Noname manuscript No.
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Three-patch models for the evolution of dispersal in advective environments: varying drift and network topology

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6/30/2021

We study the evolution of dispersal in advective three-patch models with distinct network topologies. Organisms can move between connected patches freely and they are also subject to the passive, directed drift. The carrying capacity is assumed to be the same in all patches, while the drift rates could vary. We first show that if all drift rates are the same, the faster dispersal rate is selected for all three models. For general drift rates, we show that the infinite diffusion rate is a local Convergence Stable Strategy (CvSS) for all three models. However, there are notable differences for three models: For Model I, the faster dispersal is always favored, irrespective of the drift rates, and thus the infinity dispersal rate is a global CvSS. In contrast, for Models II and III a singular strategy will exist for some ranges of drift rates and bi-stability phenomenon happens, i.e. both infinity and zero diffusion rates are local CvSSs. Furthermore, for both Models II and III, it is possible for two competing populations to coexist by varying drift and diffusion rates. Some predictions on the dynamics of n-patch models in advective environments are given along with some numerical evidence.

Keywords River patch model · network topology · evolution of dispersal · varying drift

Mathematics Subject Classification (2010) 34D20 · 92D15 · 92D40

1 Introduction

Since the pioneering work of Speirs and Gurney on the "drift paradox" [47], studying population dynamics in advective environments (such as rivers) has become an active research topic, both empirically as well as theoretically [8, 11, 18, 21–24, 27, 35–37, 42, 50]. Most mathematical models in spatial ecology assume that individuals adopt random movement, i.e. the transition probability in all directions are the same. For the organisms in advective environments, they are

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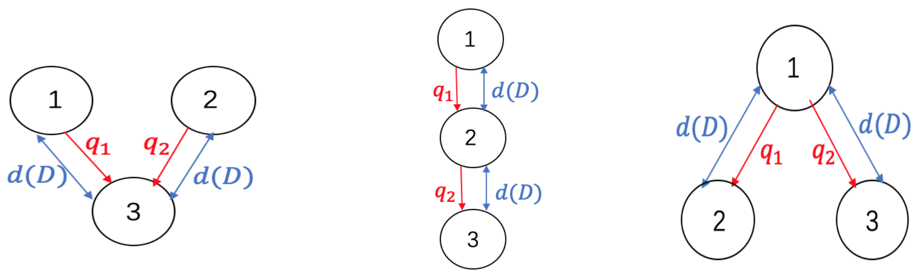
also subject to the passive, uni-directional drift. Such passive drift may push the organisms to the downstream where the environments could become unfavorable. From the mathematical point of view, the addition of drift makes the differential operators under consideration non-symmetric and thus brings new challenges to the stability analysis, especially for those models for interacting species [32, 33, 48, 51–55, 57, 58]. Almost all of these studies assume that the underlying habitat is an interval in the real line, in order to simplify the mathematical analysis. In contrast, there are rather few studies on the population dynamics in river networks, and they are mostly restricted to the case of a single species [25, 43–45, 49].

One important topic in spatial ecology is the evolution of dispersal. The seminal work of Hastings shows that random dispersal is selected against in spatially heterogeneous but temporally constant environments [7, 14], while in spatially and temporally varying environments large dispersal rate can be selected [17, 39]. See the review article [5] and the references therein. The evolution of dispersal in advective and continuous habitats has been recently considered: when the carrying capacity is spatially heterogeneous and the drift rates are constants, some intermediate dispersal rate could be selected; see [10, 26]. However, for a homogeneous environment where both carrying capacity and drift rates are spatially uniform, it was shown that when the loss at the downstream is not significant, the faster dispersal rate is favored [30, 34]; see [13] for more recent progress. Again, these studies assume that the habitat is a finite interval.

Many of the above work employ the conceptual framework of adaptive dynamics theory [6, 9]. A central idea of adaptive dynamics theory is the evolutionarily stable strategy (ESS) [38]. A strategy is called a global ESS if the resident species adopting such a strategy can not be invaded by any rare mutant species using different strategy. Another important concept is the convergence stable strategy (CvSS). A strategy is said to be a global CvSS if the mutant species is always able to invade a resident species when the mutant strategy is closer to the CvSS than the resident strategy. Local ESS and CVSS can be similarly defined and interpreted.

Our aim is to study the evolution of dispersal in discrete, advective environments using the conceptual framework of adaptive dynamics theory. Recently, the authors proposed in [20] to study the dynamics of two competing species in three-patch models with different network topology, and to investigate how the topology of directed river network modules may affect the evolution of dispersal. To be specific, we considered the following three types of river network modules in [20]:



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

Fig. 1: Three river network modules with different topology: The two-way blue arrows represent the dispersal of species between connected patches, the one-way red arrows represent the uni-directional drift. The parameters d, D are dispersal rates for the two competing species, and the parameters q_1, q_2 are drift rates from an upstream patch to a downstream patch.

In Fig. 1(a)-(c) we assume that patch 1 is upstream, patch 3 is downstream, and patch 2 is either upstream, or middle stream, or downstream. In [20] the carrying capacity of three patches are assumed to be different and the drift rates are assumed to be equal. The main findings in [20] are summarized as follows: when the drift rate is small, for all three models the mutant species can invade when rare if and only if it is the slower disperser. However, when the drift rate is large, Models I and II predict that the faster disperser wins, while Model III predicts that fast and slow dispersers may coexist, and that there exists one intermediate strategy which is evolutionarily singular. For the intermediate range of drift, Models I and II predict the existence of one singular strategy, which may or may not be evolutionarily stable, depending upon the topology of modules, while Model III predicts singular strategy may not exist and the faster disperser wins the competition.

The rest of this paper is organized as follows: In Sec. 2 we state the main results for three-patch models. In Sec. 3 we draw the main conclusions and also provide a single framework to unify our main results. In Sec. 4 we present the numerical simulations of some 4-patch models and discuss some predictions on n-patch models. The proofs of the main results for Model I to III are postponed to the Appendices.

2 Main results for three-patch models

In this paper we assume that the drift rates could be different but the carrying capacity are the same in all three patches. As in [20], in all models the two competing species are assumed to be identical except for their dispersal rates.

Our main goal in this paper is to illustrate the effects of varying drift rates and network topology on the evolution of dispersal. The main findings can briefly be summarized as follows:

- If all drift rates are identical, then the faster dispersal rate is selected across all three-patch models in which the drift network do not form a closed cycle.
- For general drift rates, infinite diffusion rate is a local CvSS for all three models.
- For Models II and III, when a singular strategy (that is neither zero nor infinity) exists, it is not a local CvSS (Numerical simulation suggests that it is not an ESS either).
- For Models II and III, when bi-stability occurs, it is possible for two competing populations with different dispersal rates to coexist, by varying the drift rates between patches.

2.1 Main results of Model I

In Model I, the species in patches 1 and 2 are washed down to patch 3 by drift with rates q_1, q_2, respectively. Two competing populations can disperse freely between the upstream patches and the downstream patch, with respective rates d, D. The two upstream patches, however, are not directly connected. The diagram of Model I is shown in Figure 1(a). The dynamics of two competing populations in this river module is described by the following system of ODEs:

$$\begin{cases} \frac{du_1}{dt} = d(u_3 - u_1) - q_1 u_1 + u_1(1 - \frac{u_1+v_1}{k}) \\ \frac{du_2}{dt} = d(u_3 - u_2) - q_2 u_2 + u_2(1 - \frac{u_2+v_2}{k}) \\ \frac{du_3}{dt} = d(u_1 + u_2 - 2u_3) + q_1 u_1 + q_2 u_2 + u_3(1 - \frac{u_3+v_3}{k}) \\ \frac{dv_1}{dt} = D(v_3 - v_1) - q_1 v_1 + v_1(1 - \frac{u_1+v_1}{k}) \\ \frac{dv_2}{dt} = D(v_3 - v_2) - q_2 v_2 + v_2(1 - \frac{u_2+v_2}{k}) \\ \frac{dv_3}{dt} = D(v_1 + v_2 - 2v_3) + q_1 v_1 + q_2 v_2 + v_3(1 - \frac{u_3+v_3}{k}) \\ u_i(0) = u_{i0}, \quad v_i(0) = v_{i0}, \quad i = 1, 2, 3. \end{cases} \tag{1}$$

Here $u_i(t), v_i(t)$ $(i = 1, 2, 3)$ denote the numbers of individuals of the respective species at time t in patch i. The parameter k is the carrying capacity for all patches. For the sake of simplicity, the intrinsic growth rates are assumed to be equal to 1. The initial data of u_i and v_i are assumed to be positive for the rest of the paper so that $u_i(t), v_i(t)$ are positive functions of time $t > 0$.

It can be shown that system (1) has a unique semi-trivial steady state of the form $(U^*, 0) = (U_1^*, U_2^*, U_3^*, 0, 0, 0)$, where $U_i^* > 0$ for $i = 1, 2, 3$.

Theorem 1 *For any $q_1 \geq 0$, $q_2 \geq 0$ and $q_1 + q_2 > 0$, if $d > D$, then $(U^*, 0)$ is globally asymptotically stable among all solutions of* (1) *with positive initial data.*

This result implies that the faster dispersal is always selected for Model I, provided that the carrying capacity is uniform in the habitat, and the conclusion is independent of the drift rates. The underlying biological intuition is that a single population at equilibrium (i.e. resident) is undermatching the resources in at least one of the two upstream patches and it is always overmatching the resource in the downstream patch; i.e. the downstream patch is always a sink and at least one of the upstream patches is a source. If a mutant with small diffusion rate is introduced, its individuals in the upstream patches will be washed to the downstream patch, where the mutant can not invade when rare as the downstream patch is a sink. Hence, small diffusion rate is selected against. In contrast, faster diffusion can counterbalance the drift by keeping more mutant individuals in upstream patches, one of which is a source patch, and thus help the mutant populations establish in this upstream source patch.

2.2 Main results of Model II

Model II assumes that individuals in patch 1 are transported to patch 2 by drift with rate q_1, and individuals in patch 2 are transported to patch 3 by drift with rate q_2. Individuals can also move between patches i and $i+1$ for $i = 1, 2$; see Fig. 1(b). The dynamics of two competing species in this network module is governed by the following ODE system:

$$\begin{cases} \frac{du_1}{dt} = d(u_2 - u_1) - q_1 u_1 + u_1(1 - \frac{u_1+v_1}{k}) \\ \frac{du_2}{dt} = d(u_1 + u_3 - 2u_2) + q_1 u_1 - q_2 u_2 + u_2(1 - \frac{u_2+v_2}{k}) \\ \frac{du_3}{dt} = d(u_2 - u_3) + q_2 u_2 + u_3(1 - \frac{u_3+v_3}{k}) \\ \frac{dv_1}{dt} = D(v_2 - v_1) - q_1 v_1 + v_1(1 - \frac{u_1+v_1}{k}) \\ \frac{dv_2}{dt} = D(v_1 + v_3 - 2v_2) + q_1 v_1 - q_2 v_2 + v_2(1 - \frac{u_2+v_2}{k}) \\ \frac{dv_3}{dt} = D(v_2 - v_3) + q_2 v_2 + v_3(1 - \frac{u_3+v_3}{k}) \\ u_i(0) = u_{i0}, \quad v_i(0) = v_{i0}, \quad i = 1, 2, 3. \end{cases} \tag{2}$$

For Model II, it can also be shown that system (2) has a unique semi-trivial steady state of the form $(U^*, 0) = (U_1^*, U_2^*, U_3^*, 0, 0, 0)$, where $U_i^* > 0, i = 1, 2, 3$.

Theorem 2 *If $q_1 \geq 1$ or $\frac{q_2}{2} < q_1 < 1$, then $(U^*, 0)$ is globally asymptotically stable for $d > D$; i.e. the faster diffuser wins.*

If $q_1 \geq 1$ and the diffusion rate of a species is small, then almost all of its individuals in patch 1 are washed out. Thus, small diffusion is not favored in this scenario. However, large diffusion will be selected as it can counterbalance the uni-dimensional drift by helping more individuals stay in patch 1. Similar intuition applies to the case $q_2/2 < q_1 < 1$, but the detail is more subtle: when diffusion rate is small, our analysis reveals that there will be more individuals in patch 2 than patch 1 when $q_2/2 < q_1 < 1$; i.e. the population in patch 1 is undermatching the resource more than in patch 2 (as carrying capacity in patches 1 and 2 are the same), so small diffusion is still not favored in this scenario.

Theorem 3 *If* $0 < q_1 < 1$ *and* $q_2 > 2q_1$*, there exists some* $d^* = d^*(q_1, q_2) > 0$ *which is an evolutionarily singular strategy. Moreover, this strategy is not a CvSS, and both zero and infinity dispersal rates are local CvSSs.*

It is interesting that zero diffusion rate emerges as a local CvSS under the assumptions of Theorem 3. Suppose the diffusion is zero or very small. On one hand, when $q_1 < 1$, the drift out of patch 1 is small enough to allow the population to persist in patch 1, which is a source. On the other hand, $q_2 > 2q_1$ drive the population in patch 2 down and that in patch 3 up. Hence, patch 2 becomes a source and patch 3 becomes a sink. Moreover, diffusion takes individuals out of patch 1, but due to the uneven drift rates those individuals are more likely to end up in patch 3 (the sink) than in patch 2 (the source). Hence, increasing diffusion will move individuals from source patch to sink patch. Thus, small diffusion can be favored in this case as the drift forces more individuals to move from patch 1 to 2 to reduce the mismatch in patch 2.

When both zero and infinity dispersal rates are local CvSSs, a natural question is whether two competing populations can coexist. Our next result answers this question partially but positively:

Theorem 4 *Fix any* $k, D, q_2 \geq 1$*. Then there exists some* $\delta > 0$ *such that for any* $d \in (0, \delta)$*,* $q_1 \in (-d, \delta)$*, Model* II *has a globally asymptotically stable positive steady state, denoted by* (U^δ, V^δ)*, which satisfies* $(U^\delta, V^\delta) \to (\hat{U}, \hat{V})$ *as* $d \to 0$ *and* $q_1 \to 0$*, where*

$$\hat{U} := (k - \hat{V}_2, 0, 0), \qquad \textit{and} \qquad \hat{V} := (\hat{V}_2, \hat{V}_2, \hat{V}_3) \tag{3}$$

such that $(\hat{V}_2, \hat{V}_3)$ *is the unique positive solution of the two-patch system*

$$\begin{cases} D(\hat{V}_3 - \hat{V}_2) - q_2\hat{V}_2 + \hat{V}_2(1 - \frac{\hat{V}_2}{k}) = 0 \\ D(\hat{V}_2 - \hat{V}_3) + q_2\hat{V}_2 + \hat{V}_3(1 - \frac{\hat{V}_3}{k}) = 0. \end{cases} \tag{4}$$

This result suggests that when the drift from patch 1 to patch 2 is very small, slow and fast diffusers can coexist in some interesting way: the slow diffuser will only occupy patch 1 and the fast diffuser is dominant in patch 2 and 3, but not in patch 1. Intuitively, the underlying mechanism for the coexistence is as follows: Consider the case $d = 0$ and $q_1 = 0$ for the sake of clarity, so that patch 1 is disconnected from patches 2 and 3 for the species u. It turns out that, due to $d = 0$ and $q_1 = 0$, the flux between patches 1 and 2 for the species v is also equal to zero. As a consequence, system (2) for patches 2 and 3 is reduced to a two-patch system for two competing species. It follows from previous work [12, 41] for two-patch models that the faster diffuser always out-competes the slower diffuser in patches 2 and 3, provided that $q_2 > 0$. As patch 2 is at the upstream for the reduced two-patch model, the equilibrium distribution of species v, denoted by $\hat{V}_2$, satisfies $\hat{V}_2 < k$; i.e. it undermatches the resource in patch 2. As there is no flux for species v between patches 1 and 2 and $q_1 = 0$, the equilibrium distribution of species v at patch 1 is also equal to $\hat{V}_2$, so that the equilibrium distribution of species u at patch 1 is given by $k - \hat{V}_2 > 0$. The case of small d, q_1 follows from a perturbation argument.

Note that $q_1 = 0$ and small negative q_1 are also covered by Theorem 4; the case of negative q_1 applies to Model III.

