

Are two-patch models sufficient?

The evolution of dispersal and topology of river network modules

Hongyan Jiang · King-Yeung Lam · Yuan Lou

We study the dynamics of two competing species in three-patch models and illustrate how the topology of directed river network modules may affect the evolution of dispersal. Each model assumes that patch 1 is at the upstream end, patch 3 is at the downstream end, but patch 2 could be upstream, or middle stream, or downstream, depending on the specific topology of the modules. We posit that individuals are subject to both unbiased dispersal between patches and passive drift from one patch to another, depending upon the connectivity of patches. When the drift rate is small, we show that for all models, the mutant species can invade when rare if and only if it is the slower disperser. However, when the drift rate is large, most models predict that the faster disperser wins, while some predict that there exists one evolutionarily singular strategy. The intermediate range of drift is much more complex: most models predict the existence of one singular strategy, but it may or may not be evolutionarily stable, again depending upon the topology of modules, while one model even predicts that for some intermediate drift rate, singular strategy does not exist and the faster disperser wins the competition.

Keywords River network module · patch model · network topology · evolution of dispersal

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1 Introduction

The dynamics of population models in advective habitats such as rivers have received increasing attention in recent years. These studies covered a wide range of topics, including flow reactors [1], persistence [25, 32–34, 38, 45], benthic-drift modeling [17, 19], seasonal environment [18, 20, 21], competition models [29, 30, 43, 46, 47, 53, 54], Allee effect [48–50], among others.

Organisms in advective environment are often subject to both unbiased dispersal and passive drift [42]. These two modes of dispersal focus on different niches. On the one hand, passive drift pushes individual to a relative downstream habitat, which can sometimes be less desirable. e.g.

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when a river meets the ocean, the downstream end of the river could be an ecological sink for fresh water organisms. On the other hand, unbiased dispersal could help organisms to overcome the drift and to explore the overall habitat without focusing on any individual patches.

One basic evolutionary questions is: How would dispersal evolve in advective habitats? It was shown in [27, 31] that for a homogeneous environment, the faster dispersal could be selected, provided that the boundary loss of individuals is not significant; see [15] for more recent progress. However, when the environment is spatially heterogeneous, some intermediate dispersal rate could be evolutionarily stable, or multiple (local) evolutionarily stable strategies could emerge; see [12, 24].

An emerging direction is the study of population dynamics in river networks [9, 22, 39–41]; see also earlier empirical works [10, 13]. Most of these studies on river networks focused on single species in continuous habitats and the corresponding mathematical models are partial differential equations of reaction-diffusion type. In this paper we consider the competition of two species with discrete dispersal in advective patchy environments, and the corresponding mathematical models are systems of ordinary differential equations. The following figure is an illustration of an advective two-patch habitat:

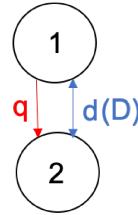


Fig. 1: Advective two-patch habitat: Patch 1 is the upstream end and patch 2 denotes the downstream end. The blue two-way arrow represents the dispersal of species between two patches with rate d or D , the red one-way arrow represents the uni-directional drift of individuals from patch 1 to patch 2 with rate q .

We can regard patch 1 in Fig. 1 as the upstream end and patch 2 as the downstream end: Individuals can move freely between two patches without cost, and those in patch 1 are washed downstream to patch 2 with rate q . The corresponding system of two competing populations can be formulated as follows:

$$\begin{cases} \frac{du_1}{dt} = d(u_2 - u_1) - qu_1 + u_1(1 - \frac{u_1 + v_1}{k_1}) \\ \frac{du_2}{dt} = d(u_1 - u_2) + qu_1 + u_2(1 - \frac{u_2 + v_2}{k_2}) \\ \frac{dv_1}{dt} = D(v_2 - v_1) - qv_1 + v_1(1 - \frac{u_1 + v_1}{k_1}) \\ \frac{dv_2}{dt} = D(v_1 - v_2) + qv_1 + v_2(1 - \frac{u_2 + v_2}{k_2}) \\ u_i(0) > 0, v_i(0) > 0, i = 1, 2, \end{cases} \quad (1)$$

where u_i, v_i ($i = 1, 2$) denote the number of individuals of the two species in patch i , with dispersal rates d and D , respectively. The parameter q is the drift rate from patch 1 to 2 for both species, and k_i ($i = 1, 2$) is the carrying capacity of patch i . The parameters d, D, k_1, k_2 are assumed to be positive constants and q is a non-negative constant. Under these assumptions, system (1) has two semi-trivial steady states, denoted by $(u_1^*, u_2^*, 0, 0)$ and $(0, 0, v_1^*, v_2^*)$. In system (1), it is assumed that both species are ecologically identical except for their dispersal rates, so that the dispersal rate can be regarded as a trait. It is subject to selection, by virtue of the competition between two phenotypes with different dispersal traits. Such a modeling framework

has become a standard approach in the study of evolution of dispersal since the seminal work of Hastings [16]. We refer to [2, 4, 5, 23, 26, 36, 51] and references therein for the evolution of dispersal in patchy environments.

It was shown in [14, 37] that the following result holds:

Theorem 1 Suppose that $k_1 > k_2$.

- (i) If $0 \leq q < \frac{k_1 - k_2}{k_1 + k_2}$ and $d < D$, then $(u_1^*, u_2^*, 0, 0)$ is globally asymptotically stable;
- (ii) If $q > \frac{k_1 - k_2}{k_1 + k_2}$ and $d < D$, then $(0, 0, v_1^*, v_2^*)$ is globally asymptotically stable.

Theorem 1 implies that when patch 1 has higher carrying capacity, the slower disperser wins the competition for slow drift. This agrees with the findings of Hastings [16] and Dockery et al. [8] on the evolution of slow dispersal. When the drift rate is large, the faster disperser will be dominant. If $q = \frac{k_1 - k_2}{k_1 + k_2}$, then both species will coexist. Indeed, the results in [8, 16] readily apply to the case $q = 0$. Thus the main contribution of Theorem 1 is the advective case $q > 0$. We refer to [28] for further discussions, including the case when $k_1 \leq k_2$.

A natural question is whether Theorem 1 can be readily extended to more general patch models. While it seems obvious that a two-patch system cannot represent stream systems in general, it is not completely intuitive how many more patches are needed for new results to arise. In this paper we study the evolution of dispersal in advective environments with three patches, and we illustrate that the predictions from three-patch models are already much more complex than those in Theorem 1.

1.1 Three-patch models

We will focus on three types of 3-patch models. Each model assumes that patch 1 is at the upstream end, patch 3 is at the downstream end, and patch 2 could be either upstream, or middle stream, or downstream, depending on the specific topology of river network modules. The following diagrams illustrate the network topology of Models (I), (II) and (III), respectively:

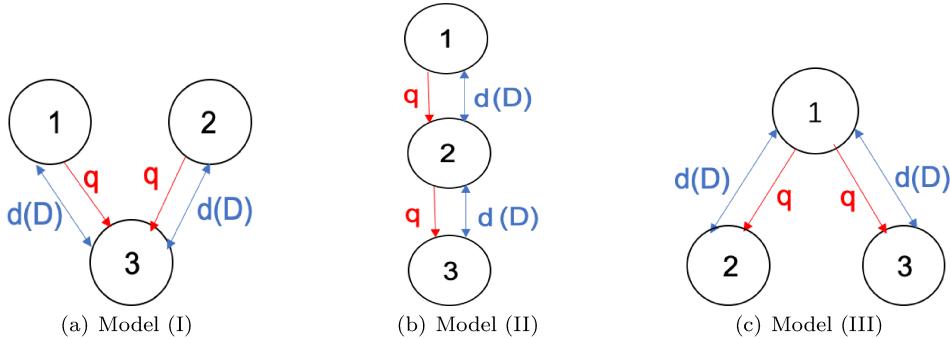


Fig. 2: Three river network modules with different topology: The two-way blue arrows represent the dispersal of species between connected patches, the one-way red arrows represent the unidirectional drift.

Model (I) assumes that the species in upstream patches 1 and 2 are washed down to the downstream patch 3 by drift with the same rate q , and two competing species can also disperse

freely between the upstream patch and the downstream patch, with rates d, D , respectively. However, the two upstream patches are not directly connected. The following ODE system describes the dynamics of two competing species in this river module:

$$\begin{cases} \frac{du_1}{dt} = d(u_3 - u_1) - qu_1 + u_1(1 - \frac{u_1+v_1}{k_1}) \\ \frac{du_2}{dt} = d(u_3 - u_2) - qu_2 + u_2(1 - \frac{u_2+v_2}{k_2}) \\ \frac{du_3}{dt} = d(u_1 + u_2 - 2u_3) + qu_1 + qu_2 + u_3(1 - \frac{u_3+v_3}{k_3}) \\ \frac{dv_1}{dt} = D(v_3 - v_1) - qv_1 + v_1(1 - \frac{u_1+v_1}{k_1}) \\ \frac{dv_2}{dt} = D(v_3 - v_2) - qv_2 + v_2(1 - \frac{u_2+v_2}{k_2}) \\ \frac{dv_3}{dt} = D(v_1 + v_2 - 2v_3) + qv_1 + qv_2 + v_3(1 - \frac{u_3+v_3}{k_3}) \\ u_i(0) = u_{i0}, v_i(0) = v_{i0}, i = 1, 2, 3. \end{cases} \quad (\text{I})$$

Here u_i, v_i ($i = 1, 2, 3$) denote the number of individuals of two species in patch i , with dispersal rates d and D , respectively. The parameter q is the rate of directed movement from one patch to another. Hence, the movement of organisms in (I) is a combination of unbiased and biased movement. For $i = 1, 2, 3$, the parameter k_i represents the carrying capacity of patch i . For the sake of simplicity, the intrinsic growth rates are assumed to be equal to one. All these parameters are assumed to be positive constants. The initial data of u_i and v_i , $1 \leq i \leq 3$, are assumed to be positive so that u_i and v_i are positive functions of time for $t \geq 0$.

