1' + m_2' < 0$. Assume to the contrary that $m_1' + m_2' \ge 0$, then $r \ge u_3^* + \tilde{\lambda}_1 + \tau q_2$. Assume $m_1' \ge 0$, then by (21) $r \le u_1^* + \tilde{\lambda}_1 < u_3^* + \tilde{\lambda}_1 \le u_3^* + \tilde{\lambda}_1 + \tau q_2 \le r$, a contradiction. Hence $m_1' + m_2' < 0$, implying $\tilde{\lambda}_1 < 0$, i.e., $(u^*, 0)$ is linearly stable. □

3 Nonexistence of positive equilibrium

In this section, we establish two nonexistence results of positive equilibrium for system (2) under Models (I) and (II). And consider the following two cases:

Case I: $d_1 \geq d_2 > 0$, $\frac{d_2}{d_1} q_1 \geq q_2 > 0$, $(d_1 - d_2)^2 + (q_1 - q_2)^2 \neq 0$, $\tau \in [0, +\infty)$.

Case II: $d_1 > d_2 > 0$, $q_2 \geq q_1 > 0$, $r_1 = r_2 = r_3 = r > 0$.

Let $(\mathbf{u}, \mathbf{v})$ be a positive equilibrium of system (2), i.e., $\mathbf{u} = (u_1, u_2, u_3)^T \gg \mathbf{0}$, $\mathbf{v} = (v_1, v_2, v_3)^T \gg \mathbf{0}$, satisfying

$$\begin{cases} \sum_{j=1}^{3} (d_1 D_{ij} + q_1 Q_{ij}) u_j + (r_i - u_i - v_i) u_i = 0, & i = 1, 2, 3, \\ \sum_{j=1}^{3} (d_2 D_{ij} + q_2 Q_{ij}) v_j + (r_i - u_i - v_i) v_i = 0, & i = 1, 2, 3. \end{cases} \tag{22}$$

Based on $(\mathbf{u}, \mathbf{v})$, we define for Model (I):

$$\begin{aligned} f_1 &= d_1 u_2 - (d_1 + q_1) u_1, \\ f_2 &= d_1 u_3 - (d_1 + q_1) u_1, \\ f_3 &= \tau q_1 u_2, \\ f_4 &= \tau q_1 u_3, \end{aligned} \tag{23}$$

and

$$\begin{aligned} g_1 &= d_2 v_2 - (d_2 + q_2) v_1, \\ g_2 &= d_2 v_3 - (d_2 + q_2) v_1, \\ g_3 &= \tau q_2 v_2, \\ g_4 &= \tau q_2 v_3. \end{aligned} \tag{24}$$

Then system (22) can be rewritten as

$$\begin{aligned} f_1 + f_2 &= -u_1 (r_1 - u_1 - v_1), \\ -(f_1 + f_3) &= -u_2 (r_2 - u_2 - v_2), \\ -(f_2 + f_4) &= -u_3 (r_3 - u_3 - v_3), \end{aligned} \tag{25}$$

$$\begin{aligned} g_1 + g_2 &= -v_1 (r_1 - u_1 - v_1), \\ -(g_1 + g_3) &= -v_2 (r_2 - u_2 - v_2), \\ -(g_2 + g_4) &= -v_3 (r_3 - u_3 - v_3). \end{aligned} \tag{26}$$

Similarly, for Model (II), we define

$$\begin{aligned} f_1' &= d_1 u_3 - (d_1 + q_1) u_1, \\ f_2' &= d_1 u_3 - (d_1 + q_1) u_2, \\ f_3' &= \tau q_1 u_3, \end{aligned} \tag{27}$$

and

$$\begin{aligned} g_1' &= d_2v_3 - (d_2+q_2)v_1, \\ g_2' &= d_2v_3 - (d_2+q_2)v_2, \\ g_3' &= \tau q_2 v_3. \end{aligned} \tag{28}$$

Then system (22) can be rewritten as

$$\begin{aligned} f_1' &= -u_1(r_1 - u_1 - v_1), \\ f_2' &= -u_2(r_2 - u_2 - v_2), \\ -(f_1' + f_2' + f_3') &= -u_3(r_3 - u_3 - v_3), \end{aligned} \tag{29}$$

$$\begin{aligned} g_1' &= -v_1(r_1 - u_1 - v_1), \\ g_2' &= -v_2(r_2 - u_2 - v_2), \\ -(g_1' + g_2' + g_3') &= -v_3(r_3 - u_3 - v_3). \end{aligned} \tag{30}$$

Using similar arguments as in [32, 33], we obtain the following identities.