2.3 Main results of Model III

Model III assumes patch 1 is upstream, whereas patches 2 and 3 are downstream. Both species in patch 1 are transported to patches 2 and 3 by drift with rates q_1 and q_2, respectively. In this case we have the following ODE system for two competing species:

$$\begin{cases} \frac{du_1}{dt} = d(u_2 + u_3 - 2u_1) - (q_1 + q_2)u_1 + u_1(1 - \frac{u_1+v_1}{k}) \\ \frac{du_2}{dt} = d(u_1 - u_2) + q_1 u_1 + u_2(1 - \frac{u_2+v_2}{k}) \\ \frac{du_3}{dt} = d(u_1 - u_3) + q_2 u_1 + u_3(1 - \frac{u_3+v_3}{k}) \\ \frac{dv_1}{dt} = D(v_2 + v_3 - 2v_1) - (q_1 + q_2)v_1 + v_1(1 - \frac{u_1+v_1}{k}) \\ \frac{dv_2}{dt} = D(v_1 - v_2) + q_1 v_1 + v_2(1 - \frac{u_2+v_2}{k}) \\ \frac{dv_3}{dt} = D(v_1 - v_3) + q_2 v_1 + v_3(1 - \frac{u_3+v_3}{k}) \\ u_i(0) = u_{i0}, \quad v_i(0) = v_{i0}, \quad i = 1, 2, 3. \end{cases} \tag{5}$$

The dynamics of (5) is more subtle than those for Models I and II. We first consider the global dynamics of Model III.

Theorem 5 *If $q_1 = q_2 > 0$, then the semi-trivial steady state $(U^*, 0)$ is globally asymptotically stable for $d > D$.*

Theorem 5 seems to agree with previous results for two-patch models that the faster diffuser always out-competes the slower diffuser [12,41]. The biological intuition is that both downstream patches are sinks under the assumption of Theorem 5; see also Corollary 6 (in Appendix C). Hence, any mutant in the upstream patch with smaller diffusion rate will more likely be pushed to two downstream sinks and thus can not invade when rare.

Next we consider the local dynamics of Model III.

Theorem 6 *If $q_1, q_2 > 0$, $|q_2 - q_1| \le \frac{1}{2}$ and $\frac{1}{\sqrt{2}} \le \frac{q_2}{q_1} \le \sqrt{2}$, then the semi-trivial steady state $(U^*, 0)$ is locally stable for $d > D$ and unstable for $d < D$.*

Theorem 6 implies that infinite diffusion rate is a global CvSS when two drift rates are comparable. This is in the same spirit as Theorem 5 since both downstream patches are still sinks under the assumption of Theorem 6; see also Corollary 8 (in Appendix C). In contrast, our next result shows that if two drift rates are not comparable, both zero and infinite diffusion rates are local CvSS.

Theorem 7 *If $1 < q_1 + q_2 < (q_1 - q_2)^2$, then there exists some $d^* = d^*(q_1, q_2) > 0$ which is an evolutionarily singular strategy. Moreover, d^* is not a CvSS, and both zero and infinity dispersal rates are local CvSSs.*

To see why zero diffusion can be a local CvSS under the assumptions of Theorem 7, first fix q_1 and choose q_2 large. This will drain almost all individuals in patch 1 to drift to patch 3, so that patch 3 becomes a sink patch due to overcrowding. Subsequently, diffusion induces a net flux of individuals from patch 2 to patch 1, so that the population in patch 2 undermatches the resource. Hence, any mutant with smaller diffusion rate can invade when rare by exploiting patch 2, which is a source patch. The same intuitive reasoning applies to the general situation: for the range of q_i in Theorem 7, our numerical results suggest that one of the two downstream patches is a sink while the other becomes a source patch, and a mutant with smaller diffusion rate can invade when rare in the downstream source patch.

3 Conclusions

In this section we first summarize the main analytical results, and then we provide a single framework to unify the main results for three models. The main findings are as follows, along with some predictions (see Sect. 4 for further discussions):

- If all drift rates are identical, then the faster dispersal rate is selected across all three-patch models in which the drift network do not form a closed cycle. A conjecture is that this result holds for n-patch river networks with uniform carrying capacity and identical drift rates, provided that the drift network is not divergence-free (a drift network with identical drift rates is called divergence-free if each individual patch has the same number of upstream and downstream patches);
- For general drift rates, infinite diffusion rate is a local CvSS for all three models. Biologically this makes good sense as with sufficiently fast dispersal, the spatial distribution of the species approaches the ideal free distribution. However, there are some notable differences for three models: For Model I, the faster dispersal is always favored and thus infinity is a global CvSS. For Models II and III, the answers depend upon the drifts rates: for some ranges of drift rates, infinity is a global CvSS (same as Model I), while for other ranges of drift rates, there exists some intermediate diffusion rate which is a singular strategy so that infinity is a local CvSS but not a global one. A conjecture is that the infinite diffusion rate is a local CvSS for n-patch river networks with uniform carrying capacity and general drift rates;
- For Models II and III, when a singular strategy (that is neither zero nor infinity) exists, it is not a local CvSS (Numerical simulation suggests that it is not an ESS either). In fact, bi-stability phenomenon happens, i.e. both infinity and zero diffusion rates are local CvSSs;
- For Models II and III, when bi-stability occurs, it is possible for two competing populations with different dispersal rates to coexist, by varying the drift rates between patches. A conjecture is that any coexistence steady state for Models II-III, if exists, is globally stable.

Next, we provide a single framework to unify the main results for Models I-III. Our idea is to use a single system of ODEs to describe all three models. Without loss of generality, consider system (2) in the $q_1 - q_2$ plane, allowing the drift rates in system (2) to take both positive and negative values. That is, we divide the $q_1 - q_2$ plane into 4 quadrants. Then the first quadrant of Fig. 2 corresponds to Model II with non-negative drift rates.

- First quadrant: Theorem 2 implies that the faster diffuser always wins for q_1, q_2 in the red region; for the blue region, Theorem 3 ensures the existence of an evolutionarily singular strategy, where both zero and infinity dispersal rates are local CvSSs.
- Second quadrant: With $q_1 < 0$ and $q_2 > 0$ in system (2), the directed flows are from patch 2 to patches 1 and 3. Hence, this corresponds to Model III with patches 1 and 2 switched. Theorem 6 implies that the faster diffuser wins for q_1, q_2 in the red region; for the blue region, Theorem 7 ensures the existence of an evolutionarily singular strategy, in which both zero and infinity dispersal rates are local CvSSs.
- Third quadrant: With $q_1 < 0$ and $q_2 < 0$ in system (2), the directed flows are from patch 3 to 2, and from patch 2 to 1. Hence, this corresponds to Model II with patches 1 and 3 switched. Hence the red and blue regions are symmetric to those in the 1st quadrant with respect to the line $q_1 + q_2 = 0$.
- 4th quadrant: With $q_1 > 0$ and $q_2 < 0$ in system (2), the directed flows are from patches 1 and 3 to patch 2. Hence, this corresponds to Model I with patches 2 and 3 switched. Theorem 1 implies that the faster diffuser always wins for q_1, q_2 in 4th quadrant.

These discussions suggest that the $q_1 - q_2$ plane can also be divided into three colored regions as in Fig. 2: For the red region, the infinite diffusion rate is a global CvSS; In the blue region, both zero and infinite diffusion rates are local CvSSs; For the white region, numerical simulations suggest that the infinite diffusion rate is a local CvSS but might not be a global one, and the zero diffusion rate might not even be a local CvSS.

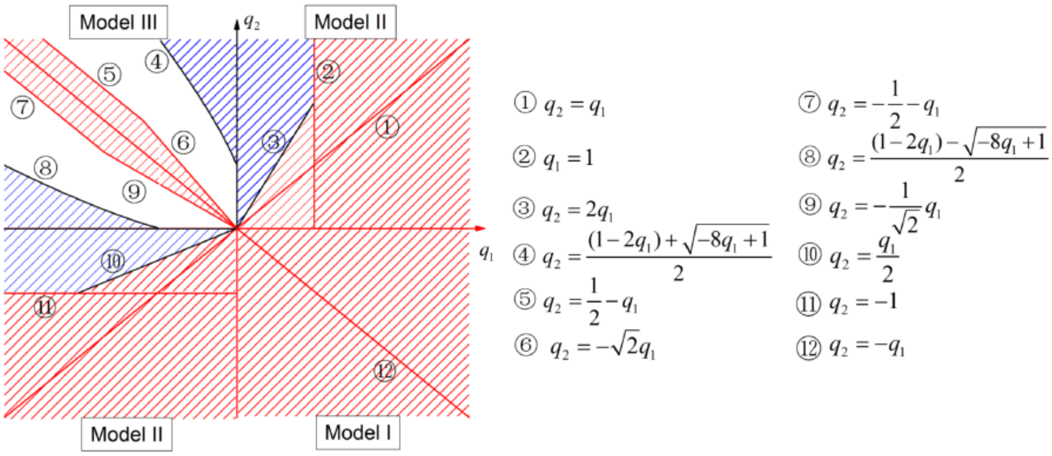


Fig. 2: The dynamics for Models I-III. The red colored regions correspond to the ranges of q_1, q_2 for which the infinite diffusion rate is a global CvSS; In the blue colored regions, there is at least one evolutionarily singular strategy and both infinity and zero diffusion rates are local CvSSs; The dynamics of Model III in the white colored regions is not fully determined theoretically.

4 Discussion and numerical results for four-patch model

In this section, we will discuss possible extensions to n-patch river network models and raise some conjectures on the evolution of faster dispersal. We will also address the issue of the invasion of slowly diffusing populations and propose to study the coexistence of slow and fast diffusing competing populations.

4.1 Evolution of fast dispersal in n-patch model

Theorems 1, 2 and 5 show that if $q_1 = q_2$, the faster diffusing population always wins the competition for Models I-III. In particular, infinity as a diffusion rate is a global CvSS for Model I and also for wider ranges of parameters in both Models II and III; see Theorems 2 and 6.

Consider the general n-patch river model, i.e.

$$\begin{cases} \frac{du_i}{dt} = d\sum_{j=1}^n m_{ij}u_j + \sum_{j=1}^n q_{ji}u_j + u_i(1 - \frac{u_i+v_i}{k_i}), & 1 \le i \le n, \\ \frac{dv_i}{dt} = D\sum_{j=1}^n m_{ij}v_j + \sum_{j=1}^n q_{ji}v_j + v_i(1 - \frac{u_i+v_i}{k_i}), & 1 \le i \le n. \end{cases}$$

Here the connectivity matrix $M := (m_{ij})$ is assumed to be symmetric, $m_{ij} = m_{ji} = 1$ when two patches i and j are directly connected, $m_{ij} = m_{ji} = 0$ when they are not directly connected, and $m_{ii} = -\sum_{j\neq i} m_{ij}$. The drift matrix $Q := (q_{ij})$ satisfies $q_{ii} = -\sum_{j\neq i} q_{ji}$, $q_{ij} > 0$ when patches i and j are connected and the directed flow is from patch i to j, and $q_{ij} = 0$ otherwise. The case $m_{ij} = 1$ but $q_{ij} = 0$ refers to the scenario when patches i, j are directly connected but there is no directed passive flow in between. Note that under our assumption, the dominant eigenvalue of Q is zero, with left eigenvector being $(1, \cdots, 1)$, i.e.

$$(1, \cdots, 1)Q = 0.$$

The positive constant k_i is the carrying capacity of patch i.

Definition 1 We say that the drift matrix $Q = (q_{ij})$ is divergence-free if its right eigenvector, corresponding to the zero eigenvalue, is given by $(1, \cdots, 1)^T$, i.e.

$$\sum_{j:j\neq i} q_{ij} = \sum_{j:j\neq i} q_{ji} \quad \text{holds for each } i.$$

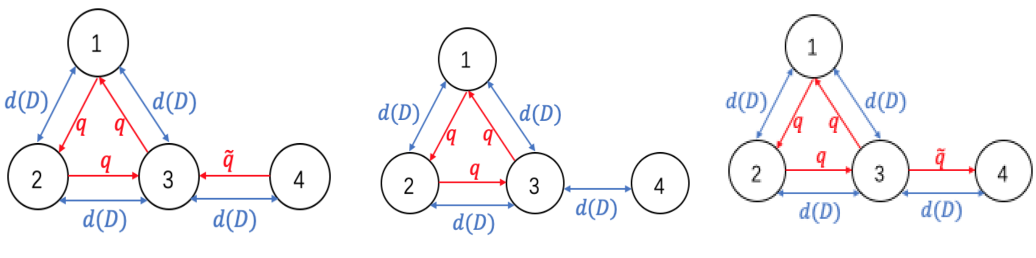
Conjecture 1 If all positive drift rates are equal, the carrying capacity is the same for all patches, and the drift network (q_{ij}) is not divergence-free, then the faster disperser always wins.

For general drift rates, Theorem 1 shows that infinite dispersal rate is a global CvSS for Model I, while for Models II and III, Lemmas 15 (in Appendix B) and 36 (in Appendix C) find that infinity is always a local CvSS.

Conjecture 2 For n-patch model with general drift rates, when the drift matrix is not divergence-free and that the carrying capacity is the same for all patches, the infinite diffusion rate is always a local CvSS.

From the biological point of view, when $k_i = k$ for all i, for a single species with sufficiently fast diffusion, its equilibrium will be close to $(k, \cdots, k)$, which is an ideal free distribution. Heuristically, if a strategy can help organisms reach the ideal free distribution at equilibrium, then the strategy is likely to be a local ESS and/or CvSS; see [1,3,4,31]. Again, we may need to exclude the exceptional case $(1, \cdots, 1)^T$ being a right eigenvector of matrix Q.

To support the above predictions for n-patch models, we performed some numerical simulations for the following four-patch models with the network topology as shown in Fig. 3:



(a) (b) (c)

Fig. 3: The two-way blue arrows represent the dispersal of species between connected patches, the one-way red arrows represent the uni-directional drift. The parameter d, D are dispersal rates for two competing species, and the parameters $q, \tilde{q}$ are drift rates. Patches 1-3 form a loop. Patch 4 is at the upstream in Fig. 3(a) and it is the downstream patch in Fig. 3(c). There is no drift between patches 3 and 4 in Fig. 3(b).

For 4-patch model with topology Fig. 3(a), our simulation results suggest that for any $\tilde{q} > 0$, the faster diffusing species always wins the competition, and the conclusion is independent of drift rates. In particular, the faster dispersal rate is selected when $\tilde{q} = q$, which is consistent with Conjectures 1 and 2.

Fig. 3(b) can also be viewed as Fig. 3(a) and 3(c) with $\tilde{q} = 0$. For this special case, $(k, \cdots, k)$ is the unique positive equilibrium for the corresponding single species model. This gives an example of the exceptional case discussed earlier for n-patch models. As predicted earlier, our numerical simulations show that two populations with different dispersal rates coexist, i.e., the faster diffusing species does not win the competition in this exceptional case.

The PIP for 4-patch model with topology Fig. 3(c) is shown in Fig. 4. We take $d \in [0, 2]$ and $D \in [0, 2]$, and then we discretize the interval $[0, 2]$ with the uniform step $\Delta = 0.02$. The parameter values (k_1, k_2, k_3, k_4) are set to be $(7, 7, 7, 7)$ and $q = 1$, $\tilde{q}$ ranges from 0.01 to 2000. Our simulations (see Fig. 4) suggest more complicated dynamics: when $\tilde{q} \in (0, q]$, the faster diffusing populations still wins. In particular, the fast dispersal rate is selected when $\tilde{q} = q$, which is consistent with Conjectures 1 and 2. However, for $\tilde{q}$ larger than q, there are two evolutionarily singular strategies, one is a local ESS and CvSS, and the other is neither an ESS not CvSS. Furthermore, the infinite diffusion rate remains as a local CvSS as predicted, while the zero diffusion rate is not a local CvSS.

4.2 Evolution of slow dispersal and coexistence

Theorems 3 and 7 illustrate the existence of evolutionarily singular strategy for Models II and III, respectively. These singular strategies are not local CvSSs, and numerical simulations suggest they are not local ESSs either. In fact, Lemmas 16 (in Appendix B) and 37 (in Appendix C) show that zero diffusion rate can be a local CvSS for some parameter ranges in both Models II and III.