Model (II) assumes that individuals in patch i are transported to patch $i + 1$ by drift with the rate q , and they can also disperse between patches i and $i + 1$ for $i = 1, 2$. i.e. Patch 2 is the stepping stone connecting patches 1 and 3. The dynamics of two competing species in this module can be described by the ODE system

$$\begin{cases} \frac{du_1}{dt} = d(u_2 - u_1) - qu_1 + u_1(1 - \frac{u_1+v_1}{k_1}) \\ \frac{du_2}{dt} = d(u_1 + u_3 - 2u_2) + qu_1 - qu_2 + u_2(1 - \frac{u_2+v_2}{k_2}) \\ \frac{du_3}{dt} = d(u_2 - u_3) + qu_2 + u_3(1 - \frac{u_3+v_3}{k_3}) \\ \frac{dv_1}{dt} = D(v_2 - v_1) - qv_1 + v_1(1 - \frac{u_1+v_1}{k_1}) \\ \frac{dv_2}{dt} = D(v_1 + v_3 - 2v_2) + qv_1 - qv_2 + v_2(1 - \frac{u_2+v_2}{k_2}) \\ \frac{dv_3}{dt} = D(v_2 - v_3) + qv_2 + v_3(1 - \frac{u_3+v_3}{k_3}) \\ u_i(0) = u_{i0}, v_i(0) = v_{i0}, i = 1, 2, 3. \end{cases} \quad (\text{II})$$

Model (III) described the situation in which both species in patch 1 are transported to patches 2 and 3 by drift with rate q , that is, patch 1 is at the upstream end, while both patches 2 and 3 are at the downstream end. Similarly, we have the following system for two competing species:

$$\begin{cases} \frac{du_1}{dt} = d(u_2 + u_3 - 2u_1) - 2qu_1 + u_1(1 - \frac{u_1+v_1}{k_1}) \\ \frac{du_2}{dt} = d(u_1 - u_2) + qu_1 + u_2(1 - \frac{u_2+v_2}{k_2}) \\ \frac{du_3}{dt} = d(u_1 - u_3) + qu_1 + u_3(1 - \frac{u_3+v_3}{k_3}) \\ \frac{dv_1}{dt} = D(v_2 + v_3 - 2v_1) - 2qv_1 + v_1(1 - \frac{u_1+v_1}{k_1}) \\ \frac{dv_2}{dt} = D(v_1 - v_2) + qv_1 + v_2(1 - \frac{u_2+v_2}{k_2}) \\ \frac{dv_3}{dt} = D(v_1 - v_3) + qv_1 + v_3(1 - \frac{u_3+v_3}{k_3}) \\ u_i(0) = u_{i0}, v_i(0) = v_{i0}, i = 1, 2, 3. \end{cases} \quad (\text{III})$$

Throughout this paper, we assume that the carrying capacities of three patches satisfy

$$k_1 > k_2 > k_3. \quad (2)$$

This serves to facilitate the comparison with Theorem 1, in which a similar condition is assumed. Biologically, condition (2) means that the upstream patch has larger carrying capacity, rendering

it more favorable for species to persist. Hence, if we increase the drift rate, more individuals from the upstream patch will be transported to the downstream, which has less favorable environmental conditions. Thus it might be more advantageous for the species to increase the dispersal rate so that individuals have better access to the more favorable upstream patch; i.e. increasing the drift rate may lead to the selection of larger dispersal rate which can counterbalance the passive drift. This was partially confirmed for two-patch model (1), but as will be seen next, the results for 3-patch are much more intricate and have subtle dependence on the topology of network modules.

We mainly study the stability of the semi-trivial steady state, denoted by

$$(u^*, 0) := (u_1^*, u_2^*, u_3^*, 0, 0, 0).$$

Biologically, we may envision the species u as the resident species which is assumed to reach the equilibrium state u^* , while species v is regarded as a mutant with low number of individuals. The question is whether the species v can invade when rare, i.e. whether $(u^*, 0)$ is unstable. Mathematically, for each of Models (I), (II) and (III), there exists an invasion fitness function, denoted by Λ_i , $i = 1, 2, 3$, respectively, such that $(u^*, 0)$ is stable when $\Lambda_i > 0$ and unstable when $\Lambda_i < 0$. Our goal is to determine the sign of Λ_i in terms of parameters d, D, q, k_i , which will in turn provide insight on the evolution of dispersal in patchy environments. **The invasion fitness function Λ_i can be characterized as the principal eigenvalue of certain irreducible cooperative matrix (see Section 3 for details).** While Λ_i generally depends on d, D, q, k_1, k_2, k_3 , we sometimes write Λ_i as $\Lambda_i(d, D)$ to emphasize the dependence of Λ_i on the strategy parameters d, D .

A well established approach to study the evolution of dispersal is the adaptive dynamics framework; see [7, 11]. A central concept of adaptive dynamics theory is that of an evolutionarily stable strategy (abbreviated as ESS henceforth), which was first introduced in [35]: A strategy is said to be an ESS (resp. a local ESS) if the resident species using it cannot be invaded by any mutant species, when the mutant species is rare and using a different strategy (resp. different but nearby strategies). Another important concept in adaptive dynamics theory is convergence stable strategy (abbreviated as CvSS henceforth): A strategy is said to be a CvSS if small changes in nearby strategies are only favored (i.e., able to invade a resident population) if they are closer to the convergence stable strategy than the resident strategy. The connection of evolutionary dynamics and ecological dynamics was investigated in [3] for a broad class of models, including reaction-diffusion equations and nonlocal diffusion equations. It is shown that frequently a species adopting an ESS dispersal strategy can displace a competitor adopting a dispersal strategy that is **in a neighborhood of the ESS**.

1.2 Slow drift

When there is no drift ($q = 0$), it is well known that $(u^*, 0)$ is stable for any $D > d$ and unstable if $D < d$. That is, the mutant can invade when rare if and only if it is the slower disperser; see [8, 16]. For slow drift, our following result for Models (I)-(III) yields the same conclusion: If the drift rate is positive and small, the species v can invade when rare if and only if $D < d$.

Theorem 2 Suppose $k_1 > k_2 > k_3$.

(i) For Model (I), if $\frac{k_2}{k_3} > 1 + \frac{k_1}{4k_2}$ and $q \in [0, q_-)$, where

$$q_- := \frac{\frac{k_2}{k_3} - \sqrt{1 + \frac{k_1}{4k_2}(1 + \frac{k_2}{k_3})}}{1 + \frac{k_2}{k_3}},$$

then for any $d > 0$,

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

(Note that the assumption $\frac{k_2}{k_3} > 1 + \frac{k_1}{4k_2}$ implies $q_- > 0$.)

(ii) For Model (II), if $0 \leq q < \min\{1 - \frac{k_2}{k_1}, \frac{k_2}{k_3} - 1\}$, then for any $d > 0$,

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

(iii) For Model (III), if $\frac{2}{k_2} > \frac{1}{k_1} + \frac{1}{k_3}$ and

$$0 \leq q \leq \frac{2 - \frac{k_2}{k_1} - \frac{k_2}{k_3}}{1 + \frac{k_2}{k_1} + \frac{k_2}{k_3}},$$

then for any $d > 0$,

$$\Lambda_3(d, D) = \begin{cases} + & D > d; \\ - & D < d. \end{cases}$$

We conjecture that if the patch qualities k_i are not all identical, then there exists some positive constant q_* , which is independent of d, D , such that if $q < q_*$, then $(u^*, 0)$ is globally asymptotically stable for all of the Models (I)-(III), provided $d < D$. We refer to the numerical computations in Figs. 3(a), 4(a)(d) and 5(a) that confirm, respectively, assertions (i), (ii) and (iii) of Theorem 2.

1.3 Fast drift

For large drift, more individuals from the upstream patch are washed to the downstream patch, which has less favorable environmental conditions. Hence, it might be natural to expect larger dispersal rate will always be selected, as in the two-patch model (1). This is indeed the case for Models (I) and (II), as shown in the following result:

Theorem 3 Assume $k_1 > k_2 > k_3$.

(i) For Model (I), further assume $\frac{2}{k_2} < \frac{1}{k_1} + \frac{1}{k_3}$. If $q \geq \frac{k_1 - k_3}{k_1 + k_3}$, then

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

(ii) For Model (II), if $q > \max\{1 - \frac{k_2}{k_1}, \frac{k_2}{k_3} - 1\}$, then

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

Theorem 3 implies that for Models (I)-(II), if the drift rate q is large, the mutant can invade when rare if and only if it is the faster disperser. This is consistent with Theorem 1 for two-patch model. We refer to Fig. 3(e) and Fig. 4(c)(f) for related numerical computations in confirmation of these analytical results.

A bit surprisingly, the result for Model (III) is completely different. We recall that a strategy $d^* > 0$ is evolutionarily singular if $\frac{\partial \Lambda_3}{\partial D}(d^*, d^*) = 0$, i.e. when there is no selection for faster nor slower dispersal.

Theorem 4 For Model (III), assume $k_1 > k_2 > k_3$. Set

$$\underline{p} := \frac{k_2^2 + k_3^2}{(k_2 - k_3)^2}, \quad \bar{p} := \frac{(1 - \frac{u_\infty}{k_2})^2 + (1 - \frac{u_\infty}{k_3})^2}{\frac{u_\infty}{k_2} + \frac{u_\infty}{k_3} - 2}, \quad \text{where} \quad u_\infty := \frac{3}{\frac{1}{k_1} + \frac{1}{k_2} + \frac{1}{k_3}}.$$

Then for $q > \max\{\underline{p}, \bar{p}\}$, we have

$$\frac{\partial \Lambda_3}{\partial D} \Big|_{D=d} = \begin{cases} + & 0 \leq d \ll 1; \\ - & d \gg 1. \end{cases}$$

i.e. $d = 0$ and $d = \infty$ are both convergence stable strategies. Furthermore, for $q > \max\{\underline{p}, \bar{p}\}$ there exists $d^* = d^*(q) > 0$ such that d^* is an evolutionarily singular strategy and the following holds:

$$\frac{\partial \Lambda_3}{\partial D} \Big|_{D=d} = \begin{cases} + & d < d^*, \text{ } d \text{ close to } d^*; \\ 0 & d = d^*; \\ - & d > d^*, \text{ } d \text{ close to } d^*. \end{cases}$$

We refer to Subsections 2.3 and 2.4 for numerical results and further discussions.

1.4 Intermediate drift

For Models (I) and (II) with intermediate drift, an evolutionarily singular strategy always exists in the course of transition from small to large drift.

Theorem 5 Assume $k_1 > k_2 > k_3$.

(i) For Model (I), set

$$\underline{q} = \frac{(k_1^2 + k_2^2)(\frac{k_1^2 + k_2^2}{k_1 + k_2} - k_3)}{k_3(k_1 + k_2)^2 + \frac{(k_1^2 + k_2^2)^2}{k_1 + k_2}}, \quad \bar{q} = \frac{(1 - \frac{u_\infty}{k_1})^2 + (1 - \frac{u_\infty}{k_2})^2}{2 - \frac{u_\infty}{k_1} - \frac{u_\infty}{k_2}}, \quad u_\infty = \frac{3}{\frac{1}{k_1} + \frac{1}{k_2} + \frac{1}{k_3}}.$$

(ii) For Model (II), set

$$\underline{q} = 1 - \frac{k_2}{k_1}, \quad \bar{q} = \frac{(1 - \frac{u_\infty}{k_1})^2 + (1 - \frac{u_\infty}{k_3})^2}{\frac{u_\infty}{k_3} - \frac{u_\infty}{k_1}}, \quad u_\infty = \frac{3}{\frac{1}{k_1} + \frac{1}{k_2} + \frac{1}{k_3}}.$$

Assume $\underline{q} \neq \bar{q}$. Then for $\min\{\underline{q}, \bar{q}\} < q < \max\{\underline{q}, \bar{q}\}$, there is some $d^*(q) > 0$ such that it is an evolutionarily singular strategy.