Lemma 3. *For Model (I), the following identities hold:*

$$\begin{aligned} &\big[(d_1-d_2)(v_2-v_1) - (q_1-q_2)v_1\big] f_1 \frac{d_1}{(d_1+q_1)^2} \\ &\quad + \big[(d_1-d_2)(v_3-v_1) - (q_1-q_2)v_1\big] f_2 \frac{d_1}{(d_1+q_1)^2} \\ &= (q_2-q_1)\tau u_2 v_2 \Big(\frac{d_1}{d_1+q_1}\Big)^2 + (q_2-q_1)\tau u_3 v_3 \Big(\frac{d_1}{d_1+q_1}\Big)^2, \end{aligned} \tag{31}$$

$$\begin{aligned} &\big[(d_1-d_2)(v_2-v_1) - (q_1-q_2)v_1\big] f_1 \frac{d_1}{(d_1+q_1)^2} - (f_2v_1 - g_2u_1)\frac{d_1}{d_1+q_1} \\ &= (q_2-q_1)\tau u_2 v_2 \Big(\frac{d_1}{d_1+q_1}\Big)^2, \end{aligned} \tag{32}$$

$$\begin{aligned} &\big[(d_1-d_2)(v_3-v_1) - (q_1-q_2)v_1\big] f_2 \frac{d_1}{(d_1+q_1)^2} - (f_1v_1 - g_1u_1)\frac{d_1}{d_1+q_1} \\ &= (q_2-q_1)\tau u_3 v_3 \Big(\frac{d_1}{d_1+q_1}\Big)^2. \end{aligned} \tag{33}$$

Proof. We first consider (31). Multiplying the three equations in (25) by $\frac{d_1}{d_1+q_1}v_1$, $\big(\frac{d_1}{d_1+q_1}\big)^2 v_2$

and $\big(\frac{d_1}{d_1+q_1}\big)^2 v_3$, respectively. Then summing them up, we obtain

$$\begin{aligned}
&(f_1+f_2)v_1\frac{d_1}{d_1+q_1}-(f_1+f_3)v_2\Big(\frac{d_1}{d_1+q_1}\Big)^2-(f_2+f_4)v_3\Big(\frac{d_1}{d_1+q_1}\Big)^2\\
&=f_1\Big[v_1\frac{d_1}{d_1+q_1}-v_2\Big(\frac{d_1}{d_1+q_1}\Big)^2\Big]+f_2\Big[v_1\frac{d_1}{d_1+q_1}-v_3\Big(\frac{d_1}{d_1+q_1}\Big)^2\Big]\\
&\quad-f_3v_2\Big(\frac{d_1}{d_1+q_1}\Big)^2-f_4v_3\Big(\frac{d_1}{d_1+q_1}\Big)^2\\
&=f_1\frac{d_1}{(d_1+q_1)^2}\big[-d_1v_2+(d_1+q_1)v_1\big]+f_2\frac{d_1}{(d_1+q_1)^2}\big[-d_1v_3+(d_1+q_1)v_1\big]. \qquad (34)
\end{aligned}$$

Similarly, multiplying the three equations in (26) by $\frac{d_1}{d_1+q_1}u_1$, $\big(\frac{d_1}{d_1+q_1}\big)^2u_2$ and $\big(\frac{d_1}{d_1+q_1}\big)^2u_3$, respectively. Then summing them up, we have

$$\begin{aligned}
&(g_1+g_2)u_1\frac{d_1}{d_1+q_1}-(g_1+g_3)u_2\Big(\frac{d_1}{d_1+q_1}\Big)^2-(g_2+g_4)u_3\Big(\frac{d_1}{d_1+q_1}\Big)^2\\
&=-f_1g_1\frac{d_1}{(d_1+q_1)^2}-f_2g_2\frac{d_1}{(d_1+q_1)^2}-g_3u_2\Big(\frac{d_1}{d_1+q_1}\Big)^2-g_4u_3\Big(\frac{d_1}{d_1+q_1}\Big)^2. \qquad (35)
\end{aligned}$$

Then, subtracting (34) from (35) yields (31). Similarly, (32) is obtained by considering the first two equations of (25) and (26), while (33) is obtained by considering the first and third equations.

□

Lemma 4. *For Model (II), the following identity holds:*

$$\begin{aligned}
&\big[(d_1-d_2)(v_1-v_3)+(q_1-q_2)v_1\big]f_1'\frac{d_1}{(d_1+q_1)^2}\\
&\quad+\big[(d_1-d_2)(v_2-v_3)+(q_1-q_2)v_2\big]f_2'\frac{d_1}{(d_1+q_1)^2}\\
&=(q_1-q_2)\tau u_3v_3\Big(\frac{d_1}{d_1+q_1}\Big)^2. \qquad (36)
\end{aligned}$$

Proof. The proof is analogous to that of Lemma 3. The difference is that the three equations in (29) are multiplied by $\frac{d_1}{d_1+q_1}v_1$, $\frac{d_1}{d_1+q_1}v_2$, and $\big(\frac{d_1}{d_1+q_1}\big)^2v_3$, respectively, and then summed. □

Now we prove the nonexistence results of positive equilibrium for the two cases under both models.

Theorem 7. *For Model (I), the following statements hold:*

(i) For Case I, $r_1 \geq r_2 = r_3$, system (2) admits no positive equilibrium.

(ii) For Case II, $\tau \in [0,1]$, system (2) admits no positive equilibrium.

Proof. We first prove (i). Assume that there exists a positive equilibrium (u,v) satisfying (22). We divide the proof into several steps.

Step 1. We claim that $f_1 + f_2 < 0$ and $g_1 + g_2 < 0$.