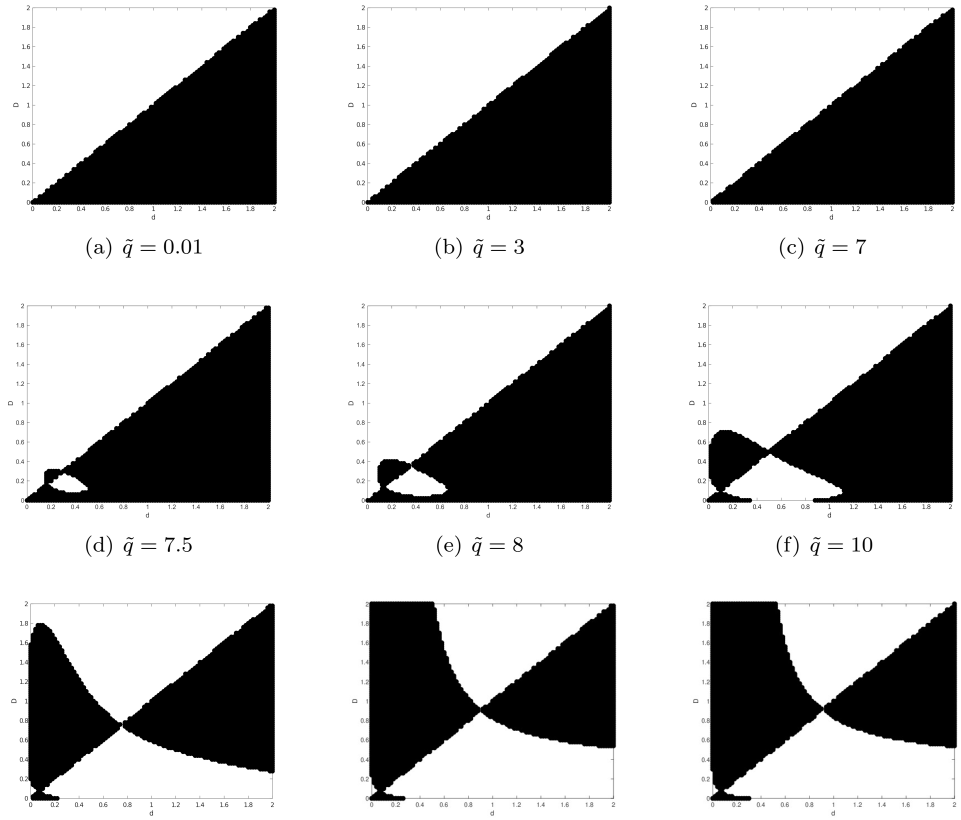
A natural question for general n-patch model is when zero diffusion rate can be a local CvSS. The analysis of Model III reveals that if there are more than one downstream patches, then it is possible for one of them to be a source patch, so that a mutant with slow diffusion rate can invade when rare in this source patch. For n-patch models it will be of interest to find sufficient conditions on the existence of some downstream source patch, by taking into account of the river network topology, so that slow diffusing populations can invade such source patch when rare.

For general n-patch models, when both zero and infinite diffusion rate are local CvSSs, it is natural to inquire whether slow and fast diffusers can coexist. It will be of interest to generalize Theorem 4 to n-patch models and to reveal the impact of network topology on the coexistence of competing species.

Appendix A The global dynamics of Model I

In this section, we mainly study the global dynamics of Model I. By the monotone dynamical system theory [16, Theorem 1.5] (see also [19,28,46]), in order to show the global stability of the semi-trivial steady state $(U^*, 0)$, we need to show the linear instability of the other semi-trivial steady state $(0, V^*)$ and the non-existence of positive steady state of (1).

By replacing u_i and v_i by ku_i and kv_i, for all i, we may assume without loss of generality that $k = 1$. **Henceforth, we will prove our theorems concerning Models I, II and III only for the case $k = 1$.**



(a) $\tilde{q} = 0.01$ (b) $\tilde{q} = 3$ (c) $\tilde{q} = 7$

(d) $\tilde{q} = 7.5$ (e) $\tilde{q} = 8$ (f) $\tilde{q} = 10$

(g) $\tilde{q} = 20$ (h) $\tilde{q} = 200$ (i) $\tilde{q} = 2000$

Fig. 4: Pairwise invasion plots (PIPs) for the four-patch model with network topology Fig. 3(c). $k_1 = k_2 = k_3 = k_4 = 7$, $q = 1$ and $\tilde{q}$ ranges from 0.01 to 2000. The horizontal axis is d and the vertical axis is D. The black regions represent the range of (d, D) for which $(U^*, 0)$ is locally stable.

A.1 Preliminary estimates on non-negative, non-trivial steady states

In this subsection, we consider non-negative and non-trivial solutions of Model I. After setting $k = 1$, they satisfy the following system:

$$\begin{cases} d(U_3 - U_1) - q_1 U_1 + U_1(1 - U_1 - V_1) = 0 \\ d(U_3 - U_2) - q_2 U_2 + U_2(1 - U_2 - V_2) = 0 \\ d(U_1 + U_2 - 2U_3) + q_1 U_1 + q_2 U_2 + U_3(1 - U_3 - V_3) = 0 \\ D(V_3 - V_1) - q_1 V_1 + V_1(1 - U_1 - V_1) = 0 \\ D(V_3 - V_2) - q_2 V_2 + V_2(1 - U_2 - V_2) = 0 \\ D(V_1 + V_2 - 2V_3) + q_1 V_1 + q_2 V_2 + V_3(1 - U_3 - V_3) = 0 \end{cases} \tag{6}$$

When $d, D > 0$, it follows from irreducibility of system (6) that there are at most three types of non-negative and non-trivial solutions, namely: semi-trivial equilibria $(U^*, 0)$, $(0, V^*)$ and positive solutions for which $U_i > 0$, $V_i > 0$, $i = 1, 2, 3$. Hence, for the simplicity of notation, in this subsection we may denote all of these different types of solutions as (U, V), with the understanding that there are only three possibilities for all $i = 1, 2, 3$: $U_i > 0$ and $V_i = 0$, or $U_i = 0$ and $V_i > 0$, or $U_i > 0$ and $V_i > 0$. We shall establish some *a prior* estimates of (U, V).

Lemma 1 *Assume* $q_1, q_2 \geq 0$, $(q_1, q_2) \neq (0, 0)$ *and* $d, D > 0$.

(i) *If* $q_1 \geq q_2$, *then* $U_1 \leq U_2$ *and* $V_1 \leq V_2$.
(ii) *If* $q_1 \leq q_2$, *then* $U_1 \geq U_2$ *and* $V_1 \geq V_2$.

In particular, if $q_1 = q_2$, *then* $U_1 = U_2$ *and* $V_1 = V_2$.

Proof For part (i) we shall prove $U_1 \leq U_2$ only, as $V_1 \leq V_2$ follows from a similar argument. We argue by contradiction: if not, assume that there exist some $q_1 \geq q_2$ and a non-negative, non-trivial solution of (6) such that $U_1 > U_2$. By the first and second equations of (6), we get

$$(-d - q_1 + 1 - U_1 - V_1)U_1 = (-d - q_2 + 1 - U_2 - V_2)U_2 = -dU_3 < 0, \tag{7}$$

so that $-d - q_i + 1 - U_i - V_i < 0$, $i = 1, 2$. Due to $U_1 > U_2$, (7) implies

$$(-d - q_1 + 1 - U_1 - V_1)U_1 > (-d - q_2 + 1 - U_2 - V_2)U_1, \tag{8}$$

and thus

$$q_2 - q_1 > (U_1 + V_1) - (U_2 + V_2), \tag{9}$$

which together with $q_1 \geq q_2$ implies that $U_1 + V_1 < U_2 + V_2$. This implies $(V_1, V_2) \neq (0, 0)$ and $V_2 > V_1 > 0$. Therefore, similar to (8), the equations of V_1 and V_2 from (6) imply

$$(-D - q_1 + 1 - U_1 - V_1)V_1 < (-D - q_2 + 1 - U_2 - V_2)V_1,$$

which implies $q_2 - q_1 < (U_1 + V_1) - (U_2 + V_2)$. This, however, contradicts (9). Therefore, $U_1 \leq U_2$ holds. This proves (i). The conclusion in (ii) follows by exchanging patches 1 and 2.

Lemma 2 *Assume* $q_1, q_2 \geq 0$ *and* $(q_1, q_2) \neq (0, 0)$. *For any* $d, D > 0$,

(i) *if* $q_1 \geq q_2$, *then* $U_1 + V_1 < 1 < U_3 + V_3$;
(ii) *if* $q_1 \leq q_2$, *then* $U_2 + V_2 < 1 < U_3 + V_3$.

In particular, when $q_1 = q_2$, $U_1 + V_1 = U_2 + V_2 < 1 < U_3 + V_3$.

Proof As the proofs of (i) and (ii) are similar, we only prove (i). Firstly, we show

$$U_1 + V_1 < 1. \tag{10}$$

We argue by contradiction: If not, there exist some $q_1 \geq q_2$ and a non-negative non-trivial solution such that $U_1 + V_1 \geq 1$; i.e. $1 - U_1 - V_1 \leq 0$. We claim that

$$U_3 + V_3 > U_1 + V_1 \geq 1. \tag{11}$$

Without loss of generality, we may assume (U_i) is non-trivial, so that the first equation of (6) implies that $U_3 \geq \frac{d+q_1}{d} U_1 > U_1$. If (V_i) is trivial then (11) holds. If not, then applying similar reasoning to the fourth equation of (6), we also get $V_3 \geq \frac{D+q_1}{D} V_1 > V_1$. This proves (11) for any non-negative solutions. Due to $q_1 \geq q_2$, we get $U_2 + V_2 \geq U_1 + V_1 \geq 1$ by Lemma 1, thus

$$U_1(1 - U_1 - V_1) + U_2(1 - U_2 - V_2) + U_3(1 - U_3 - V_3) < 0.$$

However, adding the equations of U_1, U_2, U_3 in (6), we get

$$U_1(1 - U_1 - V_1) + U_2(1 - U_2 - V_2) + U_3(1 - U_3 - V_3) = 0. \tag{12}$$

This is a contradiction. This proves (10).

Next, we claim

$$U_3 + V_3 > 1. \tag{13}$$

We again argue by contradiction and assume that there exist some $q_1 \geq q_2$ and a non-negative non-trivial solution such that (U_i) is non-trivial and $U_3 + V_3 \leq 1$. From the third equation of (6), we obtain

$$d(U_1 + U_2 - 2U_3) + q_1U_1 + q_2U_2 \leq 0,$$

which together with $U_1 \leq U_2$ (Lemma 1) implies

$$2d(U_1 - U_3) + q_1U_1 + q_2U_2 \leq 0.$$

Hence $U_1 < U_3$. If (V_i) is non-trivial, then we can get $V_1 < V_3$ by the same method. Therefore, $U_1 + V_1 < U_3 + V_3 \leq 1$. In view of (12), we have also

$$U_2 + V_2 > 1 \geq U_3 + V_3.$$

Using the second equation of (6), we get $U_3 > U_2$, which implies $V_3 < V_2$. Hence, by the equation of V_2 in (6), we get $1 - U_2 - V_2 > 0$, i.e., $U_2 + V_2 < 1$, which is again impossible. Hence, we proved (13). The proof of (i) is completed.

Lemma 3 *Assume $q_1, q_2 \geq 0$, $(q_1, q_2) \neq (0, 0)$, and $d, D > 0$.*

(i) *If $q_1 \geq q_2$, and $(U_1, U_2, U_3) \neq (0, 0, 0)$, then $U_1 \leq U_2 < U_3$.*
(ii) *If $q_1 \geq q_2$, and $(V_1, V_2, V_3) \neq (0, 0, 0)$, then $V_1 \leq V_2 < V_3$.*
(iii) *If $q_1 \leq q_2$, and $(U_1, U_2, U_3) \neq (0, 0, 0)$, then $U_2 \leq U_1 < U_3$.*
(iv) *If $q_1 \leq q_2$, and $(V_1, V_2, V_3) \neq (0, 0, 0)$, then $V_2 \leq V_1 < V_3$.*

In particular, if $q_1 = q_2$ then every positive equilibrium satisfies $U_1 = U_2 < U_3$, $V_1 = V_2 < V_3$.

Proof We only prove (i) as (ii)-(iv) follow from a similar argument. To this end, we assume $(U_1, U_2, U_3) \neq (0, 0, 0)$ and prove $U_1 \leq U_2 < U_3$. From Lemma 1, it suffices to prove $U_3 > U_2$. Suppose to the contrary that $q_1 \geq q_2$ and there is a nonnegative solution such that $(U_1, U_2, U_3) \neq (0, 0, 0)$ and $U_3 \leq U_2$. We claim that $U_3 + V_3 \leq U_2 + V_2$. This is immediate if (V_i) is trivial. If (V_i) is non-trivial, then the second equation of (6) implies

$$-q_2 + 1 - U_2 - V_2 \geq 0.$$

By way of the fifth equation of (6), we obtain $V_3 \leq V_2$, which again implies $U_3 + V_3 \leq U_2 + V_2$.

By Lemma 2, we have $1 - U_2 - V_2 \leq 1 - U_3 - V_3 < 0$. Again using the second equation of (6), we get $U_3 > U_2$, a contradiction. The assertions (ii)-(iv) are analogous, by exchanging the role of U and V or the patches one and two.

Lemma 4 *Assume $q_1, q_2 \geq 0$, $(q_1, q_2) \neq (0, 0)$, and $d, D > 0$. Then we have*

$$3 - \sum_{i=1}^{3}(U_i + V_i) > 0. \tag{14}$$

Proof By exchanging the two species if necessary, we may assume without loss of generality that (U_i) is non-trivial. Adding the equations of U_i, $i = 1, 2, 3$, in (6), we get

$$U_1(1 - U_1 - V_1) + U_2(1 - U_2 - V_2) + U_3(1 - U_3 - V_3) = 0. \tag{15}$$

If $q_1 \geq q_2$, applying (15), $U_1 + V_1 < 1 < U_3 + V_3$ (Lemma 2) and $U_1 \leq U_2 < U_3$ (Lemma 3). Hence

$$U_2(1-U_1-V_1)+U_2(1-U_2-V_2)+U_2(1-U_3-V_3)>0,$$

that is, (14) holds. The proof of the case $q_1 < q_2$ is similar and thus omitted.

Lemma 5 *Assume $q_1, q_2 \geq 0$, $(q_1, q_2) \neq (0,0)$ and $d, D > 0$.*

(i) *If (U_i) is non-trivial, then $-q_1 + 1 - U_1 - V_1 < 0$.*
(ii) *If (V_i) is non-trivial, then $-q_2 + 1 - U_2 - V_2 < 0$.*

Proof By Lemma 3 and the first and second equation of (6), we get

$$(-q_i + 1 - U_i - V_i)U_i = d(U_i - U_3) < 0, \quad i = 1, 2.$$

This proves (i). The proof of (ii) is omitted.

From the above results, we can establish the non-existence of positive solution of (6).

Lemma 6 *Assume $q_1, q_2 \geq 0$, $(q_1, q_2) \neq (0,0)$, and $d, D > 0$ satisfy $d \neq D$. Then (6) has no positive solution.*

Proof If there exists a positive solution (U, V) with $U_i > 0$ and $V_i > 0$, then we can rewrite (6) as $E_0(U_1, U_2, U_3)^T = (0,0,0)^T$ and $F_0(V_1, V_2, V_3)^T = (0,0,0)^T$, where the matrices E_0 and F_0 are defined as

$$\begin{aligned} E_0 &= \begin{pmatrix} -d - q_1 + 1 - U_1 - V_1 & 0 & d \\ 0 & -d - q_2 + 1 - U_2 - V_2 & d \\ d + q_1 & d + q_2 & -2d + 1 - U_3 - V_3 \end{pmatrix} \\ F_0 &= \begin{pmatrix} -D - q_1 + 1 - U_1 - V_1 & 0 & D \\ 0 & -D - q_2 + 1 - U_2 - V_2 & D \\ D + q_1 & D + q_2 & -2D + 1 - U_3 - V_3 \end{pmatrix}. \end{aligned} \tag{16}$$

Direct calculation gives

$$\begin{aligned} 0 = \det(E_0) =& d^2 \left(3 - \sum_{i=1}^{3}(U_i + V_i)\right) + dP \\ &+ (-q_1 + 1 - U_1 - V_1)(-q_2 + 1 - U_2 - V_2)(1 - U_3 - V_3), \end{aligned}$$

and

$$\begin{aligned} 0 = \det(F_0) =& D^2 \left(3 - \sum_{i=1}^{3}(U_i + V_i)\right) + DP \\ &+ (-q_1 + 1 - U_1 - V_1)(-q_2 + 1 - U_2 - V_2)(1 - U_3 - V_3), \end{aligned}$$

for some constant P depending only on U_i, V_i $(i = 1, 2, 3)$ and q_j $(j = 1, 2)$. Multiplying the above two equations by D, d, respectively and subtracting the resulting equations, in view of $D \neq d$, we obtain

$$\begin{aligned} &Dd \left(3 - \sum_{i=1}^{3}(U_i + V_i)\right) \\ &= (-q_1 + 1 - U_1 - V_1)(-q_2 + 1 - U_2 - V_2)(1 - U_3 - V_3). \end{aligned} \tag{17}$$

From Lemmas 2 and 5, it follows that the right hand side of (17) is negative. However, the left hand side of (17) is positive, as implied by Lemma 4. This contradiction finishes the proof.