Our numerical results indicate that, depending on $\bar{q} > \underline{q}$ or $\bar{q} < \underline{q}$, the evolutionarily singular strategy found in Theorem 5 may or may not be convergence stable/evolutionarily stable. This will be further discussed in Subsections 2.1 and 2.2.

The rest of the paper is organized as follows: In Sect. 2, we numerically compute the pairwise invasibility plots (PIPs) for each of the Models (I)-(III), which indicate the sign of the invasion fitness function as the resident and invader strategies vary, and compare their evolutionary dynamics. The proofs are postponed to Sect. 3-6. In Sect. 3, we present some general stability results of the semi-trivial equilibrium $(u^*, 0)$. Sect. 4 is devoted to the proof of Theorem 2 for small drift. In Sect. 5, we consider the large drift and establish Theorems 3 and 4. In Sect. 6 we prove Theorem 5 for intermediate drift.

2 Numerical Computations and Discussions

For Models (I) and (II), our analytical results show that the species with slower dispersal wins when q is small, whereas the species with faster dispersal wins when q is large. However, there are several different ways for which the transition can take place as q varies from 0 to ∞ .

2.1 Numerical Results for Model (I)

The PIP For Model (I) is shown in Fig. 3, where (k_1, k_2, k_3) are set to be $(2.02, 2, 0.4)$, and q takes different values. For $0 \leq q \leq 0.5729$, the dispersal strategy $d = 0$ is both ESS and convergence stable. However, when q is slightly increased to 0.572955 , there are two alternative ESS, namely, $d = 0$ and $d = \infty$. Moreover, both $d = 0$ and $d = \infty$ appear to be convergence stable. In this case, the evolutionary dynamics depends on the dispersal trait of the initial population. When q is further increased to $q = 0.57296$, then $d = 0$ is convergence stable but ceases to be an ESS. Finally, for $q \geq 0.7$, only fast dispersal rate is selected.

In Theorem 5(i), we proved that a singular strategy d^* exists for Model (I), provided $\bar{q} \neq \underline{q}$ and that $q \in (\min\{\bar{q}, \underline{q}\}, \max\{\bar{q}, \underline{q}\})$. Our numerical simulations show that d^* is not an evolutionarily stable strategy; see Fig. 3(b)(c)(f). Take Fig. 3(b) as an example, the vertical line passing through (d^*, d^*) falls into the white region, where $(u^*, 0)$ is unstable. This implies that the invading species with strategy different from d^* can invade when rare, i.e. d^* is not an ESS.

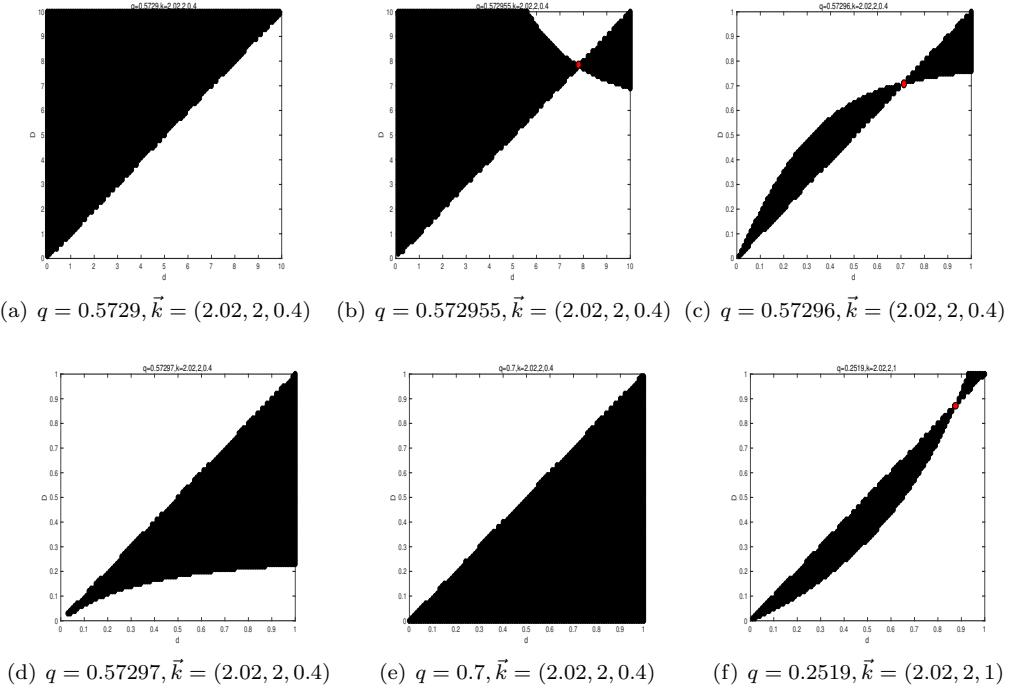


Fig. 3: The numerical simulation results of Model (I). The black regions represent the range of (d, D) for which $(u^*, 0)$ is stable. Here \vec{k} abbreviates (k_1, k_2, k_3) in the captions. Note that the value of \vec{k} of panel (f) is different. The red spots in (b)(c)(f) at the diagonal correspond to (d^*, d^*) , where the values of singular strategy d^* are approximately 7.9, 0.71, 0.88, respectively.

Furthermore, the singular strategy d^* is not convergence stable in Fig. 3(b)-(c), while it is convergence stable in Fig. 3(f). Take Fig. 3(b) again as an example. If we choose an resident strategy d_u greater than but close to d^* and envision a mutation happens so that the strategy of the mutant is given by some d_v which is larger than but close to d_u . Then from Fig. 3(b) we see that (d_u, d_v) falls into the white region, where $(u^*, 0)$ is unstable, i.e. the mutant with larger dispersal rate can invade when rare, so that the winning strategy further deviates away from the singular strategy d^* . This implies that d^* can not be convergence stable. In contrast, the opposite phenomenon occurs in Fig. 3(f), where the winning strategy is always the one which is closer to the singular strategy d^* , which explains why d^* in Fig. 3(f) is a convergence stable strategy.

It can be verified that $\underline{q} > \bar{q}$ in Fig. 3(b)(c), and $\underline{q} < \bar{q}$ in Fig. 3(f). (Note that the k_i 's take different values.) We conjecture that the sign of $\bar{q} - \underline{q}$ determines the convergence stability of d^* for Model (I).

2.2 Numerical Results for Model (II)

For Model (II), we performed numerical computations for $(k_1, k_2, k_3) = (5, 3, 2)$ (see Fig. 4(a)-(c)) and for $(k_1, k_2, k_3) = (100, 1.01, 1)$ (see Fig. 4(d)-(f)), while varying the drift rate q .

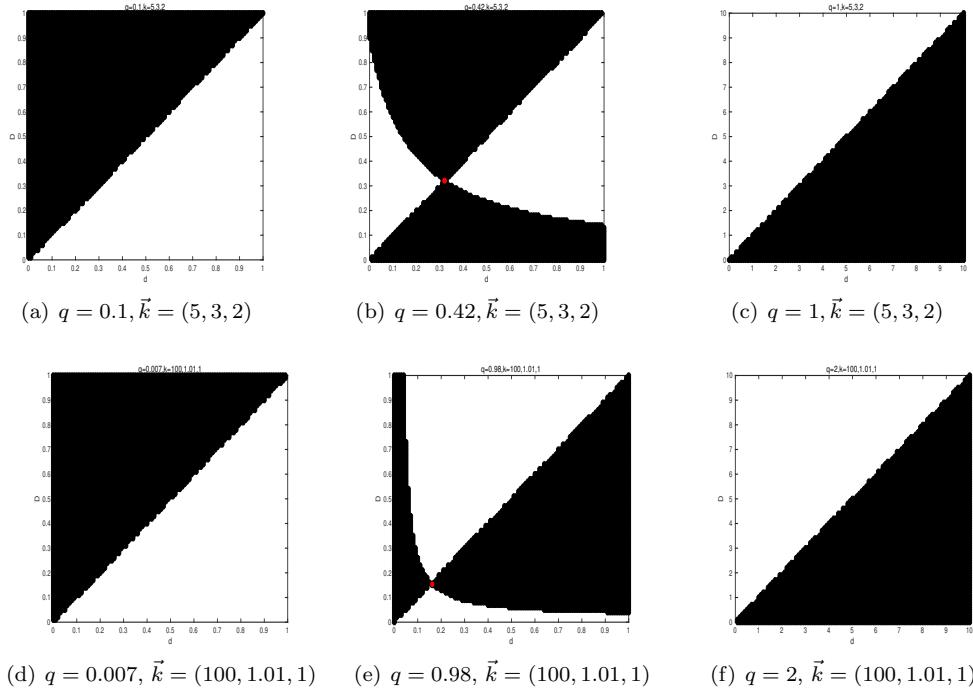


Fig. 4: The numerical simulation results of Model (II). The black regions represent the range of (d, D) for which $(u^*, 0)$ is stable. Here \vec{k} abbreviates (k_1, k_2, k_3) in the captions. The red spots in (b)(e) at the diagonal correspond to (d^*, d^*) , where the values of singular strategy d^* are approximately 0.33, 0.17, respectively.

In both cases, slow dispersal is favored when the drift is small, and fast dispersal is favored when the drift is large. Furthermore, for intermediate drift, there appears to be a unique singular strategy d^* , in agreement with Theorem 5(ii). However, the singular strategy d^* is evolutionarily stable when $(k_1, k_2, k_3) = (5, 3, 2)$ (see Fig. 4(b)) but it is not evolutionarily stable when $(k_1, k_2, k_3) = (100, 1.01, 1)$ (see Fig. 4(e)). Using the definition of \underline{q}, \bar{q} in Theorem 5(ii), it can be shown that $\underline{q} < \bar{q}$ in the first case and $\underline{q} > \bar{q}$ in the second case. We conjecture that the sign of $\bar{q} - \underline{q}$ determines the evolutionary stability of d^* for Model (II).

Observe that the spatial heterogeneity is more pronounced in case $(k_1, k_2, k_3) = (100, 1.01, 1)$ than in case $(k_1, k_2, k_3) = (5, 3, 2)$. For the first case, accessing the upstream patch (i.e. patch 1) is very important. When the drift q is intermediate, both small and large dispersal allow the species to access the superior resource in the upstream patch. This can partially account for the situation when both $d = 0$ and $d = \infty$ are evolutionarily stable simultaneously (see Fig. 4(e)).

2.3 Numerical Results for Model (III)

The PIP For Model (III) is shown in Fig. 5, where (k_1, k_2, k_3) are set to be $(1, 0.3, 0.2)$, and q takes different values. When q varies from 0 to 0.7, the transition in PIP bears similarity with Model (II) (see Fig. 5(a)-(c)), where there is a unique singular strategy that is both ESS and convergence stable. **The singular strategy increases from zero to infinity as q varies from 0 to 0.7.**

However, if we further increase q beyond 0.7, both $d = 0$ and $d = \infty$ are convergence stable strategies, and there exists at least one additional singular strategy $d^* \in (0, \infty)$. This is proved in Theorem 4. (See also Fig. 5(e)-(f).) Intuitively, the large drift confines the two species to the two downstream patches. The numerical results confirm Theorem 4 concerning the existence of a singular strategy d^* . **Moreover, they indicate that for large q , if $d, D \in (0, d^*)$, then the slower dispersing species can invade the faster species when rare but not vice versa; if $d, D \in (d^*, \infty)$, then the faster dispersing species invades the slower one when rare but not vice versa. Furthermore, the zero disperser can sometimes coexist stably with extremely fast disperser. See Fig. 5(e)-(f).** Based on the invasibility analysis, we conjecture that, for large q , the slower dispersing species can competitively exclude the faster species if $d, D \in (0, d^*)$, while the faster dispersing species excludes the slower one if $d, D \in (d^*, \infty)$.