By (25) and (26), $f_1 + f_2$ and $g_1 + g_2$ have the same sign. Thus, it suffices to consider $f_1 + f_2$. Suppose $f_1 + f_2 \geq 0$, hence $g_1 + g_2 \geq 0$. And from (25), $u_1 + v_1 > r_1$. In addition, since $f_1 + f_2 \geq 0$, at least one of f_1 and f_2 is nonnegative. Without loss of generality, assume $f_1 \geq 0$. By definition, this implies $u_2 > u_1$. From (25) and Case I, we have $r_2 > u_2 + v_2 + \tau q_1 \geq u_2 + v_2 + \tau q_2$. Thus $g_1 \geq 0$ gives $v_2 > v_1$. Consequently, $r_2 \leq r_1 \leq u_1 + v_1 < u_2 + v_2$, leading to $f_1, g_1 < 0$, a contradiction. Hence $f_1 + f_2 < 0$ and $g_1 + g_2 < 0$.

Step 2. We claim that $f_1 < 0$ and $f_2 < 0$.

It suffices to show $f_1 < 0$ and the proof for f_2 is similar. Suppose $f_1 \geq 0$, then $d_1 u_2 \geq (d_1 + q_1)u_1$. From Step 1, $f_2 < 0$, so $d_1 u_3 < (d_1 + q_1)u_1 \leq d_1 u_2$. This implies $u_3 < u_2$. A similar argument yields $v_3 < v_2$, and thus $r_3 < u_3 + v_3 + \tau q_1 < u_2 + v_2 + \tau q_1 \leq r_2$, a contradiction. Therefore $f_1 < 0$, and analogously $f_2 < 0$.

Step 3. The situation $f_i, g_i < 0$ for all $i = 1, 2$ cannot occur.

Assume to the contrary that $f_i, g_i < 0$ for $i = 1, 2$. By (31) and Case I, we have

$$\begin{aligned} M :=& \big[(d_1 - d_2)(v_2 - v_1) - (q_1 - q_2)v_1\big] f_1 \frac{d_1}{(d_1 + q_1)^2} \\ &+ \big[(d_1 - d_2)(v_3 - v_1) - (q_1 - q_2)v_1\big] f_2 \frac{d_1}{(d_1 + q_1)^2} \\ =& (q_2 - q_1)\tau u_2 v_2 \Big(\frac{d_1}{d_1 + q_1}\Big)^2 + (q_2 - q_1)\tau u_3 v_3 \Big(\frac{d_1}{d_1 + q_1}\Big)^2 \leq 0. \end{aligned}$$

If $d_1 = d_2$, then $q_1 > q_2$ and $M = -(q_1 - q_2)v_1 f_1 \frac{d_1}{(d_1+q_1)^2} - (q_1 - q_2)v_1 f_2 \frac{d_1}{(d_1+q_1)^2} > 0$, contradicting (31).

If $d_1 > d_2$ and $q_1 > q_2$, then by [32, Lemma 2.4], $\frac{q_2}{d_2} \leq \frac{q_1 - q_2}{d_1 - d_2}$. Combining this with $g_1, g_2 < 0$ yields

$$(d_1 - d_2)(v_2 - v_1) - (q_1 - q_2)v_1 < 0, \tag{37}$$

$$(d_1 - d_2)(v_3 - v_1) - (q_1 - q_2)v_1 < 0. \tag{38}$$

Since $f_1, f_2 < 0$, we obtain $M > 0$, again contradicting (31). Thus Step 3 is established.

Now we complete the final proof. From Steps 1 and 2, we have $f_1, f_2 < 0$ and $g_1 + g_2 < 0$. By Step 3 and the fact that only one of g_1 and g_2 is negative. Therefore, we consider two cases:

(a) $f_1, f_2 < 0$, $g_1 < 0$, $g_2 \geq 0$; (b) $f_1, f_2 < 0$, $g_2 < 0$, $g_1 \geq 0$.

For case (a), from (37) and (32) we obtain

$$\begin{aligned} 0 <& \big[(d_1 - d_2)(v_2 - v_1) - (q_1 - q_2)v_1\big] f_1 \frac{d_1}{(d_1 + q_1)^2} - (f_2 v_1 - g_2 u_1)\frac{d_1}{d_1 + q_1} \\ =& (q_2 - q_1)\tau u_2 v_2 \Big(\frac{d_1}{d_1 + q_1}\Big)^2 \leq 0, \end{aligned}$$

a contradiction.

For case (b), by (38) and (33) one can deduce

$$\begin{aligned} 0 &< \big[(d_1-d_2)(v_3-v_1)-(q_1-q_2)v_1\big]f_2\frac{d_1}{(d_1+q_1)^2}-(f_1v_1-g_1u_1)\frac{d_1}{d_1+q_1} \\ &= (q_2-q_1)\tau u_3v_3\Big(\frac{d_1}{d_1+q_1}\Big)^2 \le 0, \end{aligned}$$

again a contradiction. This completes the proof of (i).

We now prove (ii). The proof follows similar steps.

Step 1. We claim that $f_1+f_2<0$ and $g_1+g_2<0$.

This step can be established by the same argument as in the previous step 1, with the difference that now $q_2 \ge q_1$.

Step 2. We claim that $g_1<0$ and $g_2<0$.

It suffices to prove $g_1<0$ and the discussion for g_2 is similar. Suppose to the contrary that $g_1 \ge 0$. By definition, $d_1v_2 \ge (d_1+q_1)v_1$. Combining with the discussion in Step 1, we have $r_2 \ge u_2+v_2+\tau q_2 \ge u_2+u_2+\tau q_1$, which implies $f_2 \le 0$. By $g_1+g_2<0$ we obtain $g_2<0$. Hence $d_1v_3<(d_1+q_1)v_1 \le d_1v_2$, so $v_3<v_2$. Similarly, we get $u_3<u_2$. Then we have

$$r_3 < u_3+v_3+\tau q_2 < u_2+v_2+\tau q_2 \le r_2,$$

a contradiction. Thus $g_1<0$. Similarly, we have $g_2<0$.