A.2 The global stability of semi-trivial steady state

In this subsection, we mainly establish Theorem 1. We first study the linear instability of the semi-trivial steady state $(0, V^*) := (0, 0, 0, V_1^*, V_2^*, V_3^*)$ for Model I, where V^* satisfies

$$F_1(V_1^*, V_2^*, V_3^*)^T = (0, 0, 0)^T, \tag{18}$$

with matrix F_1 given by

$$F_1 = \begin{pmatrix} -D - q_1 + 1 - V_1^* & 0 & D \\ 0 & -D - q_2 + 1 - V_2^* & D \\ D + q_1 & D + q_2 & -2D + 1 - V_3^* \end{pmatrix}.$$

The linear instability of $(0, V^*)$ is determined by the sign of the principal eigenvalue, denoted as Λ_1, of the eigenvalue problem

$$E_1 \begin{pmatrix} \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix} + \Lambda \begin{pmatrix} \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}, \tag{19}$$

where matrix E_1 is given by

$$E_1 = \begin{pmatrix} -d - q_1 + 1 - V_1^* & 0 & d \\ 0 & -d - q_2 + 1 - V_2^* & d \\ d + q_1 & d + q_2 & -2d + 1 - V_3^* \end{pmatrix}.$$

Note that $\Lambda_1 = \Lambda_1(d, D)$ depends on D by way of V_i^*. We first study the sign of Λ_1 for the case $q_1 = q_2 = q$. From [20], we recall the following two results concerning Λ_1:

Proposition 1 ([20, Proposition 1]) *Suppose $q_1 = q_2 = q > 0$. Then the derivative of Λ_1 with respect to d, at d=D, is given by*

$$\frac{\partial \Lambda_1}{\partial d}\Big|_{d=D} = -\frac{(V_1^* - \frac{D}{D+q}V_3^*)(V_3^* - V_1^*) + (V_2^* - \frac{D}{D+q}V_3^*)(V_3^* - V_2^*)}{(V_1^*)^2 + (V_2^*)^2 + \frac{D}{D+q}(V_3^*)^2}. \tag{20}$$

Proposition 2 ([20, Proposition 2]) *Assume $q_1 = q_2 = q > 0$ and $V_1^* + V_2^* + V_3^* \neq 3$. Then* $\det(E_1) = 0$ *if and only if either $d = D$, or $d = F(D)$, where function F is given by*

$$F(D) := \frac{(-q + 1 - V_1^*)(-q + 1 - V_2^*)(1 - V_3^*)}{D(3 - V_1^* - V_2^* - V_3^*)}, \quad D > 0. \tag{21}$$

Corollary 1 *Assume $q_1 = q_2 = q > 0$. For any $d, D > 0$, we have $\frac{\partial \Lambda_1}{\partial d}\big|_{d=D} < 0$.*

Proof By Lemma 3, we have $V_3^* - V_1^* > 0$ and $V_3^* - V_2^* > 0$. Using (i) of Lemma 1 and Lemma 2, we get $V_2^* = V_1^* < 1$, which together with the equations of V_1^* and V_2^* in (18) yields

$$V_1^* - \frac{D}{D+q}V_3^* > 0 \quad \textit{and} \quad V_2^* - \frac{D}{D+q}V_3^* > 0.$$

Therefore, the right hand side of (20) is negative.

Corollary 2 *Assume $q_1 = q_2 = q > 0$. Then for any $d, D > 0$, the right hand side of* (21) *is strictly negative.*

Proof This lemma is a direct consequence of Lemmas 2, 4 and 5.

Theorem 8 *Assume $q_1 = q_2 = q > 0$. Then for any $d, D > 0$, we have*

$$\Lambda_1(d, D) = \begin{cases} + & D > d; \\ - & D < d. \end{cases}$$

Proof Since the right hand side of (21) is strictly negative (by Corollary 2), Proposition 2 says that $\Lambda_1(d, D) = 0$ if and only if $d = D$. Therefore, by Corollary 1 and the continuity of Λ_1, $\Lambda_1(d, D) > 0$ holds for $D > d > 0$ and $\Lambda_1(d, D) < 0$ holds for $0 < D < d$.

Next, we consider the sign of Λ_1 for any $q_1, q_2 \geq 0$ and $(q_1, q_2) \neq (0, 0)$.

Lemma 7 *For any $q_1, q_2 \geq 0$ and $(q_1, q_2) \neq (0, 0)$, we have $\Lambda_1(d, D) < 0$ for $d > D > 0$.*

Proof Fix $d > D > 0$. By Theorem 8, if $q_1 = q_2 = q$, then $\Lambda_1(d, D) < 0$. Then by the continuity of Λ_1 in q_1, q_2, it is sufficient to show $\Lambda_1 \neq 0$ for any $q_1 \neq q_2$. If not, we assume there exist some $q_1 \neq q_2$ such that $\Lambda_1 = 0$. By direct calculation, we get

$$0 = \det(E_1) = d^2 (3 - V_1^* - V_2^* - V_3^*) + MD + (-q_1 + 1 - V_1^*)(-q_2 + 1 - V_2^*)(1 - V_3^*).$$

By (18), we also get

$$0 = \det(F_1) = D^2 (3 - V_1^* - V_2^* - V_3^*) + Md + (-q_1 + 1 - V_1^*)(-q_2 + 1 - V_2^*)(1 - V_3^*).$$

Here M depends on $V_i^* (i = 1, 2, 3), q_1$ and q_2. Multiplying the above two equations by d, D respectively and subtracting them, we obtain

$$(D - d)[(3 - V_1^* - V_2^* - V_3^*)Dd - (-q_1 + 1 - V_1^*)(-q_2 + 1 - V_2^*)(1 - V_3^*)] = 0.$$

Due to $d > D$, we have

$$(3 - V_1^* - V_2^* - V_3^*)Dd = (-q_1 + 1 - V_1^*)(-q_2 + 1 - V_2^*)(1 - V_3^*). \tag{22}$$

Lemmas 2 and 5 imply that the right hand side of (22) is negative. However, the left hand side of (22) is positive, as implied by Lemma 4. This contradiction finishes the proof.

Proof of Theorem 1. Fix $d > D$. By Lemmas 6 and 7, $(0, V^*)$ is linearly unstable, and Model I has no positive equilibria. By the theory of monotone dynamical systems [16, Theorem 1.5], $(U^*, 0)$ is globally asymptotically stable among all non-negative, non-trivial solutions of (1).

Appendix B The dynamics of Model II

In this section, we mainly study the dynamics of Model II and establish Theorems 2 to 4.

B.1 Preliminary estimates on non-negative, non-trivial steady states

In this subsection, we study the non-negative and non-trivial solutions of the system

$$\begin{cases} d(U_2 - U_1) - q_1 U_1 + U_1(1 - U_1 - V_1) = 0 \\ d(U_1 + U_3 - 2U_2) + q_1 U_1 - q_2 U_2 + U_2(1 - U_2 - V_2) = 0 \\ d(U_2 - U_3) + q_2 U_2 + U_3(1 - U_3 - V_3) = 0 \\ D(V_2 - V_1) - q_1 V_1 + V_1(1 - U_1 - V_1) = 0 \\ D(V_1 + V_3 - 2V_2) + q_1 V_1 - q_2 V_2 + V_2(1 - U_2 - V_2) = 0 \\ D(V_2 - V_3) + q_2 V_2 + V_3(1 - U_3 - V_3) = 0. \end{cases} \tag{23}$$

Once again, we set $k = 1$ and observe that system (23) has at most three types of non-negative and non-trivial solutions, that is, semi-trivial solution $(U^*, 0), (0, V^*)$ and positive solutions for which $U_i > 0, V_i > 0$ $(i = 1, 2, 3)$. In the following, we denote by (U, V) a non-negative non-trivial solution of (23), in which $U_i > 0$ and $V_i = 0$, or $U_i = 0$ and $V_i > 0$, or $U_i > 0$ and $V_i > 0$ for all $i = 1, 2, 3$. We shall establish *a priori* estimates of the non-negative and non-trivial solutions (U, V).

Lemma 8 *For any $d, D > 0$ and $q_1, q_2 > 0$, we have $U_1 + V_1 < 1 < U_3 + V_3$.*

Proof We will prove this conclusion for the case $U_i > 0$. The case $U_i \equiv 0$ and $V_i > 0$ can be proved by a similar argument.
Step 1: We prove $U_1 + V_1 < 1$. We argue by contradiction and assume that there exist some q_1, q_2 such that $U_1 + V_1 \geq 1$. Then by the first equation of (23), we have $d(U_2 - U_1) - q_1 U_1 \geq 0$, i.e., $U_2 \geq \frac{d+q_1}{d} U_1 > U_1$. Following from the similar argument, we also get $V_i = 0$ for all i, or $V_2 > V_1$. Hence $U_2 + V_2 > U_1 + V_1 \geq 1$.

Clearly, we have $U_3 + V_3 \geq 1$. If not, assume that $U_3 + V_3 < 1$ for some q_1, q_2. By the equations of U_3 and V_3, we have $U_3 > \frac{d+q_2}{d} U_2 > U_2$ and $V_3 \geq \frac{D+q_2}{D} V_2 \geq V_2$ (where equality holds in case $V_i = 0$ for all i), which imply $U_3 + V_3 > U_2 + V_2 > 1$, a contradiction.

Therefore, we get

$$U_1(1 - U_1 - V_1) + U_2(1 - U_2 - V_2) + U_3(1 - U_3 - V_3) < 0.$$

However, adding the equations of U_i, $i = 1, 2, 3$, in (23), we find that the left hand side of the above inequality is equal to zero. This is a contradiction. Hence, $U_1 + V_1 < 1$ holds.
Step 2: We show $U_3 + V_3 > 1$. If not, we assume $U_3 + V_3 \leq 1$ for some q_1, q_2. By the equations of U_3 and V_3 in (23), we deduce that $U_2 < U_3$ and $V_2 \leq V_3$ (with equality holds if $V_i = 0$). Thus $U_2 + V_2 < U_3 + V_3 \leq 1$, which together with $U_1 + V_1 < 1$ implies

$$U_1(1 - U_1 - V_1) + U_2(1 - U_2 - V_2) + U_3(1 - U_3 - V_3) > 0.$$

Similarly, adding the equations of U_i, $i = 1, 2, 3$, in (23), we find that the left hand side of the above inequality is equal to zero. This is a contradiction.

Lemma 9 *For any $d, D > 0$, $q_1, q_2 > 0$, it holds that*

$$-q_2 + 1 - U_2 - V_2 < 0. \tag{24}$$

Proof We consider two cases:

Case I. Either $U_3 > U_2$ or $V_3 > V_2$. Without loss of generality, assume $U_3 > U_2$, so that $U_i > 0$ for all i. Adding equations of U_1 and U_2 in (23), we have

$$d(U_3 - U_2) + U_1(1 - U_1 - V_1) + U_2(-q_2 + 1 - U_2 - V_2) = 0. \tag{25}$$

It is easy to see that (24) follows from (25), $U_3 \geq U_2$ and $U_1 + V_1 < 1$ (Lemma 8).

Case II. $U_3 \leq U_2$ and $V_3 \leq V_2$. For this case,

$$-q_2 + 1 - U_2 - V_2 \leq -q_2 + 1 - U_3 - V_3 < 0.$$

The last inequality follows from Lemma 8. This completes the proof.

Lemma 10 *Let $d, D > 0$, and either $q_1 \geq 1$ or $\frac{q_2}{2} < q_1 < 1$.*

(i) *Either $U_i \equiv 0$ or $U_1 < U_2$.*
(ii) *Either $V_i \equiv 0$ or $V_1 < V_2$.*

Proof We only prove (i), as (ii) follows in a completely analogous manner. Assume $U_i > 0$ for all i, we need to show $U_1 < U_2$. Obviously, for $q_1 \geq 1$, this conclusion is true from the first equation of (23). Next, assume to the contrary that there exist some $\frac{q_2}{2} < q_1 < 1$ such that $U_1 \geq U_2$. By the first equation of (23), $-q_1 + 1 - U_1 - V_1 \geq 0$, i.e., $U_1 + V_1 \leq 1 - q_1$. Hence $U_1 + V_1 < 1 - \frac{q_2}{2}$. Using the 4th equation of (23), we get $V_2 \leq V_1$. So we have

$$U_2 + V_2 \leq U_1 + V_1 < 1 - \frac{q_2}{2}. \tag{26}$$

From the second equation of (23), we get

$$d(U_1 + U_3 - 2U_2) + q_1 U_1 - q_2 U_2 + \tfrac{q_2}{2} U_2 < 0,$$

which together with $U_1 \geq U_2$ indicates $d(U_3 - U_2) + (q_1 - \frac{q_2}{2})U_2 < 0$. Since $q_1 > \frac{q_2}{2}$, we have $U_3 < U_2$.

We claim that $U_2 + V_2 > U_3 + V_3$. If $V_i \equiv 0$, then it follows from $U_3 < U_2$ and we are done. If $V_i > 0$ for all i, then we can repeat the above argument to show that $V_3 < V_2$. Using Lemma 8, we have $U_2 + V_2 > U_3 + V_3 > 1$. This is in contradiction with (26).

Lemma 11 *For any $d, D > 0$, if $q_1 \geq 1$ or $\frac{q_2}{2} < q_1 < 1$, then*

$$3 - \sum_{i=1}^{3} (U_i + V_i) > 0. \tag{27}$$

Proof Adding all six equations of (23), we have

$$(U_1 + V_1)(1 - U_1 - V_1) + (U_2 + V_2)(1 - U_2 - V_2) + (U_3 + V_3)(1 - U_3 - V_3) = 0. \tag{28}$$

We consider two cases:

Case I. $U_2 + V_2 \leq U_3 + V_3$. For this case, by $U_3 + V_3 > 1$ we have

$$(U_3 + V_3)(1 - U_3 - V_3) \leq (U_2 + V_2)(1 - U_3 - V_3). \tag{29}$$

By Lemma 10, we have $U_1 + V_1 < U_2 + V_2$. This together with $U_1 + V_1 < 1$ implies

$$(U_1 + V_1)(1 - U_1 - V_1) < (U_2 + V_2)(1 - U_1 - V_1). \tag{30}$$

It is easy to see that (27) follows directly from (28), (29) and (30).

Case II. $U_2 + V_2 \geq U_3 + V_3$. For this case, by $U_3 + V_3 > 1 > U_1 + V_1$ (by Lemma 8) we have

$$(U_3 + V_3)(1 - U_3 - V_3) < (U_1 + V_1)(1 - U_3 - V_3). \tag{31}$$

Since $U_2 + V_2 \geq U_3 + V_3 > 1 > U_1 + V_1$, we can similarly derive

$$(U_2 + V_2)(1 - U_2 - V_2) < (U_1 + V_1)(1 - U_2 - V_2). \tag{32}$$

It is easy to see that (27) follows directly from (28), (31) and (32). Note that the above reasoning is valid also when $U_1 = U_2 = U_3 = 0$ or $V_1 = V_2 = V_3 = 0$.

Note that the above results are valid when $q_1 = q_2 > 0$. The following result implies that (23) has no positive solution when $q_1 \geq 1$ or $\frac{q_2}{2} < q_1 < 1$.

Corollary 3 *If $q_1 \geq 1$ or $\frac{q_2}{2} < q_1 < 1$, then system* (23) *has no positive solutions for $d \neq D$.*

Proof We argue by contradiction. If there exists some positive solution, denoted by (U, V), for (23). Direct calculation, as in the proof of Lemma 6, gives

$$\begin{aligned} &Dd(3 - \sum_{i=1}^{3}(U_i + V_i)) \\ &= (-q_1 + 1 - U_1 - V_1)(-q_2 + 1 - U_2 - V_2)(1 - U_3 - V_3). \end{aligned} \tag{33}$$

Due to $U_1 < U_2$, the equation of U_1 implies $-q_1+1-(U_1+V_1) < 0$. By Lemma 8, $1-(U_3+V_3) < 0$. By Lemma 9, we see $-q_2 + 1 - (U_2 + V_2) < 0$. Hence, the right hand side of (33) is negative. However, the left hand side of (33) is positive from Lemma 11, which is a contradiction.

B.2 The global dynamics of Model II when $q_1 \geq 1$ or $\frac{q_2}{2} < q_1 < 1$

In this subsection, we shall show that the faster diffuser always wins when $q_1 \geq 1$ or $\frac{q_2}{2} < q_1 < 1$. We first study the local instability of $(0, V^*) := (0, 0, 0, V_1^*, V_2^*, V_3^*)$, as determined by the sign of the principal eigenvalue Λ_2 of the eigenvalue problem

$$E_2 \begin{pmatrix} \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix} + \Lambda \begin{pmatrix} \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}, \tag{34}$$

where matrix E_2 is given by

$$E_2 = \begin{pmatrix} -d - q_1 + 1 - V_1^* & d & 0 \\ d + q_1 & -2d - q_2 + 1 - V_2^* & d \\ 0 & d + q_2 & -d + 1 - V_3^* \end{pmatrix}.$$

Proposition 3 *When $d = D$, the derivative of Λ_2 with respect to d satisfies*

$$\frac{\partial \Lambda_2}{\partial d}\Big|_{d=D} = -\frac{(D + q_1)V_1^*(V_2^* - V_1^*) + DV_2^*(V_1^* + V_3^* - 2V_2^*) + \frac{D^2}{D+q_2}V_3^*(V_2^* - V_3^*)}{(D + q_1)(V_1^*)^2 + D(V_2^*)^2 + \frac{D^2}{D+q_2}(V_3^*)^2}. \tag{35}$$

Proof Differentiate (34) with respect to d, we get

$$\begin{pmatrix} \varphi_2 - \varphi_1 \\ \varphi_1 + \varphi_3 - 2\varphi_2 \\ \varphi_2 - \varphi_3 \end{pmatrix} + E_2 \begin{pmatrix} \varphi_1' \\ \varphi_2' \\ \varphi_3' \end{pmatrix} + \frac{\partial \Lambda_2}{\partial d} \begin{pmatrix} \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix} + \Lambda_2 \begin{pmatrix} \varphi_1' \\ \varphi_2' \\ \varphi_3' \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}, \tag{36}$$

where $\varphi_i' = \frac{\partial \varphi_i}{\partial d}$, $i = 1, 2, 3$. Note that when $d = D$,

$$E_2|_{d=D} \begin{pmatrix} V_1^* \\ V_2^* \\ V_3^* \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix},$$

$$\left(E_2|_{d=D}\right)^T \begin{pmatrix} (D+q_1)V_1^* \\ DV_2^* \\ \frac{D^2}{D+q_2}V_3^* \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}, \tag{37}$$

and when $d = D$, we may choose

$$\begin{pmatrix} \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix} = \begin{pmatrix} V_1^* \\ V_2^* \\ V_3^* \end{pmatrix}. \tag{38}$$

Set $d = D$ in (36) and multiplying it by $\left((D+q_1)V_1^*, DV_2^*, \frac{D^2}{D+q_2}V_3^*\right)$, using (37), (38) and $\Lambda_2(D, D) = 0$, we obtain (35). This completes the proof.