2.4 Discussions

We consider three mathematical models for two competing species in three-patch advective environments, where the two species are identical except for their dispersal rates. Each of these models represents a river network module with distinct topology. We are interested in studying how the patch quality (k_i , $i = 1, 2, 3$), the advection rate q and the network topology affect the evolution of dispersal rate. Our main results can be summarized as follows:

- (1) **Slow drift:** For all three models, the species with slower dispersal wins.
- (2) **Intermediate drift:** There exists at least one singular strategy in Models (I) and (II). However, for Model (III), singular strategy may not exist; Indeed, for certain range of intermediate drift rates, the species with faster dispersal wins. (See Fig. 5(c).) The singular strategy, when it exists, is not evolutionarily stable for Model (I), but it can be evolutionarily stable for Models (II) and (III).
- (3) **Fast drift:** For Models (I) and (II), there is no singular strategy and the species with faster dispersal wins. For Model (III), both $d = 0$ and $d = \infty$ are convergence stable and there exists

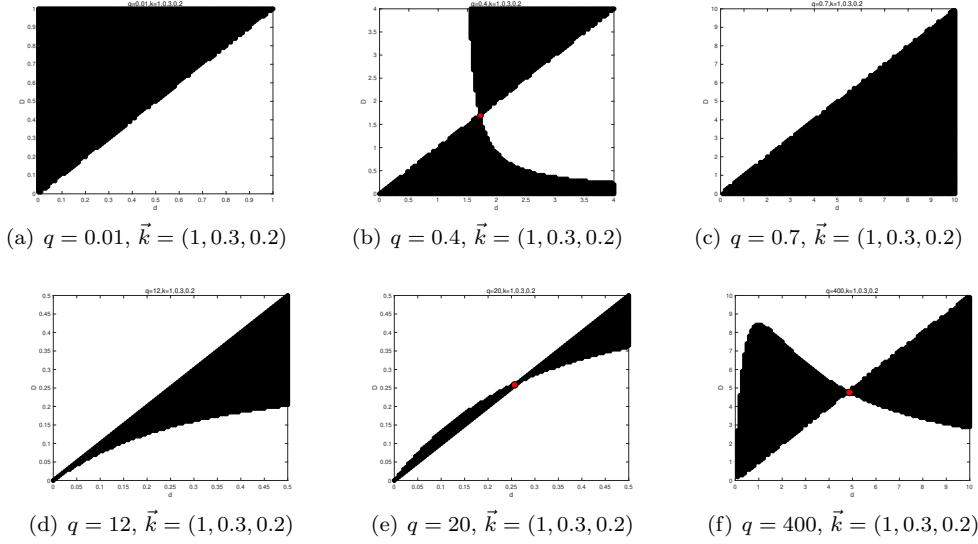


Fig. 5: The numerical simulation results of Model (III). The black regions represent the range of (d, D) for which $(u^*, 0)$ is stable. Here \vec{k} abbreviates (k_1, k_2, k_3) in the captions. The red spots in (b)(e)(f) at the diagonal correspond to (d^*, d^*) , where the values of singular strategy d^* is approximately 1.72, 0.26, 4.8, respectively.

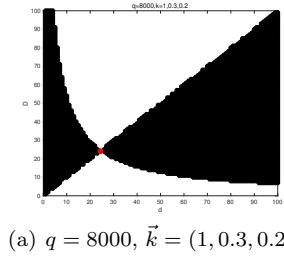


Fig. 6: A numerical simulation result of Model (III). The red spot at the diagonal corresponds to (d^*, d^*) , where the value of singular strategy d^* is approximately 25.

a singular strategy d^* . Moreover, the numerical result suggests the slower disperser wins if $0 < d, D \leq d^*$, and the faster disperser wins if $d, D \geq d^*$.

We focus our discussion on Model (III), since it behaves rather differently comparing with the other two models. From Theorem 4, there exists an evolutionarily singular strategy for Model (III) when q is sufficiently large. Our numerical simulations suggest that this singular strategy is neither evolutionarily stable nor convergence stable, and both $d = 0$ and $d = \infty$ are convergence stable; see Fig. 5(f) and Fig. 6.

While the convergence stability of $d = \infty$ can also be found in Models (I) and (II), the convergence stability of $d = 0$ may seem surprising. One way to understand this phenomenon is to notice that *Model (III) has two instead of one downstream patch*. When q is large, a single species with dispersal rate d close to zero on the upstream patch is confined to the two downstream patches. Furthermore, the two downstream patches are virtually connected by a random dispersal

rate of $d/2$. This is due to the possibility of an individual to travel to the upstream patch, with rate d , and then be quickly transported by the drift to one of the two downstream patches with equal likelihood. Hence, when we consider the competition system (III) with dispersal rates $d < D$, such that $d \ll q$ and $D \ll q$, the two species can be equivalently viewed as two competing species that have random dispersal in the two downstream patches with rates $d/2$ and $D/2$. (See Lemma 30 for a result in this direction.) It then follows by Hastings' prediction [16] that the species with slower dispersal rate wins by better utilizing the two downstream patches. In fact, when $q = 400$ and $(k_1, k_2, k_3) = (1, 0.3, 0.2)$, the species with slower dispersal rate wins whenever $1 < d < D < 5$; when $q = 8000$, then the parameter region for the selection of slower dispersal is enlarged to $[0, 20]$. See Figs. 5(f) and 6. This explains the convergence stability of $d = 0$.

However, notice that Model (III) predicts the selection of slower dispersal only when both species disperse with rates much smaller than q . Another distinct feature of Model (III) comparing to Models (I) and (II) can be observed from the interaction of extremely slow disperser and extremely fast disperser, i.e. species with zero or large dispersal rates. First, we observe from Theorem 3 that for Models (I) and (II), when q is large, the fast disperser can invade the slow one but not vice versa. In contrast, for Model (III) the extremely fast and extremely slow dispersers are sometimes mutually invasible. In such event, they can actually coexist in a stable manner. The intuitive reason is the availability of more than one downstream patch for the latter model. This is confirmed by our next result.

Theorem 6 *Assume $k_1 > k_2 > k_3$. Consider Model (III).*

(i) *For each $\underline{D} > 0$, there exist $\hat{d}_1, \hat{q}_1 > 0$ such that for $q \geq \hat{q}_1$, we have*

$$\sup_{0 \leq d < \hat{d}_1, D \geq \underline{D}} \Lambda_3(d, D) < 0.$$

(ii) *If $\frac{2}{k_2} > \frac{1}{k_1} + \frac{1}{k_3}$, then there exists $\hat{q}_2 > 0$ such that for $q \geq \hat{q}_2$,*

$$\inf_{d > \frac{1}{\epsilon}, D < \epsilon} \Lambda_3(d, D) > 0 \quad \text{for } 0 < \epsilon \ll 1.$$

(iii) *If $\frac{2}{k_2} < \frac{1}{k_1} + \frac{1}{k_3}$, then there exists $\hat{q}_3 > 0$ such that for $q \geq \hat{q}_3$,*

$$\sup_{d > \frac{1}{\epsilon}, D < \epsilon} \Lambda_3(d, D) < 0 \quad \text{for } 0 < \epsilon \ll 1.$$

In particular, when $\frac{2}{k_2} < \frac{1}{k_1} + \frac{1}{k_3}$, then Theorem 6 (i) and (iii) are applicable, so that extremely slow and extremely fast dispersers are mutually invasible and can coexist in a stable manner. This is the case, for instance, when $(k_1, k_2, k_3) = (1, 0.3, 0.2)$. Fig. 5(f) (resp. Fig. 6) shows the mutual invasibility of $(d, D) = (0, 10)$ when $q = 400$ (resp. $(d, D) = (0, 100)$ when $q = 8000$).

For Model (III) with intermediate drift rate, our numerical simulations suggest that two alternatives can happen: (i) An ESS exists; see Fig. 5(b). (ii) There is no singular strategy, and larger dispersal is favored; see Fig. 5(c)-(d). Thus we see that in contrast to Models (I)-(II), Model (III) is more complex; e.g. case (ii) does not occur for Models (I) and (II) with intermediate drift rate.

In summary, we study the dynamics of two competing species in three-patch models and illustrate how the topology of directed river network modules may affect the evolution of dispersal. The model under investigation is of Lotka-Volterra type, which is a simplification of real systems. In the future, it will be interesting to quantify the effect of travel loss [6], or to relax the assumption that the maximum growth rate being constant across patches. We also expect that part of our conclusions can be generalized to consumer-resource models in which resources on patches can be exploited. See, e.g. the Appendix B of [52] for results in this direction.

3 Preliminaries of the principal eigenvalues

In this section we present some general results on the stability of the semi-trivial equilibrium $(u^*, 0)$ for models (I)-(III), which are determined by the sign of the principal eigenvalues to some eigenvalue problems to be specified later.

We first consider Model (I), i.e. system (I). Recall that $u^* = (u_1^*, u_2^*, u_3^*)$ is the unique positive solution of the algebraic system

$$\begin{cases} d(u_3^* - u_1^*) - qu_1^* + u_1^*(1 - \frac{u_1^*}{k_1}) = 0, \\ d(u_3^* - u_2^*) - qu_2^* + u_2^*(1 - \frac{u_2^*}{k_2}) = 0, \\ d(u_1^* + u_2^* - 2u_3^*) + qu_1^* + qu_2^* + u_3^*(1 - \frac{u_3^*}{k_3}) = 0. \end{cases} \quad (3)$$

The stability of $(u^*, 0)$ is determined by the sign of the principal eigenvalue of the system

$$A_1 \begin{pmatrix} \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix} + \Lambda \begin{pmatrix} \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}, \quad (4)$$

where matrix A_1 is given by

$$A_1 = \begin{pmatrix} -D - q + 1 - \frac{u_1^*}{k_1} & 0 & D \\ 0 & -D - q + 1 - \frac{u_2^*}{k_2} & D \\ D + q & D + q & -2D + 1 - \frac{u_3^*}{k_3} \end{pmatrix}.$$

As the off-diagonal entries of A_1 are all non-negative and A_1 is irreducible, by Perron-Frobenius Theorem, A_1 has a principal eigenvalue, denoted by $\Lambda_1(d, D; q)$, such that Λ_1 is real and algebraically simple, it has the smallest real part among all eigenvalues of A_1 . Furthermore, we may choose the corresponding eigenvector such that $\varphi_i > 0$, $i = 1, 2, 3$. In contrast, the eigenvectors for other eigenvalues are either complex-valued, or real-valued but sign-changing. For simplicity, we may abbreviate $\Lambda_1(d, D; q)$ as Λ_1 or $\Lambda_1(d, D)$. As Λ_1 is a simple eigenvalue of matrix A_1 , the analytic dependence of Λ_1 on D follows from the analytic dependence of the spectral radius of A_1 on its entries.