Step 3. We claim that $v_2>v_1$ and $v_3>v_1$.

We first prove $v_2>v_1$. Since $(\mathbf{u},\mathbf{v})$ satisfies (22) and $r_i=r$, we can rewrite (22) as

$$\begin{cases} d_1(u_2+u_3-2u_1)=-(r-u_1-v_1-2q_1)u_1, \\ (d_1+q_1)(u_1-u_2)=-(r-u_2-v_2-(\tau-1)q_1)u_2, \\ (d_1+q_1)(u_1-u_3)=-(r-u_3-v_3-(\tau-1)q_1)u_3, \\ d_2(v_2+v_3-2v_1)=-(r-u_1-v_1-2q_2)v_1, \\ (d_2+q_2)(v_1-v_2)=-(r-u_2-v_2-(\tau-1)q_2)v_2, \\ (d_2+q_2)(v_1-v_3)=-(r-u_3-v_3-(\tau-1)q_2)v_3. \end{cases} \tag{39}$$

Suppose that $v_2 \le v_1$. By (39) and $q_2 \ge q_1$, we have

$$r \le u_2+v_2+(\tau-1)q_2 \le u_2+v_2+(\tau-1)q_1 \quad (\tau\in[0,1]).$$

Then from (39) we obtain $u_1 \ge u_2$. Consequently, $u_1+v_1 \ge u_2+v_2$. Thus

$$r \le u_2+v_2+(\tau-1)q_2 \le u_1+v_1+(\tau-1)q_2 \le u_1+v_1.$$

Hence $r-u_1-v_1-2q_1<0$ and $r-u_1-v_1-2q_2<0$. Substituting into (39) yields $u_2+u_3-2u_1>0$ and $v_2+v_3-2v_1>0$. Combined with $u_1 \ge u_2$ and $v_1 \ge v_2$, we deduce $u_3>u_1$ and $v_3>v_1$. One can derive

$$r > u_3+v_3+(\tau-1)q_2 > u_1+v_1+(\tau-1)q_2,$$

a contradiction. Therefore $v_2 > v_1$. A similar argument shows $v_3 > v_1$, and we omit the details.

Step 4. The situation $f_i, g_i < 0$ for all $i = 1, 2$ cannot occur.

Assume that $f_i, g_i < 0$ for $i = 1, 2$. From (31) and Case II, together with Step 3 that $v_2, v_3 > v_1$, we derive the following contradiction:

$$\begin{aligned} 0 > &\big[(d_1 - d_2)(v_2 - v_1) - (q_1 - q_2)v_1\big] f_1 \frac{d_1}{(d_1 + q_1)^2} \\ &+ \big[(d_1 - d_2)(v_3 - v_1) - (q_1 - q_2)v_1\big] f_2 \frac{d_1}{(d_1 + q_1)^2} \\ &= (q_2 - q_1)\tau u_2 v_2 \Big(\frac{d_1}{d_1 + q_1}\Big)^2 + (q_2 - q_1)\tau u_3 v_3 \Big(\frac{d_1}{d_1 + q_1}\Big)^2 \geq 0. \end{aligned}$$

Now we complete the final proof. Assume that a positive equilibrium (u, v) exists. From $f_1 + f_2 < 0$ and the above discussion, one finds that exactly one of f_1, f_2 is negative. We consider two cases:

(a) $g_1, g_2 < 0,\ f_1 < 0,\ f_2 \geq 0$; (b) $g_1, g_2 < 0,\ f_2 < 0,\ f_1 \geq 0$.

For case (a), using (32) one obtains

$$\begin{aligned} 0 > &\big[(d_1 - d_2)(v_2 - v_1) - (q_1 - q_2)v_1\big] f_1 \frac{d_1}{(d_1 + q_1)^2} - (f_2 v_1 - g_2 u_1)\frac{d_1}{d_1 + q_1} \\ &= (q_2 - q_1)\tau u_2 v_2 \Big(\frac{d_1}{d_1 + q_1}\Big)^2 \geq 0, \end{aligned}$$

a contradiction.

For case (b), using (33) one can deduce

$$\begin{aligned} 0 > &\big[(d_1 - d_2)(v_3 - v_1) - (q_1 - q_2)v_1\big] f_2 \frac{d_1}{(d_1 + q_1)^2} - (f_1 v_1 - g_1 u_1)\frac{d_1}{d_1 + q_1} \\ &= (q_2 - q_1)\tau u_3 v_3 \Big(\frac{d_1}{d_1 + q_1}\Big)^2 \geq 0, \end{aligned}$$

again a contradiction. Thus the proof of (ii) is complete. □

Theorem 8. *For Model (II), we have:*

(i) For Case I, $r_1 = r_2 \geq r_3$, system (2) admits no positive equilibrium.

(ii) For Case II, $\tau \in [0, 2]$, system (2) admits no positive equilibrium.

Proof. We first prove (i). Assume that system (2) has a positive equilibrium $(\mathbf{u}, \mathbf{v})$ satisfying (22). For clarity, we divide the proof into several steps.