B.2.1 *The sign of Λ_2 when $q_1 = q_2$*

Our goal in this subsection is to determine the sign of Λ_2 when $q_1 = q_2$. We first recall the following result:

Proposition 4 ([20, Proposition 4]) *Assume $q_1 = q_2 = q$ and $V_1^* + V_2^* + V_3^* \neq 3$. Then* $\det(E_2) = 0$ *if and only if either $d = D$, or $d = F(D)$, where $F(D)$ is given by* (21).

Lemma 12 *Suppose $d, D > 0$ and $q_1 = q_2 = q > 0$, then $V_2^* < V_3^*$.*

Proof We argue by contradiction. If not, we assume there exist some $d, D, q > 0$ such that $V_i > 0$ for all i and $V_2 \geq V_3$. By the sixth equation of (23), we get

$$qV_3^* + V_3^*(1 - V_3^*) \leq qV_2^* + V_3^*(1 - V_3^*) \leq 0,$$

which implies that $V_3^* \geq 1 + q > 1$. Therefore, $V_2^* \geq V_3^* > 1$. Hence,

$$\begin{aligned} &d(V_1^* + V_3^* - 2V_2^*) + qV_1^* - qV_2^* + V_2^*(1 - V_2^*) \\ &= (d+q)(V_1^* - V_2^*) + d(V_3^* - V_2^*) + V_2^*(1 - V_2^*) < 0, \end{aligned}$$

where we also used the assumption $V_2^* \geq V_3^*$ and $V_1^* < V_2^*$ (Lemma 10). This is in contradiction with the fifth equation of (23).

Corollary 4 *Suppose $q_1 = q_2 = q > 0$, then for any $d, D > 0$, the quantity $F(D)$ given in* (21) *is strictly negative.*

Proof By Lemmas 8 and 9, we have

$$V_3^* > 1 \quad \text{and} \quad -q + 1 - V_2^* < 0.$$

By Lemma 10 and the first equation of (23), we get $-q + 1 - V_1^* < 0$. Using also Lemma 11, the quantity $F(D)$, given in (21), is strictly negative.

Lemma 13 *Suppose $q_1 = q_2 = q > 0$, then for any $d, D > 0$, we have $\frac{D+q}{D}V_1^* > V_2^* > \frac{D}{D+q}V_3^*$.*

Proof By the fourth equation of (23) and Lemma 8, we get $d(V_2^* - V_1^*) - qV_1^* < 0$, which implies $V_2^* < \frac{D+q}{D}V_1^*$. Similarly, by the sixth equation of (23) and Lemma 8, we have $d(V_2^* - V_3^*) + qV_2^* > 0$, i.e. $V_2^* > \frac{D}{D+q}V_3^*$.

Corollary 5 *Suppose $q_1 = q_2 = q > 0$, then for any $d, D > 0$, we have $\left.\frac{\partial \Lambda_2}{\partial d}\right|_{d=D} < 0$.*

Proof If $q_1 = q_2 = q$, (35) can be rewritten as

$$\frac{\partial \Lambda_2}{\partial d}\Big|_{d=D} = -\frac{\frac{D+q}{D}V_1^*(V_2^* - V_1^*) + V_2^*(V_1^* + V_3^* - 2V_2^*) + \frac{D}{D+q}V_3^*(V_2^* - V_3^*)}{\frac{D+q}{D}(V_1^*)^2 + (V_2^*)^2 + \frac{D}{D+q}(V_3^*)^2}.$$

Note that

$$\begin{aligned}&\frac{D+q}{D}V_1^*(V_2^* - V_1^*) + V_2^*(V_1^* + V_3^* - 2V_2^*) + \frac{D}{D+q}V_3^*(V_2^* - V_3^*)\\ &= (V_2^* - V_1^*)(\frac{D+q}{D}V_1^* - V_2^*) + (V_3^* - V_2^*)(V_2^* - \frac{D}{D+q}V_3^*),\end{aligned}$$

which together with Lemmas 10, 12 and 13 yields the conclusion.

Theorem 9 *Assume $q_1 = q_2 = q > 0$. Then for any $d, D > 0$, we have*

$$\Lambda_2(d, D) = \begin{cases} + & D > d; \\ - & D < d. \end{cases}$$

Proof Since the quantity $F(D)$, which is given in (21), is strictly negative (by Corollary 4), Proposition 4 says that $\Lambda_2(d, D) = 0$ if and only if $d = D$. Therefore, by Corollary 5 and the continuity of Λ_2, $\Lambda_2(d, D) > 0$ holds for $D > d > 0$ and $\Lambda_2(d, D) < 0$ holds for $0 < D < d$.

B.2.2 The proof of Theorem 2

In this subection we will study the global dynamics of Model II for $q_1 \geq 1$ or $\frac{q_2}{2} < q_1 < 1$.

Lemma 14 *If $q_1 \geq 1$ or $\frac{q_2}{2} < q_1 < 1$, $\Lambda_2(d, D) < 0$ for $d > D$.*

Proof The proof is similar as that of Lemma 7. It follows from Theorem 9 that, if $q_1 = q_2$, then $\Lambda_2(d, D) < 0$ for $d > D$. Since Λ_2 is continuous with respect to parameters q_1, q_2, it suffices to show that $\Lambda_2 \neq 0$ for any $q_1 \neq q_2$ and $q_1 \geq 1$ or $\frac{q_2}{2} < q_1 < 1$. We argue by contradiction and assume that there exists some q satisfying the assumptions such that $\Lambda_2 = 0$. By proceeding similarly as in Lemma 7, we derive (22) again. Note that $3 - V_1^* - V_2^* - V_3^* > 0$ holds, which implies the left hand side of (22) is positive. Using $V_1^* < V_2^*$ and the first equation of (23), we deduce $-q_1 + 1 - V_1^* < 0$. By Lemma 9, $-q_2 + 1 - V_2^* < 0$. These together with $V_3^* > 1$ imply the right hand side of (22) is negative, which is a contradiction.

Proof of Theorem 2. By Corollary 3 and Lemma 14, the equilibrium $(0, V^*)$ is linearly unstable and Model II has no positive equilibria. By the theory of monotone dynamical systems [16, Theorem 1.5], the equilibrium $(U^*, 0)$ is globally asymptotically stable.

B.3 Existence of evolutionarily singular strategy

In this subsection, we consider the existence of evolutionarily singular strategy and establish Theorem 3. The linear stability of the semi-trivial steady state, $(U^*, 0) := (U_1^*, U_2^*, U_3^*, 0, 0, 0)$, is determined by the sign of the principal eigenvalue $\tilde{\Lambda}_2$ of the eigenvalue problem

$$F_2 \begin{pmatrix} \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix} + \Lambda \begin{pmatrix} \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}, \tag{39}$$

where matrix F_2 is given by

$$F_2 = \begin{pmatrix} -D - q_1 + 1 - U_1^* & D & 0 \\ D + q_1 & -2D - q_2 + 1 - U_2^* & D \\ 0 & D + q_2 & -D + 1 - U_3^* \end{pmatrix}.$$

Note that U_i^*, $i = 1, 2, 3$, satisfy

$$F_2|_{D=d} \begin{pmatrix} U_1^* \\ U_2^* \\ U_3^* \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}. \tag{40}$$

By exchanging the role of the two species, we can rewrite Proposition 3 as follows:

Proposition 5 *When $D = d$, the derivative of $\tilde{\Lambda}_2$ with respect to D satisfies*

$$\frac{\partial \tilde{\Lambda}_2}{\partial D}\Big|_{D=d} = -\frac{(d+q_1)U_1^*(U_2^* - U_1^*) + dU_2^*(U_1^* + U_3^* - 2U_2^*) + \frac{d^2}{d+q_2}U_3^*(U_2^* - U_3^*)}{(d+q_1)(U_1^*)^2 + d(U_2^*)^2 + \frac{d^2}{d+q_2}(U_3^*)^2}. \tag{41}$$

Lemma 15 *For any $q_1, q_2 > 0$, we have $\frac{\partial \tilde{\Lambda}_2}{\partial D}(d, d) < 0$ for sufficiently large d.*

Proof Set

$$M := (d+q_1)U_1^*(U_2^* - U_1^*) + dU_2^*(U_1^* + U_3^* - 2U_2^*) + \frac{d^2}{d+q_2}U_3^*(U_2^* - U_3^*). \tag{42}$$

By (23), we can rewrite (42) as

$$\begin{aligned} \frac{M}{d} &= (U_2^* - U_1^*)\left[\frac{d+q_1}{d}U_1^* - U_2^*\right] + (U_2^* - U_3^*)\left[\frac{d}{d+q_2}U_3^* - U_2^*\right] \\ &= (U_2^* - U_1^*)\frac{U_1^*(1-U_1^*)}{d} + (U_2^* - U_3^*)\frac{U_3^*(1-U_3^*)}{d+q_2} \end{aligned} \tag{43}$$

Note that $(U_1^*, U_2^*, U_3^*) \to (1, 1, 1)$ as $d \to \infty$. As (U_1^*, U_2^*, U_3^*) is the unique stable positive solution of (40), it can be shown that it is smooth at $d = \infty$ so that we can expand U_i as

$$U_i^* = 1 + \frac{\tilde{U}_i}{d} + O(\frac{1}{d^2}) \quad \text{for } i = 1, 2, 3.$$

To determine $\tilde{U}_i$, we substitute the above expansion of U_i^* into the first and third equation in (40) to get

$$\tilde{U}_1 - \tilde{U}_2 = -q_1 \quad \text{and} \quad \tilde{U}_2 - \tilde{U}_3 = -q_2. \tag{44}$$

By adding the first three equations of (40), we obtain $\sum_{i=1}^3 U_i^*(1 - U_i^*) = 0$, from which we deduce $\sum_{i=1}^3 \tilde{U}_i = 0$. Combining this with (44), we obtain

$$\tilde{U}_1 = -\frac{2q_1 + q_2}{3}, \quad \tilde{U}_2 = \frac{q_1 - q_2}{3}, \quad \tilde{U}_3 = \frac{q_1 + 2q_2}{3}. \tag{45}$$

Having determined $\tilde{U}_i$, we may substitute $U_i^* = 1 + \tilde{U}_i/d + O(1/d^2)$ into (43) to get

$$\begin{aligned} d^2 M &= (\tilde{U}_2 - \tilde{U}_1)(-\tilde{U}_1) + (\tilde{U}_2 - \tilde{U}_3)(-\tilde{U}_3) + o(1) \\ &= \frac{2}{3}(q_1^2 + q_1 q_2 + q_2^3) + o(1) > 0 \quad \text{for } d \gg 1. \end{aligned}$$

Therefore, by Proposition 5, we have $\frac{\partial \tilde{\Lambda}_2}{\partial D}(d, d) < 0$ for $d \gg 1$.

Lemma 16 *If* $0 < q_1 < 1$ *and* $q_2 > 2q_1$*, we have* $\frac{\partial \tilde{\Lambda}_2}{\partial D}(d,d) > 0$ *for sufficiently small* d.

Proof When $d \to 0$, we have $U_1^* \to \overline{U}_1 := 1 - q_1$ and, passing to a subsequence if necessary, $U_2^* \to \overline{U}_2$ for some non-negative $\overline{U}_2$. We claim that if $2q_1 < q_2$, then $\overline{U}_2 < \overline{U}_1$. If not, we assume for some $2q_1 < q_2$, $\overline{U}_2 \geq \overline{U}_1$. By the equation of U_2^* and let $d \to 0$,

$$q_1\overline{U}_1 - q_2\overline{U}_2 + \overline{U}_2(1 - \overline{U}_2) = 0.$$

Then we have $q_1\overline{U}_2 - q_2\overline{U}_2 + \overline{U}_2(1 - \overline{U}_2) \geq 0$, which implies that $\overline{U}_2 \leq 1 + q_1 - q_2$. Therefore, $1 + q_1 - q_2 \geq 1 - q_1$, i.e. $2q_1 \geq q_2$. This contradiction shows that $\overline{U}_2 < \overline{U}_1$.

Note that $M \to q_1\overline{U}_1(\overline{U}_2 - \overline{U}_1) < 0$ as $d \to 0$, where M is given by (42). Note that $0 < q_1 < 1$. Hence, for sufficiently small d, we have $\frac{\partial \tilde{\Lambda}_2}{\partial D}(d,d) > 0$.

Proof of Theorem 3. Since $d \mapsto \frac{\partial \tilde{\Lambda}_2}{\partial D}(d,d)$ is analytic, all the roots are discrete. By Lemmas 15 and 16, $\frac{\partial \tilde{\Lambda}_2}{\partial D}(d,d) < 0$ for $d \gg 1$ and $\frac{\partial \tilde{\Lambda}_2}{\partial D}(d,d) > 0$ for $0 < d \ll 1$. This says that the infinity and zero diffusion rates are local CvSSs. Furthermore, there exists at least one $d^* = d^*(q_1, q_2)$ such that $\frac{\partial \tilde{\Lambda}_2}{\partial D}(d^*, d^*) = 0$, and $\frac{\partial \tilde{\Lambda}_2}{\partial D}(d,d)$ change sign from positive to negative in a neighborhood of d^*; i.e. d^* is an evolutionary singular strategy which is not a CvSS.

B.4 The proof of Theorem 4

The proof of Theorem 4 is divided into a series of lemmas. First, we recall that $(\hat{V}_2, \hat{V}_3)$ is the unique positive solution of (4) with $k = 1$.

Lemma 17 *Let* $d = q_1 = 0$ *and* $D, d_2 > 0$ *and let* $(\hat{V}_2, \hat{V}_3)$ *be the unique positive solution of* (4)*. Then* $\hat{V}_2 < 1 < \hat{V}_3$ *and* $(1 - \hat{V}_2, 0, 0, \hat{V}_2, \hat{V}_2, \hat{V}_3)$ *is a non-negative solution of system* (23)*.*

Proof It is clear that $(1 - \hat{V}_2, 0, 0, \hat{V}_2, \hat{V}_2, \hat{V}_3)$ is a non-negative solution of system (23) when $d = q_1 = 0$. Adding the equations of (4), we have

$$\hat{V}_2(1 - \hat{V}_2) + \hat{V}_3(1 - \hat{V}_3) = 0. \tag{46}$$

In view of (46), it is enough to show $\hat{V}_3 > 1$. Suppose not, then $\hat{V}_3 \leq 1$ and the 2nd equation of (4) implies $\hat{V}_2 < \hat{V}_3 \leq 1$, which contradicts (46).

Lemma 18 *The matrix*

$$\hat{E}_1 = \begin{pmatrix} -D - q_2 + 1 - 2\hat{V}_2 & D \\ D & -D + q_2 + 1 - 2\hat{V}_3 \end{pmatrix}$$

is invertible.

Proof Observe that zero is an eigenvalue of the cooperative matrix

$$\hat{E}_2 := \hat{E}_1 + \begin{pmatrix} \hat{V}_2 & 0 \\ 0 & \hat{V}_3 \end{pmatrix}$$

with a strictly positive eigenvector $(\hat{V}_2, \hat{V}_3)$. Hence, zero is the principal eigenvalue of $\hat{E}_2$. Since the principal eigenvalue is strictly monotone with respect to the diagonal entries, we deduce that zero is not an eigenvalue of $\hat{E}_1$.