It is well known that $(u^*, 0)$ is stable if $\Lambda_1 > 0$ and unstable when $\Lambda_1 < 0$. Furthermore, $\Lambda_1(d, d) = 0$ holds for any $d > 0$, with $\varphi_i = u_i^*$, $1 \leq i \leq 3$.

Proposition 1 *The derivative of Λ_1 with respect to D , at $D=d$, is given by*

$$\frac{\partial \Lambda_1}{\partial D} \Big|_{D=d} = - \frac{(u_1^* - \frac{d}{d+q} u_3^*)(u_3^* - u_1^*) + (u_2^* - \frac{d}{d+q} u_3^*)(u_3^* - u_2^*)}{(u_1^*)^2 + (u_2^*)^2 + \frac{d}{d+q} (u_3^*)^2}. \quad (5)$$

Proof Differentiate (4) with respect to D , we get

$$\begin{pmatrix} \varphi_3 - \varphi_1 \\ \varphi_3 - \varphi_2 \\ \varphi_1 + \varphi_2 - 2\varphi_3 \end{pmatrix} + A_1 \begin{pmatrix} \varphi'_1 \\ \varphi'_2 \\ \varphi'_3 \end{pmatrix} + \frac{\partial \Lambda_1}{\partial D} \begin{pmatrix} \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix} + \Lambda_1 \begin{pmatrix} \varphi'_1 \\ \varphi'_2 \\ \varphi'_3 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}, \quad (6)$$

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

$$A_1 \Big|_{D=d} \begin{pmatrix} u_1^* \\ u_2^* \\ u_3^* \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix},$$

$$A_1^T \Big|_{D=d} \begin{pmatrix} (d+q)u_1^* \\ (d+q)u_2^* \\ du_3^* \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}, \quad (7)$$

and when $D = d$, we may choose

$$\begin{pmatrix} \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix} = \begin{pmatrix} u_1^* \\ u_2^* \\ u_3^* \end{pmatrix}. \quad (8)$$

Set $D = d$ in (6) and multiplying it by $((d+q)u_1^*, (d+q)u_2^*, du_3^*)$, using (7), (8) and $\Lambda_1(d, d) = 0$, we obtain (5). This completes the proof.

Let $|A_1|$ be the determinant of A_1 . By direct calculations, we have

Proposition 2 Assume $\frac{u_1^*}{k_1} + \frac{u_2^*}{k_2} + \frac{u_3^*}{k_3} \neq 3$. Then $|A_1| = 0$ if and only if either $D = d$, or $D = F(d)$, where function F is given by

$$F(d) := \frac{(-q+1-\frac{u_1^*}{k_1})(-q+1-\frac{u_2^*}{k_2})(1-\frac{u_3^*}{k_3})}{d(3-\frac{u_1^*}{k_1}-\frac{u_2^*}{k_2}-\frac{u_3^*}{k_3})}, \quad d > 0. \quad (9)$$

Proof The determinant of A_1 is given by

$$\begin{aligned} |A_1| = & D^2(3 - \frac{u_1^*}{k_1} - \frac{u_2^*}{k_2} - \frac{u_3^*}{k_3}) - D[2(-q+1-\frac{u_1^*}{k_1})(-q+1-\frac{u_2^*}{k_2}) \\ & + (-q+1-\frac{u_1^*}{k_1}-q+1-\frac{u_2^*}{k_2})(1-\frac{u_3^*}{k_3}) \\ & + q(-q+1-\frac{u_1^*}{k_1}-q+1-\frac{u_2^*}{k_2})] + (-q+1-\frac{u_1^*}{k_1})(-q+1-\frac{u_2^*}{k_2})(1-\frac{u_3^*}{k_3}). \end{aligned}$$

Note that

$$A_1 \Big|_{D=d} \begin{pmatrix} u_1^* \\ u_2^* \\ u_3^* \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix},$$

which implies that

$$\begin{aligned} & d^2(3 - \frac{u_1^*}{k_1} - \frac{u_2^*}{k_2} - \frac{u_3^*}{k_3}) - d[2(-q+1-\frac{u_1^*}{k_1})(-q+1-\frac{u_2^*}{k_2}) + (-q+1-\frac{u_1^*}{k_1}-q+1-\frac{u_2^*}{k_2})(1-\frac{u_3^*}{k_3}) \\ & + q(-q+1-\frac{u_1^*}{k_1}-q+1-\frac{u_2^*}{k_2})] + (-q+1-\frac{u_1^*}{k_1})(-q+1-\frac{u_2^*}{k_2})(1-\frac{u_3^*}{k_3}) = 0. \end{aligned}$$

Multiplying the above two equations by d, D , respectively and subtracting the results, we have

$$(D-d) \left[Dd \left(3 - \frac{u_1^*}{k_1} - \frac{u_2^*}{k_2} - \frac{u_3^*}{k_3} \right) - (-q+1-\frac{u_1^*}{k_1})(-q+1-\frac{u_2^*}{k_2})(1-\frac{u_3^*}{k_3}) \right] = 0.$$

The proof is complete.

If $D = d$, then zero is the principal eigenvalue of A_1 . By Proposition 2, $|A_1| = 0$ at $D = F(d)$ for all $d > 0$, i.e. zero is an eigenvalue of A_1 when $D = F(d)$. However, 0 may not be the principal eigenvalue of A_1 when $D = F(d)$. As Λ_1 is the principal eigenvalue of matrix A_1 , we see that $\Lambda_1(d, F(d)) \leq 0$. These discussions lead to the following result:

Corollary 1 Assume that $F(d)$ is defined for $d > 0$. Then $\Lambda_1(d, F(d)) \leq 0$.

For Model (II), i.e. system (II), $u^* = (u_1^*, u_2^*, u_3^*)$ is the unique positive solution of the algebraic system

$$\begin{cases} d(u_2^* - u_1^*) - qu_1^* + u_1^*(1 - \frac{u_1^*}{k_1}) = 0, \\ d(u_1^* + u_3^* - 2u_2^*) + qu_1^* - qu_2^* + u_2^*(1 - \frac{u_2^*}{k_2}) = 0, \\ d(u_2^* - u_3^*) + qu_2^* + u_3^*(1 - \frac{u_3^*}{k_3}) = 0. \end{cases} \quad (10)$$

Similarly, the stability of $(u^*, 0)$ in (II) is determined by the sign of the principal eigenvalue, denoted by $\Lambda_2(d, D; q)$, of the eigenvalue problem

$$A_2 \begin{pmatrix} \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix} + \Lambda \begin{pmatrix} \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}, \quad (11)$$

where matrix A_2 is defined by

$$A_2 := \begin{pmatrix} -D - q + 1 - \frac{u_1^*}{k_1} & D & 0 \\ D + q & -2D - q + 1 - \frac{u_2^*}{k_2} & D \\ 0 & D + q & -D + 1 - \frac{u_3^*}{k_3} \end{pmatrix}.$$

Similar to the proof of Proposition 1, we have the following result:

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

$$\frac{\partial \Lambda_2}{\partial D} \Big|_{D=d} = -\frac{\frac{d+q}{d}u_1^*(u_2^* - u_1^*) + u_2^*(u_1^* + u_3^* - 2u_2^*) + \frac{d}{d+q}u_3^*(u_2^* - u_3^*)}{\frac{d+q}{d}(u_1^*)^2 + (u_2^*)^2 + \frac{d}{d+q}(u_3^*)^2}. \quad (12)$$

By direct calculations, we can obtain the following same result for (II):

Proposition 4 *Assume $\frac{u_1^*}{k_1} + \frac{u_2^*}{k_2} + \frac{u_3^*}{k_3} \neq 3$. Then $|A_2| = 0$ if and only if either $D = d$, or $D = F(d)$, where F is given by (9).*

For Model (III), i.e. system (III), u^* is given by

$$\begin{cases} d(u_2^* + u_3^* - 2u_1^*) - 2qu_1^* + u_1^*(1 - \frac{u_1^*}{k_1}) = 0, \\ d(u_1^* - u_2^*) + qu_1^* + u_2^*(1 - \frac{u_2^*}{k_2}) = 0, \\ d(u_1^* - u_3^*) + qu_1^* + u_3^*(1 - \frac{u_3^*}{k_3}) = 0. \end{cases} \quad (13)$$

The principal eigenvalue Λ_3 is determined by

$$A_3 \begin{pmatrix} \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix} + \Lambda \begin{pmatrix} \varphi_1 \\ \varphi_2 \\ \varphi_3 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}, \quad (14)$$

where matrix A_3 is defined by

$$A_3 := \begin{pmatrix} -2D - 2q + 1 - \frac{u_1^*}{k_1} & D & D \\ D + q & -D + 1 - \frac{u_2^*}{k_2} & 0 \\ D + q & 0 & -D + 1 - \frac{u_3^*}{k_3} \end{pmatrix}.$$

Similar to the proof of Proposition 1, we have the following result:

Proposition 5 When $D = d$, the derivative of Λ_3 with respect to D satisfies

$$\frac{\partial \Lambda_3}{\partial D} \Big|_{D=d} = -\frac{(u_2^* - \frac{d+q}{d}u_1^*)(u_1^* - u_2^*) + (u_3^* - \frac{d+q}{d}u_1^*)(u_1^* - u_3^*)}{\frac{d+q}{d}(u_1^*)^2 + (u_2^*)^2 + (u_3^*)^2}. \quad (15)$$

By direct calculations, we can obtain the following result for (III):

Proposition 6 Assume $\frac{u_1^*}{k_1} + \frac{u_2^*}{k_2} + \frac{u_3^*}{k_3} \neq 3$. Then $|\Lambda_3| = 0$ if and only if either $D = d$, or

$$D = \frac{(-2q + 1 - \frac{u_1^*}{k_1})(1 - \frac{u_2^*}{k_2})(1 - \frac{u_3^*}{k_3})}{d(3 - \frac{u_1^*}{k_1} - \frac{u_2^*}{k_2} - \frac{u_3^*}{k_3})}. \quad (16)$$

For subsequent applications, we make some comments on the analytic dependence of u^* and Λ_i ($i = 1, 2, 3$) on dispersal and drift rates $d > 0, q \geq 0$. Consider $i = 1$ for instance, the existence of positive solution u^* for system (3) follows from the upper and lower solution method. Using (7) we can show that any positive solution of (3), as an equilibrium of the corresponding time-dependent system, is linearly stable. In fact, it follows from the theory of strongly monotone dynamical system that Model (I) has a unique positive solution and it is globally stable among all positive solutions of (here ' denotes the time derivative)

$$\begin{cases} u'_1 = d(u_3 - u_1) - qu_1 + u_1(1 - \frac{u_1}{k_1}), \\ u'_2 = d(u_3 - u_2) - qu_2 + u_2(1 - \frac{u_2}{k_2}), \\ u'_3 = d(u_1 + u_2 - 2u_3) + qu_1 + qu_2 + u_3(1 - \frac{u_3}{k_3}), \end{cases} \quad (17)$$

which is the time-dependent problem corresponding to (3).