Step 1. We claim that $f_1' + f_2' < 0$ and $g_1' + g_2' < 0$.

First consider $g_1' + g_2' < 0$. Suppose to the contrary that $g_1' + g_2' \geq 0$. Then at least one of g_1', g_2' is nonnegative. Without loss of generality, assume $g_1' \geq 0$. By (28) and (30), we have $v_3 > v_1$ and $r_1 \leq u_1 + v_1$. Since f_1' and g_1' have the same sign, and f_2' and g_2' have the same sign, thus $f_1' \geq 0$. Consequently $u_3 > u_1$. Then $r_3 \leq r_1 \leq u_1 + v_1 < u_3 + v_3$. On the other

hand, $g_1' + g_2' \geq 0$ implies $r_3 \geq u_3 + v_3$, a contradiction. Hence $g_1' + g_2' < 0$. A similar argument shows $f_1' + f_2' < 0$.

Step 2. We claim that $f_i', g_i' < 0$, $i = 1, 2$.

Since f_1' and g_1' have the same sign, f_2' and g_2' have the same sign, it suffices to show $f_i' < 0$, $i = 1, 2$. Suppose $f_1' \geq 0$. Then from $f_1' + f_2' < 0$ we get $f_2' < 0$. Thus $g_1' \geq 0$, $g_2' < 0$. Using (27) and (28), we have $(d_1 + q_1)u_2 > d_1u_3 \geq (d_1 + q_1)u_1$ and $(d_2 + q_2)v_2 > d_2v_3 \geq (d_2 + q_2)v_1$, so $u_2 > u_1$ and $v_2 > v_1$. From (29), $r_1 \leq u_1 + v_1 < u_2 + v_2$, thus $r_2 < u_2 + v_2$. However, $f_2' < 0$ gives $r_2 > u_2 + v_2$, a contradiction. A similar argument yields $f_2' < 0$.

Now we complete the remaining proof of (i). Assume a positive equilibrium $(\mathbf{u}, \mathbf{v})$ exists. By (37) and (38) we have

$$(d_1 - d_2)(v_3 - v_1) - (q_1 - q_2)v_1 < 0, \quad (d_1 - d_2)(v_3 - v_2) - (q_1 - q_2)v_2 < 0.$$

Combining with (36) we obtain

$$\begin{aligned} 0 > & \big[(d_1 - d_2)(v_1 - v_3) + (q_1 - q_2)v_1\big] f_1' \frac{d_1}{(d_1 + q_1)^2} \\ & + \big[(d_1 - d_2)(v_2 - v_3) + (q_1 - q_2)v_2\big] f_2' \frac{d_1}{(d_1 + q_1)^2} \\ = & (q_1 - q_2)\tau u_3 v_3 \Big(\frac{d_1}{d_1 + q_1}\Big)^2 \geq 0, \end{aligned}$$

a contradiction. This completes the proof of (i).

Now we prove (ii). Assume that system (2) has a positive equilibrium $(\mathbf{u}, \mathbf{v})$ satisfying (22). We divide the proof into steps.

Step 1. We claim that $f_1' + f_2' < 0$, $g_1' + g_2' < 0$, and $f_i', g_i' < 0$.
This step can be established by the same arguments as in Step 1 and Step 2 of the previous proof.

Step 2. We claim that $v_3 > v_1$ and $v_3 > v_2$.
We first prove $v_3 > v_1$. Since $(\mathbf{u}, \mathbf{v})$ satisfies (22) and $r_i = r$, we can rewrite the system as

$$\begin{cases} d_1(u_3 - u_1) = -(r - u_1 - v_1 - q_1)u_1, \\ d_1(u_3 - u_2) = -(r - u_2 - v_2 - q_1)u_2, \\ (d_1 + q_1)(u_1 + u_2 - 2u_3) = -(r - u_3 - v_3 - (\tau - 2)q_1)u_3, \\ d_2(v_3 - v_1) = -(r - u_1 - v_1 - q_2)v_1, \\ d_2(v_3 - v_2) = -(r - u_2 - v_2 - q_2)v_2, \\ (d_2 + q_2)(v_1 + v_3 - 2v_3) = -(r - u_3 - v_3 - (\tau - 2)q_2)v_3. \end{cases} \tag{40}$$

Suppose that $v_3 \leq v_1$. From (40) and $q_2 \geq q_1$, we have

$$r \geq u_1 + v_1 + q_2 \geq u_1 + v_1 + q_1.$$

From (40) we get $u_3 \le u_1$. Using $f_1' < 0$ we obtain $r > u_1 + v_1 \ge u_3 + v_3$. Hence

$$r > u_3 + v_3 + (\tau - 2)q_1 \ge u_3 + v_3 + (\tau - 2)q_2 \quad (\tau \in [0, 2]).$$

Then $u_1 + u_2 - 2u_3 < 0$ and $v_1 + v_2 - 2v_3 < 0$, which imply $u_2 < u_3 \le u_1$ and $v_2 < v_3 \le v_1$. Therefore,

$$r \ge u_1 + v_1 + q_2 \ge u_2 + v_2 + q_2.$$

Substituting into (40) yields $v_3 < v_2$, a contradiction. Hence $v_3 > v_1$. A similar argument shows $v_3 > v_2$.