Set $U = (U_1, U_2, U_3)$ and $V = (V_1, V_2, V_3)$. Define map $F(d, q_1, U, V) : \mathbb{R}^8 \to \mathbb{R}^6$ by

$$F(d, q_1, U, V) = \begin{pmatrix} d(U_2 - U_1) - q_1 U_1 + U_1(1 - U_1 - V_1) \\ d(U_1 + U_3 - 2U_2) + q_1 U_1 - q_2 U_2 + U_2(1 - U_2 - V_2) \\ d(U_2 - U_3) + q_2 U_2 + U_3(1 - U_3 - V_3) \\ D(V_2 - V_1) - q_1 V_1 + V_1(1 - U_1 - V_1) \\ D(V_1 + V_3 - 2V_2) + q_1 V_1 - q_2 V_2 + V_2(1 - U_2 - V_2) \\ D(V_2 - V_3) + q_2 V_2 + V_3(1 - U_3 - V_3) \end{pmatrix} \tag{47}$$

It is clear that $(U, V) = (U_1, U_2, U_3, V_1, V_2, V_3)$ is a steady state of Model II if and only if $F(d, q_1, U, V) = 0$. Now, observe that $F(0, 0, \hat{U}, \hat{V}) = 0$. One can further compute

$$\begin{aligned} &D_{(U,V)} F(0, 0, \hat{U}, \hat{V}) \\ &= \begin{pmatrix} -(1 - \hat{V}_2) & 0 & 0 & -(1 - \hat{V}_2) & 0 & 0 \\ 0 & -q_2 + 1 - \hat{V}_2 & 0 & 0 & 0 & 0 \\ 0 & q_2 & 1 - \hat{V}_3 & 0 & 0 & 0 \\ -\hat{V}_2 & 0 & 0 & -D - \hat{V}_2 & D & 0 \\ 0 & -\hat{V}_2 & 0 & D & -2D - q_2 + 1 - 2\hat{V}_2 & D \\ 0 & 0 & -\hat{V}_3 & 0 & D + q_2 & -D + 1 - 2\hat{V}_3 \end{pmatrix}. \end{aligned}$$

Lemma 19 *Let $D > 0$ and $q_2 \geq 1$ and consider the eigenvalue problem*

$$D_{(U,V)} F(0, 0, \hat{U}, \hat{V}) \begin{pmatrix} \varphi \\ \psi \end{pmatrix} = \lambda \begin{pmatrix} \varphi \\ \psi \end{pmatrix} \qquad \text{for } \varphi, \psi \in \mathbb{R}^3. \tag{48}$$

Then every eigenvalue of (48) *lies in $\{z \in \mathbb{C} : \operatorname{Re} z < 0\}$. In particular, $D_{(U,V)} F(0, 0, \hat{U}, \hat{V})$ is invertible.*

Proof First, note that the system (4) implies

$$\frac{D}{D + q_2 - 1 + \hat{V}_2} = \frac{\hat{V}_2}{\hat{V}_3} = \frac{D - 1 + \hat{V}_3}{D + q_2}. \tag{49}$$

It suffices to show that the principal eigenvalue of (48), denoted as λ_1^*, is strictly negative. Suppose to the contrary that (48) holds for some $\varphi, \psi \in \mathbb{R}^3$ and $\lambda_1^* \in \mathbb{R}$ such that

$$\sum_{i=1}^{3} (|\varphi_i| + |\psi_i|) = 1, \quad \varphi_i \leq 0, \quad \psi_i \geq 0, \quad \text{for } i = 1, 2, 3, \quad \text{and} \quad \lambda_1^* \geq 0. \tag{50}$$

We will show that $D = 0$, which gives a contradiction.

Now, multiply both sides of the equation (48) with $\lambda = \lambda_1^*$ on the left by the row vector

$$\vec{r}_1 := \left(-\frac{\hat{V}_2}{1 - \hat{V}_2} (D - 1 + \hat{V}_3), -M^2, -M, D - 1 + \hat{V}_3, D - 1 + \hat{V}_3, D \right),$$

with $M > 0$ to be chosen later. We obtain

$$\vec{R}^T \begin{pmatrix} \varphi \\ \psi \end{pmatrix} = \lambda_1^* \vec{r}_1 \begin{pmatrix} \varphi \\ \psi \end{pmatrix} \quad \text{and} \quad \vec{r}_1 \begin{pmatrix} \varphi \\ \psi \end{pmatrix} > 0, \tag{51}$$

where the strict inequality follows from (50), and $\vec{R}$ can be computed (using (49) for R_5) as

$$\vec{R} = \begin{pmatrix} R_1 \\ R_2 \\ R_3 \\ R_4 \\ R_5 \\ R_6 \end{pmatrix} = \begin{pmatrix} 0 \\ M^2(q_2 - 1 + \hat{V}_2) - Mq_2 - \hat{V}_2(D - 1 + \hat{V}_3) \\ M(\hat{V}_3 - 1) - \hat{V}_3 D \\ 0 \\ -\hat{V}_2(D - 1 + \hat{V}_3) \\ -\hat{V}_3 D \end{pmatrix}$$

Next choose $M \gg 1$ so that $R_2, R_3 < 0$ and $R_5, R_6 < 0$. By inspecting (51) in conjunction with (50), we deduce that

$$\varphi_1 = -\frac{1}{2}, \quad \varphi_2 = \varphi_3 = \psi_2 = \psi_3 = 0, \quad \psi_1 = \frac{1}{2} \quad \text{and} \quad \lambda_1^* = 0.$$

But if we substitute this into the 5th component of (48), we have $D/2 = 0$. This is a contradiction.

Lemma 20 *Fix any $D > 0$ and $q_2 \geq 1$. Then there exists some $\delta > 0$ such that for any $d \in (0, \delta)$, $q_1 \in (-\delta, \delta)$ and $d + q_1 > 0$, Model* II *has a positive steady state, denoted by (U^δ, V^δ), which satisfies $(U^\delta, V^\delta) \to (\hat{U}, \hat{V})$ as $(d, q_1) \to (0, 0)$, where $(\hat{U}, \hat{V})$ is given in* (3) *and* (4) *with $k = 1$.*

Proof It is easy to check that $F(0, 0, \hat{U}, \hat{V}) = 0$. Moreover, we have shown in Lemma 19 that $D_{(U,V)}F(0, 0, \hat{U}, \hat{V})$ is invertible. By the implicit function theorem, there exists some $\delta > 0$ such that for $|d|, |q_1| \leq \delta$, there exists $(U^\delta, V^\delta) \in \mathbb{R}^6$ such that

$$F(d, q_1, U^\delta, V^\delta) = (0, 0, 0, 0, 0, 0)^T,$$

and $(U^\delta, V^\delta) \to (\hat{U}, \hat{V})$ as $d, q_1 \to 0$. Finally we show that for all d, q_1 small such that $d > 0$ and $d + q_1 > 0$, each component of (U^δ, V^δ) is also positive. Since $\hat{U}_1, \hat{V}_2, \hat{V}_3 > 0$, it suffices to show that $U_2^\delta > 0$ and $U_3^\delta > 0$. Recall from Lemma 17 that $\hat{V}_2 < 1 < \hat{V}_3$. By setting the second component of (47) to zero we have

$$\left(2d + q_2 - 1 + U_2^\delta + V_2^\delta\right) U_2^\delta = (d + q_1)U_1^\delta + dU_3 = (d + q_1)(1 - \hat{V}_2 + o(1)) + o(d) > 0.$$

Using $q_2 \geq 1$, we deduce that $U_2^\delta > 0$. Next, we set the third component of (47) to get

$$\left(d - 1 + \hat{V}_3 + o(1)\right) U_3^\delta = \left(d - 1 + U_3^\delta + V_3^\delta\right) U_3^\delta = (d + q_2)U_2^\delta > 0.$$

Since $\hat{V}_3 > 1$, we deduce that $U_3^\delta > 0$. In summary, we have proved that $U_2^\delta > 0$ and $U_3^\delta > 0$ for $d \in (0, \delta)$, $q_1 \in (-\delta, \delta)$ and $d + q_1 > 0$.

Lemma 21 *Suppose that $q_2 \geq 1$. Let (U, V) denote any positive solution of Model* II*. Then as $d \to 0$ and $q_1 \to 0$, $(U, V) \to (\hat{U}, \hat{V})$.*

Proof First it is easy to see that U_i, V_i, $i = 1, 2, 3$, are uniformly bounded with respect to small d, q_1. Hence, passing to a sub-sequence if necessary we may assume $U_i \to \bar{U}_i$ and $V_i \to \bar{V}_i$ as $d, q_1 \to 0$, where $\bar{U}_i, \bar{V}_i \geq 0$ satisfy $F(0, 0, \bar{U}, \bar{V}) = 0$, with F defined in (47).

Step 1: $\bar{U}_2 = 0$.

This is a consequence of assumption $q_2 \geq 1$ and

$$-q_2\bar{U}_2 + \bar{U}_2(1 - \bar{U}_2 - \bar{V}_2) = 0.$$

Step 2: If $\bar{U}_3 > 0$, then $\bar{U}_1 > 0$.

Suppose to the contrary that $\bar U_3 > 0$ and $\bar U_1 = 0$. The first component of $F(0,0,\bar U,\bar V) = 0$ yields $\bar U_3 + \bar V_3 = 1$. Therefore, the 4th to 6th component of $F(0,0,\bar U,\bar V) = 0$ can be rewritten as

$$\begin{cases} D(\bar V_2 - \bar V_1) + \bar V_1(1-\bar V_1) = 0 \\ D(\bar V_1 + \bar V_3 - 2\bar V_2) - q_2\bar V_2 + \bar V_2(1-\bar V_2) = 0 \\ D(\bar V_2 - \bar V_3) + q_2\bar V_2 = 0. \end{cases}$$

By $\bar U_3+\bar V_3 = 1$ and $\bar U_3 > 0$, we have $\bar V_3 < 1$. By the third equation above, $\bar V_2 = D/(D+q_2)\bar V_3 < 1$. Adding three equations we find

$$\bar V_1(1-\bar V_1) + \bar V_2(1-\bar V_2) = 0,$$

which together with $\bar V_2 < 1$ implies $\bar V_1 > 1$. By the first equation we then obtain $\bar V_2 > \bar V_1$, which is a contradiction. This completes Step 2.

Step 3: If $\bar U_3 = 0$, then $\bar U_1 > 0$.

Suppose to the contrary that $\bar U_1 = \bar U_3 = 0$. Then $\bar U_3$ and $\bar V_i$ satisfy

$$\begin{cases} \bar U_3(1-\bar U_3-\bar V_3) = 0 \\ D(\bar V_2 - \bar V_1) + \bar V_1(1-\bar V_1) = 0 \\ D(\bar V_1 + \bar V_3 - 2\bar V_2) - q_2\bar V_2 + \bar V_2(1-\bar V_2) = 0 \\ D(\bar V_2 - \bar V_3) + q_2\bar V_2 + \bar V_3(1-\bar U_3-\bar V_3) = 0 \end{cases}$$

If $\bar U_3 = 0$, then either $\bar V_i = 0$ for $i = 1,2,3$, or $\bar V_i = V_i^* > 0$ for $i = 1,2,3$, where $(0, V^*)$ is one of the semi-trivial steady states of Model II. We rule out both cases as follows:

1. For the case $(\bar U,\bar V) = (0,0,0,0,0,0)$, we have $(U,V) \to (0,0,0,0,0,0)$ as $d, q_1 \to 0$, which implies that $1-(U_i+V_i) > 0$ for small d, q_1. Adding the equations of U_i for $i = 1,2,3$, we have
$$U_1(1-U_1-V_1) + U_2(1-U_2-V_2) + U_3(1-U_3-V_3) = 0,$$
which is a contradiction as each term in the left hand side is positive.
2. For the case $(\bar U,\bar V) = (0,V^*)$, we normalize U_i by setting $\tilde U_i = U_i/(U_1+U_2+U_3)$. Then by similar argument we have, by passing to a subsequence if necessary, $\tilde U_i \to \check U_i \geq 0$ as $d, q_1 \to 0$, and $\check U_i$ satisfy $\check U_1 + \check U_2 + \check U_3 = 1$ and
$$\check U_1(1-V_1^*) = -q_2\check U_2 + \check U_2(1-V_2^*) = q_2\check U_2 + \check U_3(1-V_3^*) = 0$$
Since $V_1^* < 1$, so $\check U_1 = 0$. It follows from $q_2 \geq 1$ that $\check U_2 = 0$. This together with the last equation and $V_3^* > 1$ imply that $\check U_3 = 0$. This contradicts $\check U_1 + \check U_2 + \check U_3 = 1$.

Having ruled out both cases above, we proved Step 3.

Step 4: $\bar U_1 > 0$.

This is a consequence of Steps 2 and 3.

Step 5: $\bar U_3 = 0$.

If not, then $\bar U_3 > 0$, which leads to $\bar U_3 + \bar V_3 = 1$. Therefore,

$$\begin{cases} D(\bar V_3 - \bar V_2) - q_2\bar V_2 + \bar V_2(1-\bar V_2) = 0 \\ D(\bar V_2 - \bar V_3) + q_2\bar V_2 = 0. \end{cases}$$

Adding the above two equations we find $\bar V_2(1-\bar V_2) = 0$. Since $\bar V_2 < 1$, the only possibility is $\bar V_2 = 0$, from which we have $\bar V_i = 0$ for $i = 1,2,3$ and $\bar U_1 = \bar U_3 = 1$. That is, $(U,V) \to (1,0,1,0,0,0)$ as

$d, q_1 \to 0$. We normalize V_i by setting $\tilde{V}_i = V_i/(V_1+V_2+V_3)$. Then by passing to a subsequence if necessary, $\tilde{V}_i \to \check{V}_i \geq 0$ as $d, q_1 \to 0$, and $\check{V}_i$ satisfy $\check{V}_1+\check{V}_2+\check{V}_3 = 1$, and

$$\begin{cases} \check{V}_1 = \check{V}_2 \\ D(\check{V}_1+\check{V}_3-2\check{V}_2) - q_2\check{V}_2 + \check{V}_2 = 0 \\ D(\check{V}_3-\check{V}_2) + q_2\check{V}_2 = 0, \end{cases}$$

from which we conclude that $\check{V}_i = 0$ for all i, which is a contradiction. This completes Step 5.

Step 6: $\bar{V}_1 = \hat{V}_2$ and $\bar{U}_1 = 1 - \hat{V}_2$.

As $\bar{U}_1 > 0$ and $\bar{U}_2 = \bar{U}_3 = 0$, we have $\bar{U}_1 + \bar{V}_1 = 1$, $\bar{V}_1 = \bar{V}_2$, and

$$\begin{cases} D(\bar{V}_3-\bar{V}_2) - q_2\bar{V}_2 + \bar{V}_2(1-\bar{V}_2) = 0 \\ D(\bar{V}_2-\bar{V}_3) + q_2\bar{V}_2 + \bar{V}_3(1-\bar{V}_3) = 0. \end{cases}$$

By similar normalization argument we can show that $\bar{V}_i > 0$ for all i. Hence, $\bar{V}_i = \hat{V}_i$ for $i = 2, 3$. Thus $\bar{V}_1 = \hat{V}_2$ and $\bar{U}_1 = 1 - \hat{V}_2$. This completes the proof.

Lemma 22 *Fix any $D, q_2 > 0$. Then there exists some $\delta > 0$ such that for any $d \in (0, \delta)$ and $q_1 \in (-d, \delta)$, the positive steady state (U^δ, V^δ), which is given by Lemma 20, is locally stable.*

Proof By previous result, there exists some $\delta > 0$ such that for $|d|, |q_1| \leq \delta$, there exist $(U^\delta, V^\delta) \in \mathbb{R}^6_+$ such that $F(d, q_1, U^\delta, V^\delta) = (0,0,0,0,0,0)^T$. Since the two-species competition models II and III are strongly monotone, the linearized system at (U^δ, V^δ) has a principal eigenvalue (it is real, simple and has the largest real part among all eigenvalues), which we denote as λ_1^δ; i.e.

$$D_{(U,V)}F(d, q_1, U^\delta, V^\delta)\begin{pmatrix}\varphi^\delta \\ \phi^\delta\end{pmatrix} = \lambda_1^\delta \begin{pmatrix}\varphi^\delta \\ \phi^\delta\end{pmatrix},$$

where $\varphi^\delta := (\varphi_1^\delta, \varphi_2^\delta, \varphi_3^\delta)^T$ and $\phi^\delta := (\phi_1^\delta, \phi_2^\delta, \phi_3^\delta)^T$. Furthermore, we may choose $\varphi_i^\delta < 0$ and $\phi_i^\delta > 0$ for $i = 1, 2, 3$, and normalize by

$$\sum_{i=1}^{3}(|\varphi_i^\delta| + |\phi_i^\delta|) = 1.$$

We proceed to show that (U^δ, V^δ) is stable, that is, $\lambda_1^\delta < 0$. To this end, we argue by contradiction and assume $\lambda_1^\delta \geq 0$. Let $\delta \to 0$ (so that $d \to 0, q_1 \to 0$), by passing to a subsequence, we may assume that $\lambda_1^\delta \to \lambda_1^* \geq 0$, so that $D_{(U,V)}F(0, 0, \hat{U}, \hat{V})$ has at least one non-negative eigenvalue, i.e. that (48) holds for some non-trivial eigenvector (φ, ψ) and non-negative eigenvalue λ_1^*. However, Lemma 19 asserts that $\lambda_1^* < 0$. This is a contradiction.