Since the left hand side of (3) depends on parameters d and q analytically, by the linear stability of u^* and the implicit function theorem, u^* also depends on $d > 0$ and $q \geq 0$ analytically. Note also that Λ_1 is a simple eigenvalue of matrix A_1 , and hence depends analytically on the entries of A_1 . As a consequence, Λ_1 is a real analytic function of the parameters d, q . The arguments for $i = 2, 3$ are similar and thus omitted.

4 The small drift case

The goal of this section is to establish Theorem 2 for the small drift case. We consider three Models (I)-(III) and establish part (i)-(iii) of Theorem 2 in Subsections 4.1-4.3, respectively.

4.1 Model (I)

In this subsection, we study the sign of the principal eigenvalue Λ_1 in Model (I) when q is small. To this end, we first establish some estimates on solutions of (3). In this subsection $u^* = (u_1^*, u_2^*, u_3^*)$ denotes the unique positive solution of (3).

Lemma 1 Suppose $k_1 > k_2 > k_3$. Then $u_3^* > k_3$ holds for any $d > 0$ and $q \geq 0$.

Proof We first prove $u_3^* > k_3$ holds for $q = 0$. We argue by contradiction: If not, assume that when $q = 0$, $u_3^* \leq k_3$. Adding three equations of (3), we have

$$u_1^*(1 - \frac{u_1^*}{k_1}) + u_2^*(1 - \frac{u_2^*}{k_2}) + u_3^*(1 - \frac{u_3^*}{k_3}) = 0,$$

which implies that

$$u_1^*(1 - \frac{u_1^*}{k_1}) + u_2^*(1 - \frac{u_2^*}{k_2}) \leq 0.$$

Hence, without loss of generality we may assume that $1 - u_1^*/k_1 \leq 0$. Therefore, by the first equation of (3), $u_3^* \geq u_1^*$. This implies that $k_3 \geq u_3^* \geq u_1^* \geq k_1$, which contradicts assumption $k_1 > k_3$.

Notice that $u_i^* = u_i^*(q)$ is a smooth function of q , so it suffices to prove that $u_3^* \neq k_3$ when $q > 0$. Again we argue by contradiction and assume that there exists some $q > 0$ such that $u_3^* = k_3$. By (3), we get

$$u_i^* = \frac{k_i(-d - q + 1) + \sqrt{k_i^2(-d - q + 1)^2 + 4dk_ik_3}}{2}, \quad i = 1, 2.$$

By the third equation of (3) and $u_3^* = k_3$, we know $u_1^* + u_2^* = \frac{2dk_3}{d+q}$, so we obtain

$$\begin{aligned} \frac{2dk_3}{d+q} &= \frac{k_1(-d - q + 1) + \sqrt{k_1^2(-d - q + 1)^2 + 4dk_1k_3}}{2} \\ &\quad + \frac{k_2(-d - q + 1) + \sqrt{k_2^2(-d - q + 1)^2 + 4dk_2k_3}}{2}. \end{aligned}$$

For $x > 0$, set

$$f(x) = \frac{x(-d - q + 1) + \sqrt{x^2(-d - q + 1)^2 + 4dk_3x}}{2}.$$

As $f'(x) > 0$ for $x > 0$, by $k_1 > k_2 > k_3$ we have

$$\frac{2dk_3}{d+q} = f(k_1) + f(k_2) > 2f(k_3) = k_3(-d - q + 1) + k_3\sqrt{(-d - q + 1)^2 + 4d}.$$

Rationalizing the right hand side, we get

$$\frac{2dk_3}{d+q} > \frac{4dk_3}{\sqrt{(d+q-1)^2 + 4d} + d + q - 1}.$$

Cancelling $2dk_3$ on both sides, the above can be further simplified to

$$\sqrt{(d+q-1)^2 + 4d} > d + q + 1,$$

which implies that $q < 0$, a contradiction.

Lemma 2 *Assume that $k_1 > k_2 > k_3$, then $\frac{u_1^*}{k_1} < \frac{u_2^*}{k_2}$ holds for any $d > 0$ and $q \geq 0$.*

Proof Clearly, we know that $\frac{u_1^*}{k_1} < \frac{u_2^*}{k_2}$ holds for sufficiently large d . Thus, as $\frac{u_1^*}{k_1}$ and $\frac{u_2^*}{k_2}$ are continuous functions of d, q , it suffices to prove that $\frac{u_1^*}{k_1} \neq \frac{u_2^*}{k_2}$ for any $d > 0$. We assume that there exists some $d > 0$ such that $\frac{u_1^*}{k_1} = \frac{u_2^*}{k_2}$. Set $a := \frac{u_1^*}{k_1} = \frac{u_2^*}{k_2}$. By the first and second equation of (3), we get

$$(u_2^* - u_1^*)(d + q - 1 + a) = 0.$$

Due to $\frac{u_1^*}{k_1} = \frac{u_2^*}{k_2}$ and $k_1 > k_2$, we see that $u_1^* \neq u_2^*$. Hence, $d + q - 1 + a = 0$, i.e.

$$1 - \frac{u_1^*}{k_1} = d + q.$$

By the first equation of (3) we have $u_3^* = 0$, which is a contradiction.

Lemma 3 Assume that $k_1 > k_2 > k_3$, then $u_1^* > u_2^*$ holds for any $d > 0$ and $q \geq 0$.

Proof By the first and second equation of (3), we obtain

$$(-d - q + 1 - \frac{u_1^*}{k_1})u_1^* = (-d - q + 1 - \frac{u_2^*}{k_2})u_2^* = -du_3^* < 0.$$

By Lemma 2, we have

$$(-d - q + 1 - \frac{u_2^*}{k_2})u_1^* < (-d - q + 1 - \frac{u_2^*}{k_2})u_2^* < 0.$$

Therefore, $u_1^* > u_2^*$.

Lemma 4 Assume that $k_1 > k_2 > k_3$, then $u_1^* < k_1$ holds for any $d > 0, q \geq 0$.

Proof By the third equation of (3) and Lemma 3, we get

$$2d(u_1^* - u_3^*) + 2qu_1^* + u_3^*(1 - \frac{u_3^*}{k_3}) > 0,$$

which together with the first equation of (3) implies that

$$2u_1^*(1 - \frac{u_1^*}{k_1}) + u_3^*(1 - \frac{u_3^*}{k_3}) > 0.$$

Then by Lemma 1, we get $u_1^* < k_1$.

Lemma 5 Suppose $k_1 > k_2 > k_3$. If $\frac{k_2}{k_3} > 1 + \frac{k_1}{4k_2}$, then $u_2^* < k_2$ holds for any $q \geq 0$ and $d > 0$.

Proof Obviously, $u_2^* < k_2$ when $d = 0$ and $q > 0$. Note that u_2^* is continuous in d and q , it suffices to show for any $d > 0, q \geq 0$, $u_2^* \neq k_2$. If not, we assume that there exist $d > 0$ and $q \geq 0$ such that $u_2^* = k_2$. So $u_3^* = \frac{d+q}{d}k_2$. Rewrite (3) as

$$\begin{cases} d(u_3^* - u_1^*) - qu_1^* + u_1^*(1 - \frac{u_1^*}{k_1}) = 0, \\ d(u_1^* - u_3^*) + qu_1^* + u_3^*(1 - \frac{u_3^*}{k_3}) = 0. \end{cases}$$

Thus

$$u_1^*(1 - \frac{u_1^*}{k_1}) = u_3^*(\frac{u_3^*}{k_3} - 1). \quad (18)$$

We only need to prove there is no positive solution of (18) in the interval (k_2, k_1) . Rewrite (18) as $\frac{1}{k_1}(u_1^*)^2 - u_1^* + u_3^*(\frac{u_3^*}{k_3} - 1) = 0$, we know (18) has solution if and only if

$$1 - \frac{4u_3^*}{k_1}(\frac{u_3^*}{k_3} - 1) \geq 0. \quad (19)$$

By $u_3^* = \frac{d+q}{d}k_2$ and assumption $\frac{k_2}{k_3} > 1 + \frac{k_1}{4k_2}$, we see that (19) can not hold, i.e. (18) has no solution, which is a contradiction.

For the rest of this subsection, we define

$$q_- := \frac{\frac{k_2}{k_3} - \sqrt{1 + \frac{k_1}{4k_2}(1 + \frac{k_2}{k_3})}}{1 + \frac{k_2}{k_3}}.$$

Lemma 6 Suppose $k_1 > k_2 > k_3$. If $\frac{k_2}{k_3} > 1 + \frac{k_1}{4k_2}$, then $u_2^* > u_3^*$ holds for all $d > 0$ and $q \in [0, q_-)$.

Proof The proof is similar to that of Lemma 5. By Lemma 5, we know that when $q = 0$, $u_2^* < k_2$. By the second equation of (3), $u_2^* > u_3^*$ holds for $q = 0$ and $d > 0$. Thus we just need to verify when $q \in (0, q_-)$, $u_2^* \neq u_3^*$ for any $d > 0$. We argue by contradiction and assume that there exist some $q \in (0, q_-)$ and $d > 0$ such that $u_2^* = u_3^*$. By the second equation of (3), we get $u_2^* = u_3^* = k_2(1 - q)$ and

$$\begin{cases} d(u_3^* - u_1^*) - qu_1^* + u_1^*(1 - \frac{u_1^*}{k_1}) = 0, \\ d(u_1^* - u_3^*) + qu_1^* + qu_3^* + u_3^*(1 - \frac{u_3^*}{k_3}) = 0, \end{cases}$$

so that

$$\frac{1}{k_1}(u_1^*)^2 - u_1^* + k_2(1 - q)[-q - 1 + \frac{k_2}{k_3}(1 - q)] = 0,$$

for which we only need to show there is no positive solution. If not, we must have

$$1 - \frac{4k_2(1-q)}{k_1}[-q - 1 + \frac{k_2}{k_3}(1 - q)] \geq 0.$$

By assumption $q < q_-$, we get $1 - \frac{4k_2(1-q)}{k_1}[-q - 1 + \frac{k_2}{k_3}(1 - q)] < 0$, which is a contradiction.

Corollary 2 Assume $k_1 > k_2 > k_3$. If $\frac{k_2}{k_3} > 1 + \frac{k_1}{4k_2}$, then for $q \in [0, q_-)$, $d > 0$, $\frac{\partial A_1}{\partial D}|_{D=d} > 0$.