Now we complete the remaining proof of (ii). Assume a positive equilibrium $(\mathbf{u}, \mathbf{v})$ exists. From the above discussion and (36) we obtain

$$\begin{aligned} 0 < & \big[(d_1 - d_2)(v_1 - v_3) + (q_1 - q_2)v_1\big] f_1' \frac{d_1}{(d_1 + q_1)^2} \\ & + \big[(d_1 - d_2)(v_2 - v_3) + (q_1 - q_2)v_2\big] f_2' \frac{d_1}{(d_1 + q_1)^2} \\ = & (q_1 - q_2)\tau u_3 v_3 \Big(\frac{d_1}{d_1 + q_1}\Big)^2 \le 0, \end{aligned}$$

a contradiction. Thus the proof of (ii) is complete. □

4 Global dynamics of system (2)

In this section, we obtain the global dynamics results for both models. First, for Model (I), we obtain the following results.

Theorem 9. *For Model (I), assume that $d_1 = d_2 = d > 0$, $q_1 > q_2 > 0$, $r_1 \ge r_2 = r_3$, $\tau \in [0, +\infty)$. Then we have:*

(i) If $(\mathbf{0}, \mathbf{v}^*)$ exists, then it is globally asymptotically stable.

(ii) If $(\mathbf{0}, \mathbf{v}^*)$ does not exist, then $(\mathbf{0}, \mathbf{0})$ is globally asymptotically stable.

Proof. We consider two cases: (i) $(\mathbf{0}, \mathbf{v}^*)$ exists, and (ii) $(\mathbf{0}, \mathbf{v}^*)$ does not exist.

For case (i), if $(\mathbf{u}^*, \mathbf{0})$ does not exist, then by Theorem 3 and the theory of monotone dynamical systems, $(\mathbf{0}, \mathbf{v}^*)$ is globally asymptotically stable. If $(\mathbf{u}^*, \mathbf{0})$ exists, Theorem 3 shows that $(\mathbf{u}^*, \mathbf{0})$ is linearly unstable while $(\mathbf{0}, \mathbf{v}^*)$ is linearly stable. Combined with Theorem 7, there is no positive equilibrium, so $(\mathbf{0}, \mathbf{v}^*)$ is globally asymptotically stable.

For case (ii), if $(\mathbf{u}^*, \mathbf{0})$ does not exist, combined with Theorem 7, there is no positive equilibrium, so $(\mathbf{0}, \mathbf{0})$ is globally asymptotically stable. If $(\mathbf{u}^*, \mathbf{0})$ exists, Theorem 3 gives that $(\mathbf{u}^*, \mathbf{0})$ is linearly unstable, and again $(\mathbf{0}, \mathbf{0})$ is globally asymptotically stable. □

Theorem 10. *For Model (I), assume that $d_1 > d_2 > 0$, $q_2 \ge q_1 > 0$, $r_1 = r_2 = r_3 = r > 0$, $\tau \in [0, 1]$, the following statements hold:*

(i) If $(\mathbf{u}^*, \mathbf{0})$ *exists, then it is globally asymptotically stable.*

(ii) If $(\mathbf{u}^*, \mathbf{0})$ *does not exist, then* $(\mathbf{0}, \mathbf{0})$ *is globally asymptotically stable.*

Next, for Model (II), we establish the following global dynamics:

Theorem 11. *For Model (II), assume that* $d_1 = d_2 = d > 0$, $q_1 > q_2 > 0$, $r_1 = r_2 \geq r_3$, $\tau \in [0, +\infty)$. *Then the following statements are valid:*

(i) If $(\mathbf{0}, \mathbf{v}^*)$ *exists, then it is globally asymptotically stable.*

(ii) If $(\mathbf{0}, \mathbf{v}^*)$ *does not exist, then* $(\mathbf{0}, \mathbf{0})$ *is globally asymptotically stable.*

Theorem 12. *For Model (II), assume that* $d_1 > d_2 > 0$, $q_2 \geq q_1 > 0$, $r_1 = r_2 = r_3 = r > 0$, *and* $\tau \in [0, 2]$, *we obtain:*

(i) If $(\mathbf{u}^*, \mathbf{0})$ *exists, then it is globally asymptotically stable.*

(ii) If $(\mathbf{u}^*, \mathbf{0})$ *does not exist, then* $(\mathbf{0}, \mathbf{0})$ *is globally asymptotically stable.*

Remark 1. The proofs of Theorems 10, 11, and 12 are analogous to that of Theorem 9, using the corresponding lemmas for local stability and nonexistence. We omit the details.

Biologically, these results reveal that in an open environment with a distributary three-patch structure, when upstream resources are better than downstream resources and the two species have identical dispersal abilities, a higher advection velocity may become a disadvantage regardless of the magnitude of the downstream loss rate τ. This is because excessive advection intensifies the downstream loss of individuals, making it difficult for the population to sustain itself, whereas a relatively lower advection velocity favors population persistence. In an environment where resources are uniformly distributed and the downstream loss rate τ is small, the species with greater dispersal ability and a lower advection rate gains a competitive advantage.

5 Numerical simulations

In this section, we present numerical simulations for system (2) under Models (I) and (II).