Therefore, $\lambda_1^\delta < 0$ for sufficiently small $\delta > 0$, i.e. (U^δ, V^δ) is stable.

In the following two results, we consider the linear instability of the semi-trivial steady states of (2), denoted by $(U^*, 0) := (U_1^*, U_2^*, U_3^*, 0, 0, 0)$ and $(0, V^*) := (0, 0, 0, V_1^*, V_2^*, V_3^*)$.

Lemma 23 *If $q_2 \geq 1$, then there exists $\delta > 0$ such that $(U^*, 0)$ is linearly unstable for every $0 \leq d, q_1 \leq \delta$.*

Proof Setting $d = 0, q_1 = 0$, (U_1^*, U_2^*, U_3^*) is the unique solution of

$$\begin{cases} U_1^*(1 - U_1^*) = 0 \\ -q_2 U_2^* + U_2^*(1 - U_2^*) = 0 \\ q_2 U_2^* + U_3^*(1 - U_3^*) = 0. \end{cases}$$

By direct calculations and using $q_2 \geq 1$, we get

$$(U_1^*, U_2^*, U_3^*) = (1, \max(1 - q_2, 0), \frac{1 + \sqrt{1 + 4q_2 U_2^*}}{2}).$$

For $q_2 \geq 1$, we have $(U_1^*, U_2^*, U_3^*) = (1, 0, 1)$, and its linear stability of $(U^*, 0)$ is determined by eigenvalue problem

$$\tilde{E}_2 \varphi + \Lambda \varphi = 0,$$

where $\varphi = (\varphi_1, \varphi_2, \varphi_3)^T$ and

$$\tilde{E}_2 = \begin{pmatrix} -D & D & 0 \\ D & -2D - q_2 + 1 & D \\ 0 & D + q_2 & -D \end{pmatrix}.$$

We will test $\tilde{E}_2$ by multiplying on the right with the vector $(\hat{V}_2 - \epsilon, \hat{V}_2, \hat{V}_3)^T$, where $\hat{V}_2, \hat{V}_3$ is given in Theorem 4 and ϵ is a small positive constant.

$$\tilde{E}_2 \begin{pmatrix} \hat{V}_2 - \epsilon \\ \hat{V}_2 \\ \hat{V}_3 \end{pmatrix} = \begin{pmatrix} \epsilon D \\ (\hat{V}_2)^2 - \epsilon D \\ \hat{V}_3(\hat{V}_3 - 1) \end{pmatrix}.$$

Since all of the entries of the right hand side is positive, we can apply the Collatz-Wielandt Formula [40, P. 667] to get

$$-\Lambda = \max_{\{\varphi \geq 0 : \varphi \neq 0\}} \min_{1 \leq i \leq 3, \varphi_i > 0} \frac{[\tilde{E}_2 \varphi]_i}{\varphi_i} \geq \min \left\{ \frac{\epsilon D}{\hat{V}_2 - \epsilon}, \frac{(\hat{V}_2)^2 - \epsilon D}{\hat{V}_2}, \frac{\hat{V}_3(\hat{V}_3 - 1)}{\hat{V}_3} \right\} > 0,$$

that is, $(U^*, 0)$ is linearly unstable when $d = q_1 = 0$. By continuity, it remains linearly unstable for all small d and q_1.

Lemma 24 *For each $D, q_2 > 0$, there exists $\delta > 0$ such that $(0, V^*)$ is linearly unstable for every $0 \leq d, q_1 \leq \delta$.*

Proof Setting $d = 0$ and $q_1 = 0$, the linear instability of $(0, V^*)$ is determined by the principal eigenvalue of the following problem

$$\begin{pmatrix} 1 - V_1^* & 0 & 0 \\ 0 & -q_2 + 1 - V_2^* & 0 \\ 0 & q_2 & 1 - V_3^* \end{pmatrix} \begin{pmatrix} \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix} + \Lambda \begin{pmatrix} \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}.$$

Clearly, $\Lambda = V_3^* - 1$ is an eigenvalue with eigenfunction $(0, 0, 1)^T$. Recalling that $V_1^* < 1$ (Lemma 8), we deduce that there is at least one negative eigenvalue. Thus $(0, V^*)$ is linearly unstable.

Proof of Theorem 4. By Lemma 20, there exists some $\delta > 0$ such that for any $d \in (0, \delta)$, $q_1 \in (-d, \delta)$, Model II has a unique positive steady state (U^δ, V^δ) in a small neighborhood of $(\hat{U}, \hat{V})$. Lemma 21 further ensures that this is the only positive steady state for small positive d and q_1. By Lemma 22, (U^δ, V^δ) is locally stable. We can then conclude by the theory of monotone dynamical systems [15, 16, 46] and Lemmas 23 and 24 that (U^δ, V^δ) is globally stable.

Appendix C The dynamics of Model III

In this section, we mainly consider the dynamics of Model III, i.e., system (5), in homogeneous environments. We consider the non-negative and non-trivial solutions of

$$\begin{cases} d(U_2+U_3-2U_1)-(q_1+q_2)U_1+U_1(1-U_1-V_1)=0 \\ d(U_1-U_2)+q_1U_1+U_2(1-U_2-V_2)=0 \\ d(U_1-U_3)+q_2U_1+U_3(1-U_3-V_3)=0 \\ D(V_2+V_3-2V_1)-(q_1+q_2)V_1+V_1(1-U_1-V_1)=0 \\ D(V_1-V_2)+q_1V_1+V_2(1-U_2-V_2)=0 \\ D(V_1-V_3)+q_2V_1+V_3(1-U_3-V_3)=0 \end{cases} \tag{52}$$

There are three types of non-negative and non-trivial solutions of this system. We denote three different types of solutions as (U,V), in which $U_i>0$ and $V_i=0$, or $U_i=0$ and $V_i>0$, or $U_i>0$ and $V_i>0$ for all $i=1,2,3$. The semi-trivial steady state $(U^*,0):=(U_1^*,U_2^*,U_3^*,0,0,0)$ satisfies

$$\begin{cases} d(U_2^*+U_3^*-2U_1^*)-(q_1+q_2)U_1^*+U_1^*(1-U_1^*)=0 \\ d(U_1^*-U_2^*)+q_1U_1^*+U_2^*(1-U_2^*)=0 \\ d(U_1^*-U_3^*)+q_2U_1^*+U_3^*(1-U_3^*)=0 \end{cases} \tag{53}$$

The linear stability of $(U_1^*,U_2^*,U_3^*,0,0,0)$ is determined by the sign of the principal eigenvalue $\tilde{\Lambda}_3$ of the eigenvalue problem

$$F_3\begin{pmatrix}\varphi_1\\ \varphi_2\\ \varphi_3\end{pmatrix}+\Lambda\begin{pmatrix}\varphi_1\\ \varphi_2\\ \varphi_3\end{pmatrix}=\begin{pmatrix}0\\0\\0\end{pmatrix}, \tag{54}$$

where matrix F_3 is given by

$$F_3=\begin{pmatrix}-2D-(q_1+q_2)+1-U_1^* & D & D\\ D+q_1 & -D+1-U_2^* & 0\\ D+q_2 & 0 & -D+1-U_3^*\end{pmatrix}.$$

Proposition 6 *When $D=d$, the derivative of $\tilde{\Lambda}_3$ with respect to D satisfies*

$$\frac{\partial\tilde{\Lambda}_3}{\partial D}\Big|_{D=d}=-\frac{U_1^*(U_2^*+U_3^*-2U_1^*)+\frac{d}{d+q_1}U_2^*(U_1^*-U_2^*)+\frac{d}{d+q_2}U_3^*(U_1^*-U_3^*)}{(U_1^*)^2+\frac{d}{d+q_1}(U_2^*)^2+\frac{d}{d+q_2}(U_3^*)^2}. \tag{55}$$

Proof Differentiate (54) with respect to D, we get

$$\begin{pmatrix}\varphi_2+\varphi_3-2\varphi_1\\ \varphi_1-\varphi_2\\ \varphi_1-\varphi_3\end{pmatrix}+F_3\begin{pmatrix}\varphi_1'\\ \varphi_2'\\ \varphi_3'\end{pmatrix}+\frac{\partial\tilde{\Lambda}_3}{\partial D}\begin{pmatrix}\varphi_1\\ \varphi_2\\ \varphi_3\end{pmatrix}+\tilde{\Lambda}_3\begin{pmatrix}\varphi_1'\\ \varphi_2'\\ \varphi_3'\end{pmatrix}=\begin{pmatrix}0\\0\\0\end{pmatrix}, \tag{56}$$

where $\varphi_i'=\frac{\partial\varphi_i}{\partial D}$, $i=1,2,3$. Note that when $D=d$,

$$F_3|_{D=d}\begin{pmatrix}U_1^*\\ U_2^*\\ U_3^*\end{pmatrix}=\begin{pmatrix}0\\0\\0\end{pmatrix},$$

$$F_3^T\Big|_{D=d}\begin{pmatrix}U_1^*\\ \frac{d}{d+q_1}U_2^*\\ \frac{d}{d+q_2}U_3^*\end{pmatrix}=\begin{pmatrix}0\\0\\0\end{pmatrix}, \tag{57}$$

and when $D = d$, we may choose

$$\begin{pmatrix}\varphi_1\\ \varphi_2\\ \varphi_3\end{pmatrix} = \begin{pmatrix}U_1^*\\ U_2^*\\ U_3^*\end{pmatrix}. \tag{58}$$

Set $D = d$ in (56) and multiplying it by $\left(U_1^*, \frac{d}{d+q_1}U_2^*, \frac{d}{d+q_2}U_3^*\right)$, using (57), (58) and $\tilde{\Lambda}_3(d,d) = 0$, we obtain (55). This completes the proof.

Next, we establish some *a prior* estimates of U_i^*, $i = 1, 2, 3$.

Lemma 25 *For any $d, D > 0$ and $q_1, q_2 > 0$, the following results hold:*

(i) *If $q_1 \geq q_2$, then $U_2^* \geq U_3^*$;*
(ii) *If $q_1 \leq q_2$, then $U_2^* \leq U_3^*$.*

In particular, if $q_1 = q_2$, $U_2^* = U_3^*$ holds.

Proof We prove (i) only and (ii) can be shown similarly. We will assume $U_2^* < U_3^*$ and deduce $q_1 < q_2$. By the second and third equation of (53),

$$\begin{cases}(-d + 1 - U_2^*)U_2^* = -(d + q_1)U_1^* < 0,\\ (-d + 1 - U_3^*)U_3^* = -(d + q_2)U_1^* < 0.\end{cases}$$

This implies

$$0 < U_2^* < U_3^* \quad \text{and} \quad 0 > -d + 1 - U_2^* > -d + 1 - U_3^*.$$

Combining the above, we have

$$-(d + q_2)U_1^* = (-d + 1 - U_2^*)U_2^* > (-d + 1 - U_3^*)U_3^* = -(d + q_2)U_1^*.$$

This implies $q_2 > q_1$. This proves (i).

Lemma 26 *For any $d, D > 0$ and $q_1, q_2 > 0$, $U_1^* < 1$ always holds.*

Proof By exchanging patches 2 and 3 if necessary (the river network is symmetric), we may assume without loss of generality that $q_1 \geq q_2$.

We argue by contradiction and assume that $U_1^* \geq 1$ for some $q_1 \geq q_2 > 0$. By the first equation of (53), we get

$$d(U_2^* + U_3^* - 2U_1^*) - (q_1 + q_2)U_1^* \geq 0.$$

Using $U_2^* \geq U_3^*$ (from Lemma 25), we have

$$2d(U_2^* - U_1^*) \geq (q_1 + q_2)U_1^* > 0,$$

so $U_2^* > U_1^* \geq 1$. In view of $\sum_{i=1}^3 U_i^*(1 - U_i^*) = 0$ (upon summing (53)), we must have $U_3^* < 1$. By the third equation of (53), we get $U_3^* > \frac{d+q_2}{d}U_1^* > U_1^* \geq 1$. This is a contradiction. This finishes the proof for the case $q_1 \geq q_2$, and the case $q_1 \leq q_2$ can be treated similarly.

C.1 The global dynamics of Model III when $q_1 = q_2$

In this part, we shall show Theorem 5. We first establish some *a priori* estimates of non-negative and non-trivial steady state of (52) as $q_1 = q_2$.

C.1.1 Preliminary results on non-negative, non-trivial steady states

Lemma 27 *Suppose* $q_1 = q_2 > 0$*, then for any* $d, D > 0$*, we have* $U_2 = U_3$ *and* $V_2 = V_3$*.*

Proof By the similar argument in the proof of Lemma 1, we can obtain this lemma.

Lemma 28 *Suppose* $q_1 = q_2 := q > 0$*, then for any* $d, D > 0$*, we have* $U_3 + V_3 > 1$*.*

Proof Assume that (U_i) is non-trivial and is thus positive for all i. The same argument applies to the case $U_1 = U_2 = U_3 = 0$. Assume to the contrary that $U_3 + V_3 \leq 1$ for some $d, D, q > 0$, then by the third equation of (52), we get $d(U_1 - U_3) + qU_1 \leq 0$. Thus $U_3 \geq \frac{d+q}{d} U_1 > U_1$. Similarly, we can show $V_3 > V_1$, if $V_i > 0$ for all i. Hence $1 \geq U_3 + V_3 > U_1 + V_1$ holds. By the first equation of (52) and Lemma 27, we obtain

$$2d(U_3 - U_1) - 2qU_1 = d(U_2 + U_3 - 2U_1) - 2qU_1 < 0,$$

i.e., $d(U_3 - U_1) - qU_1 < 0$. This together with the third equation of (52) implies that $U_3 + V_3 > 1$, which is a contradiction with our assumption.

Lemma 29 *Suppose* $q_1 = q_2 = q > 0$*, then for any* $d, D > 0$*, we have* $U_1 + V_1 < 1$*.*

Proof We argue by contradiction. If $U_1 + V_1 \geq 1$ for some $d, D, q > 0$, then by the first equation of (52) and Lemma 27, we have

$$2d(U_2 - U_1) - 2qU_1 = d(U_2 + U_3 - 2U_1) - 2qU_1 \geq 0,$$

so that $d(U_2 - U_1) - qU_1 \geq 0$, which together with the second equation of (52) implies $U_2 + V_2 \leq 1$. Using Lemma 27, we have $U_3 + V_3 = U_2 + V_2 \leq 1$. But this contradicts Lemma 28.

Lemma 30 *Suppose* $q_1 = q_2 := q > 0$ *and* $d, D > 0$*.*

(i) *If* $U_i > 0$ *for all* i*, then* $U_1 < U_3$*.*
(i) *If* $V_i > 0$ *for all* i*, then* $V_1 < V_3$*.*

Proof In case of $(U^*, 0)$ and $(0, V^*)$, the lemma follows from Lemmas 28 and 29. It therefore suffices to consider positive equilibria (U, V). We will prove (i), as (ii) follows from a similar argument. If $U_1 \geq U_3$ for some $d, D, q > 0$, by Lemmas 28 and 29, we have $V_3 > V_1$, which together with the 6th equation of (52) implies

$$(q + 1 - U_3 - V_3)V_3 > qV_1 + V_3(1 - U_3 - V_3) = D(V_3 - V_1) > 0;$$

i.e. $q + 1 - U_3 - V_3 > 0$. However, by the third equation of (52) and $U_1 \geq U_3$, we get

$$(q + 1 - U_3 - V_3)U_3 \leq qU_1 + U_3(1 - U_3 - V_3) = d(U_3 - U_1) \leq 0;$$

i.e. $q + 1 - U_3 - V_3 \leq 0$. This is a contradiction.

The following result is a direct consequence of Lemmas 27 and 30, and it provides some insight for the biological interpretation of Theorem 5.

Corollary 6 *Assume* $q_1 = q_2 > 0$ *and* $d, D > 0$*. Then we have*

$$U_1 < 1 < U_2 = U_3 \quad \text{and} \quad V_1 < 1 < V_2 = V_3.$$

Lemma 31 *Suppose $q_1 = q_2 > 0$, then for any $d, D > 0$, we have*

$$3 - \sum_{i=1}^{3}(U_i + V_i) > 0. \tag{59}$$

Proof By possibly exchanging the role of U and V, we may assume $U_i > 0$ for all i. Adding the equations of U_i $(i = 1, 2, 3)$ in (52) and using $U_2 + V_2 = U_3 + V_3 > 1$ (Lemmas 27 and 28), $U_1 + V_1 < 1$ (Lemma 29) and $U_1 < U_3 = U_2$ (Corollary 6), we obtain

$$\begin{aligned} &U_3(1 - U_1 - V_1) + U_3(1 - U_2 - V_2) + U_3(1 - U_3 - V_3) \\ &> U_1(1 - U_1 - V_1) + U_2(1 - U_2 - V_2) + U_3(1 - U_3 - V_3) = 0, \end{aligned}$$

which establishes (59).