Proof By Lemmas 3 and 6, we have $u_1^* > u_2^* > u_3^*$. In particular, $u_3^* - u_1^* < 0$, $u_3^* - u_2^* < 0$. It follows from Lemmas 4 and 5 that $u_1^* < k_1$, $u_2^* < k_2$. Then by the first and second equation of (3), $u_1^* - \frac{d}{d+q}u_3^* > 0$, $u_2^* - \frac{d}{d+q}u_3^* > 0$. Therefore, the right hand side of (5) is positive.

Lemma 7 Assume $k_1 > k_2 > k_3$ and $\frac{k_2}{k_3} > 1 + \frac{k_1}{4k_2}$. If $q \in [0, q_-)$ and $d > 0$, then

$$3 - \frac{u_1^*}{k_1} - \frac{u_2^*}{k_2} - \frac{u_3^*}{k_3} < 0. \quad (20)$$

Proof We first show that (20) holds when $q = 0$. For $q = 0$, dividing the i -th equation of (3) by u_i and adding the results, we have

$$3 - \frac{u_1^*}{k_1} - \frac{u_2^*}{k_2} - \frac{u_3^*}{k_3} = -d(\frac{u_1^*}{u_3^*} + \frac{u_3^*}{u_1^*} - 2) - d(\frac{u_2^*}{u_3^*} + \frac{u_3^*}{u_2^*} - 2) < 0,$$

where the last equality is strict as k_1, k_2, k_3 are not equal to each other.

Note that u_i , $i = 1, 2, 3$, are continuous functions of q , so it suffices to prove $3 - \frac{u_1^*}{k_1} - \frac{u_2^*}{k_2} - \frac{u_3^*}{k_3} \neq 0$ for any $q > 0$. If not, assume that there exists $q > 0$ satisfying the assumption such that

$$3 - \frac{u_1^*}{k_1} - \frac{u_2^*}{k_2} - \frac{u_3^*}{k_3} = 0. \quad (21)$$

Adding the equations in (3), we have

$$u_1^*(1 - \frac{u_1^*}{k_1}) + u_2^*(1 - \frac{u_2^*}{k_2}) + u_3^*(1 - \frac{u_3^*}{k_3}) = 0,$$

which together with (21) implies that

$$(u_1^* - u_2^*)(1 - \frac{u_1^*}{k_1}) + (u_2^* - u_3^*)(\frac{u_3^*}{k_3} - 1) = 0.$$

By Lemmas 1, 3, 4 and 6, the left side of the above equation is positive. This contradiction completes the proof.

Recall that $F(d)$ was defined in (9). By Lemma 7, if $q \in [0, q_-)$, then $F(d)$ is well defined for any $d > 0$. Hence, by Corollary 1 we see that $\Lambda_1(d, F(d)) \leq 0$ for $d > 0$.

Lemma 8 *Suppose $k_1 > k_2 > k_3$, $\frac{k_2}{k_3} > 1 + \frac{k_1}{4k_2}$. If $q \in [0, q_-)$, then $\Lambda_1(d, D) > 0$ for all $D > d > 0$.*

Proof We argue by contradiction and assume that $\Lambda_1(\hat{d}, \hat{D}) \leq 0$ for some $\hat{D} > \hat{d} > 0$. By Corollary 2, $\Lambda_1(d, D) > 0$ for $D > d$ and D close to d . Hence we may assume that $\Lambda_1(\hat{d}, \hat{D}) = 0$. By Proposition 2, $\hat{D} = F(\hat{d})$ and $F(\hat{d}) > \hat{d}$. Clearly, we have $F(d) < d$ as $d \rightarrow +\infty$. By the continuity of F , $D = F(d)$ crosses the diagonal line $D = d$ at some $d = d^* > 0$. By Corollary 2, there exists some $\delta > 0$ such that $\Lambda_1(d, D) > 0$ for $d \in (d^* - \delta, d^* + \delta)$ and $0 < D - d < \delta$. This contradicts the fact that $\Lambda_1(d, F(d)) \leq 0$ for $d > 0$.

Proof of Theorem 2-(i). It follows from Lemma 8 and Corollary 2.

4.2 Model (II)

In this subsection, we study the sign of the principal eigenvalue Λ_2 in Model (II) when q is small. We first establish a few preliminary estimates on solutions of (10). Let $u^* = (u_1^*, u_2^*, u_3^*)$ denote the unique positive solution of (10) throughout this subsection.

Lemma 9 *Assume $k_1 > k_2 > k_3$. For any $d > 0$, $q \geq 0$, $u_1^* < k_1$ always holds.*

Proof If not, assume that there exist $d > 0, q \geq 0$ such that $u_1^* \geq k_1$. By the first equation of (10),

$$u_2^* \geq \frac{d+q}{d} u_1^* \geq u_1^* \geq k_1 > k_2.$$

Then by the second equation of (10), $u_3^* > u_2^* > k_2 > k_3$. Thus $u_1^*(1 - \frac{u_1^*}{k_1}) + u_2^*(1 - \frac{u_2^*}{k_2}) + u_3^*(1 - \frac{u_3^*}{k_3}) < 0$. By (10) we have $u_1^*(1 - \frac{u_1^*}{k_1}) + u_2^*(1 - \frac{u_2^*}{k_2}) + u_3^*(1 - \frac{u_3^*}{k_3}) = 0$, which is a contradiction.

Next, we have

Lemma 10 *Assume $k_1 > k_2 > k_3$. For any $d > 0$, $q \geq 0$, $u_3^* > k_3$ always holds.*

The proof of Lemma 10 is similar to that of Lemma 9 and is thus omitted.

Lemma 11 *Suppose $k_1 > k_2 > k_3$. If $0 \leq q < \min\{1 - \frac{k_2}{k_1}, \frac{k_2}{k_3} - 1\}$, then $u_1^* > u_2^* > u_3^*$ for $d > 0$.*

Proof Firstly, we prove $u_1^* > u_2^*$. We argue by contradiction and assume that there exists $0 \leq q < \min\{1 - \frac{k_2}{k_1}, \frac{k_2}{k_3} - 1\}$ such that $u_1^* \leq u_2^*$. From the first equation of (10), $u_1^* \geq k_1(1 - q)$, and using $q < 1 - \frac{k_2}{k_1}$, we obtain $u_2^* \geq u_1^* > k_2$. By the second equation of (10) and $u_2^* \geq u_1^* > k_2$, we get $u_2^* < u_3^*$. Again using the equation of u_3^* , $u_3^* < k_3(1 + q)$. Thus $k_2 < u_2^* < u_3^* < k_3(1 + q)$, i.e., $q > \frac{k_2}{k_3} - 1$, which contradicts assumption $q < \frac{k_2}{k_3} - 1$.

Next, we prove $u_2^* > u_3^*$. When $q = 0$, $u_2^* > u_3^*$ follows from $u_3^* > k_3$ and the equation of u_3^* . By the continuous dependence of u_i^* on q , it suffices to show $u_2^* \neq u_3^*$. Suppose to the contrary that there is some q satisfying the assumption such that $u_2^* = u_3^*$. Using the 3rd equation of (10), we get $u_2^* = u_3^* = k_3(1 + q)$. The second equation of (10) is reduced to

$$d(u_1^* - u_2^*) + qu_1^* - qu_2^* + u_2^*(1 - \frac{u_2^*}{k_2}) = 0.$$

As we have shown $u_1^* > u_2^*$, thus $u_2^* > k_2$ holds. This together with $u_2^* = k_3(1 + q)$ implies $q > \frac{k_2}{k_3} - 1$, which is impossible since $q \in [0, \frac{k_2}{k_3} - 1]$.

Proposition 7 Suppose $k_1 > k_2 > k_3$. If $0 \leq q < \min\{1 - \frac{k_2}{k_1}, \frac{k_2}{k_3} - 1\}$, then

$$\frac{\partial \Lambda_2}{\partial D} \Big|_{D=d} > 0 \quad \text{for any } d > 0.$$

Proof By Lemma 11, we have

$$\frac{d+q}{d} u_1^* (u_2^* - u_1^*) + u_2^* (u_1^* + u_3^* - 2u_2^*) + \frac{d}{d+q} u_3^* (u_2^* - u_3^*) < -(u_1^* - u_2^*)^2 - (u_2^* - u_3^*)^2 < 0.$$

Thus the right hand side of (12) is positive and the conclusion follows from Proposition 3.

Lemma 12 Assume $k_1 > k_2 > k_3$. If $0 \leq q < \min\{1 - \frac{k_2}{k_1}, \frac{k_2}{k_3} - 1\}$, then

$$3 - \frac{u_1^*}{k_1} - \frac{u_2^*}{k_2} - \frac{u_3^*}{k_3} < 0 \quad \text{for } d > 0.$$

Proof To repeat the proof of Lemma 7, we need

$$u_1^* < k_1, \quad u_3^* > k_3, \quad \text{and} \quad u_1^* > u_2^* > u_3^*,$$

which are already proved in Lemmas 9, 10 and 11.

Recall that F is defined as in (9). By Lemma 12, if $0 \leq q < \min\{1 - \frac{k_2}{k_1}, \frac{k_2}{k_3} - 1\}$, then $F(d)$ is well defined for all $d > 0$. The rest of the proof for Theorem 2-(ii) is identical to that of Theorem 2-(i) and is thus omitted.

4.3 Model (III)

In this subsection, we study the sign of the principal eigenvalue Λ_3 in Model (III) when q is small. Again, the key is to establish a few preliminary estimates on solutions of (13), denoted by $u^* = (u_1^*, u_2^*, u_3^*)$ throughout this subsection.

Lemma 13 Suppose that $k_1 > k_2 > k_3$. Then for all $d > 0$, $q \geq 0$, $u_1^* < k_1$ holds.

Proof Clearly $u_1^* < k_1$ holds when $q = 0$, so it suffices to show that for $q > 0$, $u_1^* \neq k_1$. If not, we may assume that there exists some $q > 0$ such that $u_1^* = k_1$. Substituting $u_1^* = k_1$ into the first equation of (13), we get

$$u_2^* + u_3^* = (2 + 2q/d)k_1. \quad (22)$$

Substituting $u_1^* = k_1$ into the second and third equation of (13), we obtain

$$u_i^* = \frac{k_i(1-d) + \sqrt{k_i^2(d-1)^2 + 4k_1k_i(d+q)}}{2} \quad \text{for } i = 2, 3.$$

For $x > 0$, set

$$g(x) := \frac{x(1-d) + \sqrt{x^2(d-1)^2 + 4k_1(d+q)x}}{2},$$

and observe that $g'(x) > 0$ for $x > 0$. By (22), we have

$$\frac{2(d+q)}{d} k_1 = g(k_2) + g(k_3) < 2g(k_1) = k_1(1-d) + \sqrt{k_1^2(d-1)^2 + 4k_1^2(d+q)}.$$

Cancelling k_1 on both sides, and multiplying $\sqrt{(d-1)^2 + 4(d+q)} + (d-1)$ on both sides, we get

$$\frac{2(d+q)}{d} [\sqrt{(d+1)^2 + 4q} + (d-1)] = \frac{2(d+q)}{d} [\sqrt{(d-1)^2 + 4(d+q)} + (d-1)] < 4(d+q).$$

Cancelling $2(d+q)$ on both sides, the above can be simplified to

$$\sqrt{(d+1)^2 + 4q} < d+1,$$

from which it follows that $q < 0$, a contradiction.