For Model (I) we choose initial values $u(0) = (0.5, 0.3, 0.6)^T$ and $v(0) = (0.5, 0.3, 0.6)^T$. For spatially heterogeneous environment, fix parameters $r_1 = 3$, $r_2 = r_3 = 2$, and $\tau = 1.5$. When $d_1 = d_2 = 1$, $q_1 = 2 > q_2 = 1.5$, as shown in Fig. 2(a)–(b), as time increases, v_i converges to a positive number while u_i tends to zero, i.e., species v wins the competition. This is consistent with the theoretical results.

For spatially homogeneous environment, fix parameters $r_1 = r_2 = r_3 = 1 > 0$ and $\tau = 0.5$. When $d_1 = 1.5 > d_2 = 1$, $q_1 = 1 < q_2 = 2$, as shown in Fig. 2(c)–(d), as time increases, u_i converges to a positive number while v_i tends to zero, again consistent with the theoretical results.

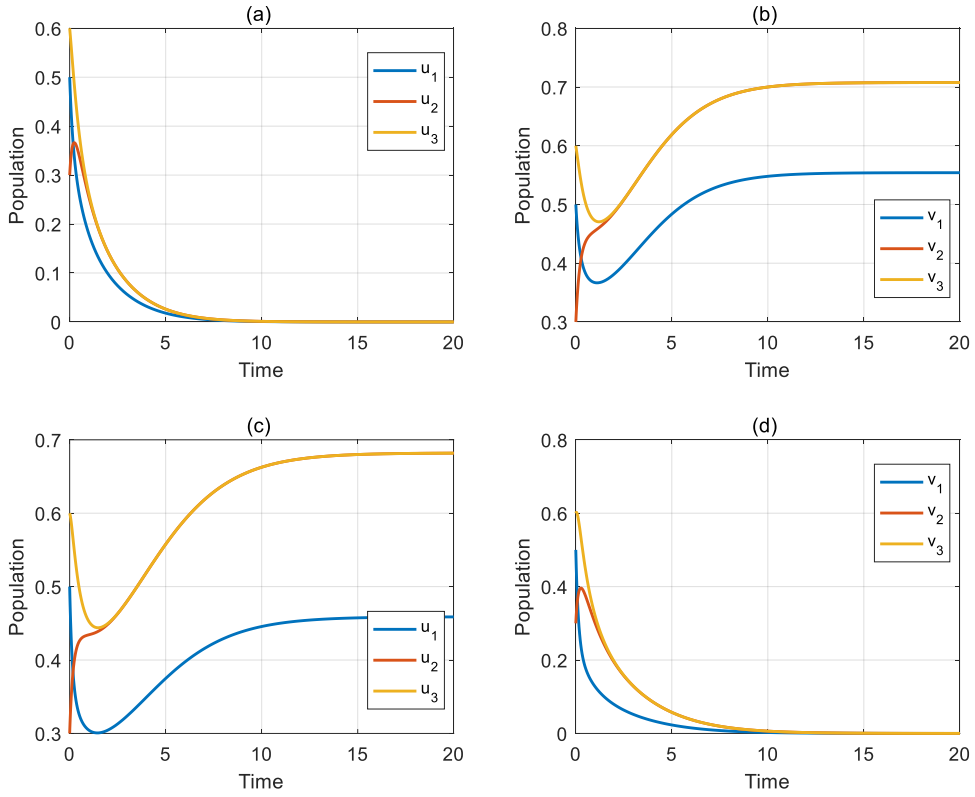


图 2: Numerical simulations of system (2) for Model (I) under two parameter regimes. The initial data are fixed as $u(0) = (0.5, 0.3, 0.6)^T$ and $v(0) = (0.5, 0.3, 0.6)^T$. Panels (a)–(b) correspond to the spatially heterogeneous case with parameters $r_1 = 3$, $r_2 = r_3 = 2$, $\tau = 1.5$, $d_1 = d_2 = 1$, $q_1 = 2 > q_2 = 1.5$. Panels (c)–(d) correspond to the spatially homogeneous case with parameters $r_1 = r_2 = r_3 = 1 > 0$ and $\tau = 0.5$, $d_1 = 1.5 > d_2 = 1$, $q_1 = 1 < q_2 = 2$.

For Model (II) we choose initial values $u(0) = (0.5, 0.3, 0.6)^T$ and $v(0) = (0.5, 0.3, 0.6)^T$.

For spatially heterogeneous environment, fix parameters $r_1 = r_2 = 2 > r_3 = 1$, and $\tau = 3$. When $d_1 = d_2 = 1$, $q_1 = 2 > q_2 = 1.5$, as shown in Fig. 3(a)–(b), as time increases, v_i converges to a positive number while u_i tends to zero, i.e., species v wins the competition, consistent with the theoretical results.

For spatially homogeneous environment, fix parameters $r_1 = r_2 = r_3 = 2$ and $\tau = 2$. When $d_1 = 1.5 \geq d_2 = 1$, $q_1 = 1 < q_2 = 2$, as shown in Fig. 3(c)–(d), as time increases, u_i converges to a positive number while v_i tends to zero, again consistent with the theoretical results.