Lemma 32 *Suppose $q_1 = q_2 := q > 0$ and $d, D > 0$. Then we have $-2q + 1 - U_1 - V_1 < 0$.*

Proof Corollary 6 and the first equation of (52) indicate that $-2q + 1 - U_1 - V_1 < 0$.

Theorem 10 *If $q_1 = q_2 > 0$ and $d, D > 0$, then system (52) has no positive solution.*

Proof We argue by contradiction. If there exists a positive solution (U, V) for (52), by direct calculation, we obtain

$$Dd(3 - \sum_{i=1}^{3}(U_i + V_i)) = (-2q + 1 - U_1 - V_1)(1 - U_2 - V_2)(1 - U_3 - V_3). \tag{60}$$

Lemma 31 shows that the left hand side of (60) is positive, but the right hand side of (60) is negative, due to Lemmas 27, 28 and 32. This completes the proof.

C.1.2 Global stability of $(U^*, 0)$ when $q_1 = q_2$

We assume $q_1 = q_2 := q$ throughout this subsection. The local instability of $(0, V^*)$ is determined by the sign of the principal eigenvalue, denoted as Λ_3, of the system

$$E_3 \begin{pmatrix} \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix} + \Lambda \begin{pmatrix} \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix},$$

where E_3 is rewritten as

$$E_3 = \begin{pmatrix} -2d - 2q + 1 - V_1^* & d & d \\ d + q & -d + 1 - V_2^* & 0 \\ d + q & 0 & -d + 1 - V_3^* \end{pmatrix}.$$

Setting $q_1 = q_2 := q$ and exchanging the role of the two species, (55) can be rewritten as

$$\frac{\partial \Lambda_3}{\partial d}\Big|_{d=D} = -\frac{(V_2^* - \frac{D+q}{D}V_1^*)(V_1^* - V_2^*) + (V_3^* - \frac{D+q}{d}V_1^*)(V_1^* - V_3^*)}{\frac{D+q}{D}(V_1^*)^2 + (V_2^*)^2 + (V_3^*)^2}. \tag{61}$$

We can obtain the following result by direct calculations:

Propositon 7 ([20, Propositon 6]) *Assume* $q_1 = q_2 := q > 0$ *and* $V_1^* + V_2^* + V_3^* \neq 3$. *Then* $\det(E_3) = 0$ *if and only if either* $d = D$, *or*

$$d = \frac{(-2q + 1 - V_1^*)(1 - V_2^*)(1 - V_3^*)}{D(3 - V_1^* - V_2^* - V_3^*)}. \tag{62}$$

Corollary 7 *Suppose* $q_1 = q_2 := q > 0$, *then for any* $d, D > 0$, $\frac{\partial \Lambda_3}{\partial d}\big|_{d=D} < 0$.

Proof By Corollary 6, we have $V_1^* - V_2^* < 0, V_1^* - V_3^* < 0$. Using $V_2^* > 1$ and the fifth equation of (52), we get

$$\frac{D+q}{D} V_1^* - V_2^* > 0.$$

Similarly, by $V_3^* > 1$ and the sixth equation of (52), we get

$$\frac{D+q}{D} V_1^* - V_3^* > 0.$$

Therefore, the right hand side of (61) is strictly negative.

Lemma 33 *Suppose* $q_1 = q_2 > 0$, *then for any* $d, D > 0$, *the right hand side of* (62) *is negative.*

Proof Using Lemmas 27 and 28, we get $V_2^* = V_3^* > 1$, hence $(1-V_2^*)(1-V_3^*) > 0$, which together with Lemmas 31 and 32 shows that the right hand side of (62) is strictly negative.

Theorem 11 *Suppose* $q_1 = q_2 > 0$, *then for any* $d, D > 0$, *we have*

$$\Lambda_3(d, D) = \begin{cases} + & D > d; \\ - & D < d; \end{cases} \quad \text{and} \quad \tilde{\Lambda}_3(d, D) = \begin{cases} - & D > d; \\ + & D < d. \end{cases}$$

Proof The equation (62) cannot hold since the right hand side is strictly negative, by Lemma 33. Hence, Proposition 7 says that $\Lambda_3(d, D) = 0$ if and only if $d = D$. Therefore, by Corollary 7 and the continuity of Λ_3, $\Lambda_3(d, D) > 0$ holds for $D > d > 0$ and $\Lambda_3(d, D) < 0$ holds for $0 < D < d$. The result for $\tilde{\Lambda}_3$ follows from the identity $\tilde{\Lambda}_3(d, D) = \Lambda_3(D, d)$ for all d, D.

Proof of Theorem 5. For $d > D$, Theorems 11 and 10 says that $(0, V^*)$ is linearly unstable, and that Model III has no positive equilibria. It follows from the theory of monotone dynamical systems [16, Theorem 1.5] that the equilibrium $(U^*, 0)$ is globally asymptotically stable.

C.2 The local stability of $(U^*, 0)$

In this subsection, we determine the local stability of the semi-trivial steady sate $(U^*, 0)$ for more general q_1, q_2.

Lemma 34 *Suppose* $0 < q_2 \leq q_1 + \frac{1}{2}$, $0 < \frac{q_2}{q_1} \leq \sqrt{2}$. *Then* $U_2^* > 1$ *holds for all* $d > 0$.

Proof Since we have shown $U_2^* > 1$ for $q_1 = q_2$, it is sufficient to show $U_2^* \neq 1$ for any q_1, q_2 satisfying the assumptions. We argue by contradiction: Suppose that $U_2^* = 1$ for some q_1, q_2. By the second equation of (53), we have

$$U_1^* = \frac{d}{d + q_1}. \tag{63}$$

Adding the equations of U_1^*, U_2^*, U_3^* in (53) and using $U_2^* = 1$, we get

$$U_1^*(1 - U_1^*) + U_3^*(1 - U_3^*) = 0. \tag{64}$$

Substituting (63) and (64) into the third equation of (53), we get

$$U_3^* = \frac{1}{d + q_1}(d + q_2 - \frac{q_1}{d + q_1}). \tag{65}$$

By $U_1^* < 1$ (from (63)) and (64), we see that $U_3^* > 1$. This, together with (65), implies that

$$\frac{q_1}{d + q_1} < q_2 - q_1. \tag{66}$$

Hence, $q_2 - q_1 > 0$. Therefore, we can rewrite (66) to get

$$d > \frac{q_1(1 - q_2 + q_1)}{q_2 - q_1} > 0, \tag{67}$$

which the last inequality follows from $0 < q_2 - q_1 \leq \frac{1}{2}$. By (63), (64) and (65), after simplifications, we have

$$dq_1 = (q_2 - q_1 - \frac{q_1}{d + q_1})(d + q_2 - \frac{q_1}{d + q_1}). \tag{68}$$

It follows from (68) that $dq_1 < (q_2 - q_1)(d + q_2)$, which can be rewritten as

$$d(2q_1 - q_2) < q_2(q_2 - q_1). \tag{69}$$

By (67) and (69), note that $2q_1 - q_2 > 0$ by assumption, we have

$$0 < \left(\frac{q_1}{q_2 - q_1} - q_1 \right)(2q_1 - q_2) < q_2(q_2 - q_1). \tag{70}$$

By assumption $0 < q_2 - q_1 \leq \frac{1}{2}$, we have $\frac{q_1}{q_2 - q_1} \geq 2q_1$. Hence, by (70)

$$q_1(2q_1 - q_2) < q_2(q_2 - q_1),$$

which is equivalent to $q_2 > \sqrt{2}q_1$, a contradiction to assumption $q_2 \leq \sqrt{2}q_1$.

Lemma 35 *Suppose that $0 < q_1 \leq q_2 + \frac{1}{2}$ and $\frac{q_2}{q_1} \geq \frac{1}{\sqrt{2}}$, then $U_3^* > 1$ holds for all $d > 0$.*

Proof This proof is similar to Lemma 34, by exchanging the role of patches 2 and 3. We omit the proof.

Directly by Lemmas 34, and 35, we obtain the following result, which also provides some insight for the biological interpretation of Theorem 6.

Corollary 8 *Let q_1, q_2, d, D be positive. If $|q_2 - q_1| \leq \frac{1}{2}$ and $\frac{1}{\sqrt{2}} \leq \frac{q_2}{q_1} \leq \sqrt{2}$, then $U_2^* > 1$ and $U_3^* > 1$ hold.*

Proof of Theorem 6. Fix $d > D$. We have shown that if $q_1 = q_2$, $\tilde{\Lambda}_3(d, D) > 0$ in Theorem 11. By the continuity of $\tilde{\Lambda}_3$ in q_1, q_2, we just need to prove $\tilde{\Lambda}_3 \neq 0$. By contradiction, we assume that there exist some q_1, q_2 such that $\tilde{\Lambda}_3 = 0$. Then by direct calculation, we get

$$Dd(3 - U_1^* - U_2^* - U_3^*) = [-(q_1 + q_2) + (1 - U_1^*)](1 - U_2^*)(1 - U_3^*). \tag{71}$$

Adding the equations of (53), we get

$$U_1^*(1 - U_1^*) + U_2^*(1 - U_2^*) + U_3^*(1 - U_3^*) = 0. \tag{72}$$

Due to $U_2^* > 1$ and $U_3^* > 1$, we have $U_1^* < 1$, so

$$U_i^*(1 - U_i^*) < (1 - U_i^*), \quad \text{for } i = 1, 2, 3.$$

Substituting this into (72), we obtain $3 - U_1^* - U_2^* - U_3^* > 0$. Again using $U_1^* < U_2^*, U_1^* < U_3^*$ and the first equation of (53), $-(q_1 + q_2) + (1 - U_1^*) < 0$. This together with $U_2^* > 1$ and $U_3^* > 1$ (Corollary 8) yields the right hand side of (71) is negative. This contradiction finishes the proof.

C.3 Existence of evolutionarily singular strategy

The goal of this subsection is to establish Theorem 7.

Lemma 36 *For any $q_1, q_2 > 0$, we have $\frac{\partial \tilde{\Lambda}_3}{\partial D}(d, d) < 0$ for sufficiently large d.*

Proof By Proposition 6, the sign of $\frac{\partial \tilde{\Lambda}_3}{\partial D}(d, d)$ is the opposite of that of N, where

$$N := U_1^*(U_2^* + U_3^* - 2U_1^*) + \frac{d}{d + q_1} U_2^*(U_1^* - U_2^*) + \frac{d}{d + q_2} U_3^*(U_1^* - U_3^*). \tag{73}$$

By (53), we can rewrite (73) as

$$\begin{aligned} N &= (U_2^* - U_1^*)(U_1^* - \frac{d}{d + q_1} U_2^*) + (U_3^* - U_1^*)(U_1^* - \frac{d}{d + q_2} U_3^*) \\ &= \frac{1}{d + q_1}(U_2^* - U_1^*)U_2^*(U_2^* - 1) + \frac{1}{d + q_2}(U_3^* - U_1^*)U_3^*(U_3^* - 1) \end{aligned} \tag{74}$$

Note that $(U_1^*, U_2^*, U_3^*) \to (1, 1, 1)$ as $d \to \infty$. As (U_1^*, U_2^*, U_3^*) is the unique stable positive solution of (53), it can be shown that it is smooth at $d = \infty$ so that we can expand U_i as $U_i^* = 1 + \tilde{U}_i/d + O(1/d^2)$, $i = 1, 2, 3$, for sufficiently large d. From the second and third equation of (53) we have

$$\tilde{U}_2 = \tilde{U}_1 + q_1, \quad \tilde{U}_3 = \tilde{U}_1 + q_2. \tag{75}$$

Recall (72) (resulting from adding three equations in (53)), it follows that

$$\tilde{U}_1 + \tilde{U}_2 + \tilde{U}_3 = 0. \tag{76}$$

By solving (75) and (76), $\tilde{U}_1 = -(q_1 + q_2)/3$, $\tilde{U}_2 = (2q_1 - q_2)/3$, $\tilde{U}_3 = (2q_2 - q_1)/3$. Hence, for large d it holds that

$$\begin{cases} U_1^* = 1 - \dfrac{q_1 + q_2}{3d} + O(1/d^2), \\ U_2^* = 1 + \dfrac{2q_1 - q_2}{3d} + O(1/d^2), \\ U_3^* = 1 + \dfrac{2q_2 - q_1}{3d} + O(1/d^2). \end{cases}$$

Substituting into (74), we obtain

$$d^3 N \to \frac{2}{3}(q_1^2 + q_2^2 - q_1 q_2) > 0 \quad \text{as } d \to \infty, \tag{77}$$

provided that $(q_1, q_2) \neq (0, 0)$. Therefore, we conclude by Proposition 6 that $\frac{\partial \tilde{\Lambda}_3}{\partial D}(d,d) < 0$ for sufficiently large d.

Lemma 37 *Let $q_1, q_2 > 0$. For sufficiently small d, we have*

$$\frac{\partial \tilde{\Lambda}_3}{\partial D}(d,d) = \begin{cases} - & \text{if } q_1 + q_2 \leq 1 \ \text{ or } \ q_1 + q_2 > (q_1 - q_2)^2; \\ + & \text{if } 1 < q_1 + q_2 < (q_1 - q_2)^2. \end{cases} \tag{78}$$

Proof We consider three cases:

Case I. $q_1 + q_2 < 1$. By the first equation of (53), we see that $U_1^* \to \overline{U}_1 := 1 - (q_1 + q_2) > 0$ as $d \to 0$. By the second and third equation of (53), $U_2^* \to \overline{U}_2 \geq 1, U_3^* \to \overline{U}_3 \geq 1$. Thus $N \to \overline{U}_1(\overline{U}_2 + \overline{U}_3 - 2\overline{U}_1) > 0$ as $d \to 0$, where N is given by (73). Here we used $q_1 > 0$ and $q_2 > 0$. By Proposition 6, we have $\frac{\partial \tilde{\Lambda}_3}{\partial D}(d,d) < 0$ for sufficiently small d when $q_1 + q_2 < 1$.

Case II. $q_1 + q_2 = 1$. For this case, we have $U_1^* \to 0$ and $U_i^* \to 1$ $(i = 2, 3)$ as $d \to 0$. By the first equation of (53), we get

$$\frac{U_1^*}{\sqrt{d}} \to \sqrt{2} \qquad as \quad d \to 0. \tag{79}$$

Thus $N = 2\sqrt{2}d^{1/2} + o(1)$ is positive for sufficiently small d. Therefore, $\frac{\partial \tilde{\Lambda}_3}{\partial D}(d,d) < 0$ when $q_1 + q_2 = 1$.

Case III. $q_1 + q_2 > 1$. For this case, we have $U_1^* \to 0$ and $U_i^* \to 1$ $(i = 2, 3)$ as $d \to 0$. By the first equation of (53), we get

$$\frac{U_1^*}{d} \to \frac{2}{q_1 + q_2 - 1}, \qquad as \quad d \to 0. \tag{80}$$

Substituting into (73), we get

$$\frac{N}{d} = \frac{2}{q_1 + q_2 - 1}(1 + 1 - o(1)) + \frac{1}{d + q_1} \cdot 1 \cdot (o(1) - 1) + \frac{1}{d + q_2} \cdot 1 \cdot (o(1) - 1) + o(1).$$

Hence,

$$\lim_{d \to 0+} \frac{N}{d} = \frac{(q_1 + q_2) - (q_1 - q_2)^2}{(q_1 q_2)(q_1 + q_2 - 1)}.$$

Having determined the sign of N for d sufficiently small, (78) follows from Proposition 6.

Proof of Theorem 7. Since $d \mapsto \frac{\partial \tilde{\Lambda}_3}{\partial D}(d,d)$ is analytic, all the roots are discrete. By Lemmas 36 and 37, $\frac{\partial \tilde{\Lambda}_3}{\partial D}(d,d) > 0$ for d small and $\frac{\partial \tilde{\Lambda}_3}{\partial D}(d,d) < 0$ for $d \gg 1$. This says that the infinity and zero diffusion rates are local CvSSs. Furthermore, there exists at least one $d^* = d^*(q_1, q_2)$ such that $\frac{\partial \tilde{\Lambda}_3}{\partial D}(d^*, d^*) = 0$, and $\frac{\partial \tilde{\Lambda}_3}{\partial D}(d,d)$ change sign from positive to negative in a neighborhood of d^*; i.e. d^* is an evolutionary singular strategy which is not a CvSS.

Acknowledgment. The authors sincerely thank Prof. Mark Lewis and the referees for their suggestions which help improve the presentation of the manuscript. HYJ is partially supported by the NSFC grant No. 11571364. KYL and YL are partially supported by the NSF grant DMS-1853561.

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