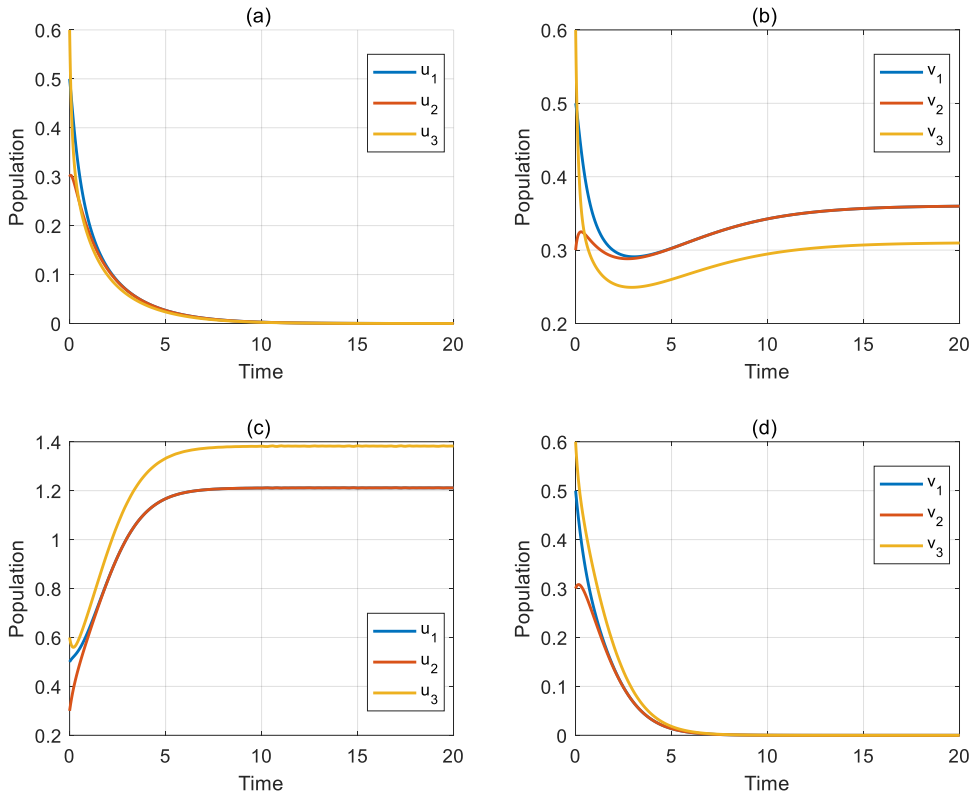


图 3: Numerical simulations of system (2) for Model (II) under two parameter regimes. The initial data are fixed as $u(0) = (0.5, 0.3, 0.6)^T$ and $v(0) = (0.5, 0.3, 0.6)^T$. Panels (a)–(b) correspond to the spatially heterogeneous case with parameters $r_1 = r_2 = 2 > r_3 = 1$, $\tau = 3$, $d_1 = d_2 = 1$, $q_1 = 2 > q_2 = 1.5$. Panels (c)–(d) correspond to the spatially homogeneous case with parameters $r_1 = r_2 = r_3 = 2$ and $\tau = 2$, $d_1 = 1.5 > d_2 = 1$, $q_1 = 1 < q_2 = 2$. The numerical results confirm the global stability predictions in Theorems 11–12.

6 Conclusion and discussion

In this paper, we studied two classes of Lotka–Volterra competition patch models in open branched river networks with downstream loss. For both distributary and confluent structures, we obtained the following conclusions. When upstream resources are superior to or equal to downstream resources, the species with a slower advection rate wins the competition. This result is robust with respect to the downstream loss rate τ. When resources are uniformly distributed, the species with a faster diffusion rate and weaker advection gains the competitive advantage. These results reveal a fundamental ecological rule in open advective environments: advection acts as a net loss mechanism, while larger diffusion can compensate for the directional loss caused by advection.

Our results share similarities with those of Jiang, Lam and Lou [12, 13] and Liu, Liu and Chen [14] in closed three-patch networks, where competitive outcomes are also determined by the relative magnitude of diffusion and advection rates. However, key differences arise due to the open boundary. In closed environments, advection only changes spatial distributions and causes no net loss, whereas in open environments advection leads to permanent loss at the downstream boundary. As a result, fast advection becomes a clear disadvantage, and competitive exclusion is stronger in open systems. Moreover, open environments exhibit an extinction threshold: when advection or loss rates are too large, a single species may fail to establish a positive equilibrium, a phenomenon that does not occur in closed environments. Branching effects are also amplified: distributary structures have losses in two downstream branches separately, while confluent structures have concentrated loss at the downstream junction.

The biological implications of our results can be summarized as slow advection advantage and fast diffusion compensation. Slower advection means longer residence time in upstream patches and reduced risk of being washed out of the system. Larger diffusion helps individuals return to favorable upstream habitats, compensating for advective loss. From a management perspective, species with slower advection and faster diffusion should be prioritized for conservation, while invaders with slow advection plus fast diffusion strategies may pose higher invasion risks. The topology of branched networks should also be considered in river management and reserve design, since distributary and confluent structures differ in their effects on species protection.

Finally, we point out some limitations of this work. Our analysis relies mainly on symmetry assumptions for the three-patch branched structures: for the distributary case, we assume $r_2 = r_3$ and $\tau_1 = \tau_2$ and for the confluent case, we assume $r_1 = r_2$. For non-symmetric branches, where $r_2 \neq r_3$ or $\tau_1 \neq \tau_2$, the proof of nonexistence of positive equilibria becomes more complicated and requires new mathematical tools. In addition, we have only considered the case where both species share the same pattern of resource utilization. Future work will investigate non-symmetric branching structures and the effects of species-specific resource preferences on competition outcomes.

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