Lemma 14 *Assume $k_1 > k_2 > k_3$, then $\frac{u_2^*}{k_2} < \frac{u_3^*}{k_3}$ for all $d > 0$ and $q \geq 0$.*

Proof As $d \rightarrow \infty$, $u_1^*, u_2^*, u_3^* \rightarrow 3/(\frac{1}{k_1} + \frac{1}{k_2} + \frac{1}{k_3})$, so $\frac{u_2^*}{k_2} < \frac{u_3^*}{k_3}$ for large d . By virtue of the continuity of u_2^*, u_3^* with respect to d , we just need to prove that $\frac{u_2^*}{k_2} \neq \frac{u_3^*}{k_3}$ for $d > 0$. We argue by contradiction and assume that there exists $d > 0$ such that $a := \frac{u_2^*}{k_2} = \frac{u_3^*}{k_3}$. Then by the second and third equation of (13), we have

$$(d-1+a)(u_3^* - u_2^*) = 0.$$

Since $u_2^* = \frac{k_2}{k_3}u_3^* > u_3^*$, we have $u_2^* \neq u_3^*$ and hence $a = 1-d < 1$. Next, by adding all three equations of (13), we get

$$u_1^*(1 - \frac{u_1^*}{k_1}) + u_2^*(1 - a) + u_3^*(1 - a) = 0.$$

But this implies $u_1^* > k_1$, which is impossible, in view of Lemma 13.

Lemma 15 *Assume $k_1 > k_2 > k_3$, then $u_2^* > u_3^*$ holds for all $d > 0$, $q \geq 0$.*

Proof From Lemma 14 and (13), we have

$$\begin{cases} d(u_1^* - u_3^*) + qu_1^* + u_3^*(1 - \frac{u_2^*}{k_2}) > 0, \\ d(u_1^* - u_2^*) + qu_1^* + u_2^*(1 - \frac{u_3^*}{k_2}) = 0. \end{cases} \quad (23)$$

Subtracting, we get $(u_2^* - u_3^*)(d-1 + \frac{u_2^*}{k_2}) > 0$. Now, it is easy to see that $d-1 + \frac{u_2^*}{k_2} > 0$ (otherwise the second equation of (23) says $u_1^* \leq 0$). Thus, $u_2^* > u_3^*$.

Lemma 16 *Assume $k_1 > k_2 > k_3$, then $u_3^* > k_3$ for all $d > 0$, $q \geq 0$.*

Proof By Lemma 14 and (13), we know

$$0 = u_1^*(1 - \frac{u_1^*}{k_1}) + u_2^*(1 - \frac{u_2^*}{k_2}) + u_3^*(1 - \frac{u_3^*}{k_3}) > u_1^*(1 - \frac{u_1^*}{k_1}) + (u_2^* + u_3^*)(1 - \frac{u_3^*}{k_3}).$$

Now, by noting that $u_1^* > k_1$ (which is proved in Lemma 13), we have $u_3^* > k_3$.

Let (u_1, u_2) denote the unique positive solution of the following two-patch model:

$$\begin{cases} d(u_2 - u_1) - qu_1 + u_1(1 - \frac{u_1}{k_1}) = 0, \\ d(u_1 - u_2) + qu_1 + u_2(1 - \frac{u_2}{k_2}) = 0. \end{cases} \quad (24)$$

Lemma 17 *Assume $k_1 > k_2$. Then for any $d > 0$, $q \geq 0$, $u_2 > k_2$.*

Proof Assume that there exist some $d > 0$, $q \geq 0$ such that $u_2 \leq k_2$. By the second equation of (24), we get $u_1 \leq u_2$. Adding the equations of (24), we have

$$u_1(1 - \frac{u_1}{k_1}) + u_2(1 - \frac{u_2}{k_2}) = 0.$$

Hence, $u_1 \geq k_1$. Therefore, $k_1 \leq u_1 \leq u_2 \leq k_2$, which is a contradiction.

Lemma 18 *Assume $k_1 > k_2$.*

- (i) *If $q < \frac{k_1 - k_2}{k_1 + k_2}$, then $u_1 > \frac{2k_1 k_2}{k_1 + k_2}$;*
- (ii) *If $q > \frac{k_1 - k_2}{k_1 + k_2}$, then $u_1 < \frac{2k_1 k_2}{k_1 + k_2}$.*

Proof We first prove that u_1 is decreasing with respect to q . Note that

$$(d + q - 1 + 2\frac{u_1}{k_1})(d - 1 + 2\frac{u_2}{k_2}) - d(d + q) > 0.$$

Taking the derivative of two equations with respect to q in (24), we have

$$\begin{cases} d(u_2)' - (d + q - 1 + 2\frac{u_1}{k_1})(u_1)' - u_1 = 0, \\ (-d + 1 - 2\frac{u_2}{k_2})(u_2)' + (d + q)(u_1)' + u_1 = 0. \end{cases} \quad (25)$$

Multiplying the above two equations by $(-d + 1 - 2\frac{u_2}{k_2})$, d and subtracting them, we get

$$(u_1)' = \frac{1 - 2\frac{u_2}{k_2}}{(d + q - 1 + 2\frac{u_1}{k_1})(d - 1 + 2\frac{u_2}{k_2}) - d(d + q)} u_1.$$

By Lemma 17, $(u_1)' < 0$. Note that when $q = \frac{k_1 - k_2}{k_1 + k_2}$, $u_1 = u_2 = \frac{2k_1 k_2}{k_1 + k_2}$, then the conclusion follows from the monotonicity of u_1 in q .

Lemma 19 *Suppose $k_1 > k_2 > k_3$ and $\frac{2}{k_2} > \frac{1}{k_1} + \frac{1}{k_3}$. Then $u_2^* > k_2$ for $d > 0$, $0 \leq q \leq \frac{k_1 - k_3}{k_1 + k_3}$.*

Proof For fixed q , by assumption we have $u_2^* > k_2$ for sufficiently large d . Hence, it suffices to show that $u_2^* \neq k_2$ for all $d > 0$. If not, assume that there exists $d > 0$ such that $u_2^* = k_2$, so that the second equation of (13) implies $d(u_1^* - u_2^*) + qu_1^* = 0$, and the first and third equation of (13) is equivalent to (24). As $q \leq \frac{k_1 - k_3}{k_1 + k_3}$, it follows from Lemma 18 that

$$u_1^* \geq \frac{2k_1 k_3}{k_1 + k_3}.$$

Therefore, by $u_2^* = k_2$ and the second equation of (13), $u_1^* = \frac{d}{d+q}u_2^* \leq u_2^*$. Hence, we obtain $\frac{2k_1 k_3}{k_1 + k_3} \leq k_2$, i.e., $\frac{2}{k_2} \leq \frac{1}{k_3} + \frac{1}{k_1}$, which is a contradiction.

For the rest of this subsection, we assume in addition that $\frac{2}{k_2} > \frac{1}{k_1} + \frac{1}{k_3}$ and define the positive number \underline{q} as

$$\underline{q} := \frac{\frac{2}{k_2} - \frac{1}{k_1} - \frac{1}{k_3}}{\frac{1}{k_2} + \frac{1}{k_1} + \frac{1}{k_3}}.$$

Lemma 20 *Suppose $k_1 > k_2 > k_3$ and $\frac{2}{k_2} > \frac{1}{k_1} + \frac{1}{k_3}$. Then*

$$u_1^* > u_2^* \quad \text{for } d > 0 \text{ and } 0 \leq q \leq \underline{q}.$$

Proof Step 1. $q = 0$. Note that

$$\frac{q}{\frac{1}{k_2} + \frac{1}{k_1} + \frac{1}{k_3}} < \frac{k_1 - k_3}{k_1 + k_3},$$

where we used $0 < \frac{1}{k_1} < \frac{1}{k_2} < \frac{1}{k_3}$. It follows from Lemma 19 that $u_1^* > u_2^*$.

Step 2. $0 < q \leq \underline{q}$. In this case, we only need to show that $u_1^* \neq u_2^*$. If not, $u_1^* = u_2^*$. Then (13) can be reduced to

$$\begin{cases} d(u_3^* - u_1^*) - 2qu_1^* + u_1^*(1 - \frac{u_1^*}{k_1}) = 0, \\ u_1^* = u_2^* = k_2(1 + q), \\ d(u_1^* - u_3^*) + qu_1^* + u_3^*(1 - \frac{u_3^*}{k_3}) = 0. \end{cases} \quad (26)$$

By the first and second equation of (26), we have

$$u_3^* = \frac{k_2(1 + q)[d + (2 + \frac{k_2}{k_1})q - (1 - \frac{k_2}{k_1})]}{d}. \quad (27)$$

By our assumption on q , we have

$$q \leq \frac{\frac{2}{k_2} - \frac{1}{k_1} - \frac{1}{k_3}}{\frac{1}{k_2} + \frac{1}{k_1} + \frac{1}{k_3}} < \frac{\frac{1}{k_2} - \frac{1}{k_1}}{\frac{2}{k_2} + \frac{1}{k_1}} = \frac{1 - \frac{k_2}{k_1}}{2 + \frac{k_2}{k_1}}. \quad (28)$$

Substituting (28) into (27), we deduce that

$$u_3^* < k_2(1 + q). \quad (29)$$

Next, deduce from the first and third equation of (26) that

$$(d + q) \frac{u_1^*}{u_3^*} = d - 1 + \frac{u_3^*}{k_3} \quad \text{and} \quad d \frac{u_3^*}{u_1^*} = d + 2q - 1 + \frac{u_1^*}{k_1}. \quad (30)$$

Note that the latter implies that (using $u_1^* = k_2(1 + q)$ and (28))

$$d > \underline{d} := - \left(2 + \frac{k_2}{k_1} \right) q + \left(1 - \frac{k_2}{k_1} \right) > 0. \quad (31)$$

Multiplying the two equations, we obtain

$$d(d + q) = (d - \underline{d})(d - 1 + \frac{u_3^*}{k_3}).$$

Cancelling d^2 on both sides, the above can be simplified as

$$u_3^* = k_3 \frac{d(1 + q + \underline{d}) - \underline{d}}{d - \underline{d}}. \quad (32)$$

Since $d > \underline{d}$ (by (31)), and that the expression on the right hand side of (32) is monotone decreasing in $d \in (\underline{d}, \infty)$, it holds that

$$u_3^* > k_3(1 + q + \underline{d}) = k_3[(2 - \frac{k_2}{k_1}) - (1 + \frac{k_2}{k_1})q]. \quad (33)$$

By using the assumption of q , (33) implies

$$u_3^* > k_3[(2 - \frac{k_2}{k_1}) - (1 + \frac{k_2}{k_1})q] \geq k_2(1 + q), \quad (34)$$

which is a contradiction to (29).

Corollary 3 Suppose $k_1 > k_2 > k_3$ and $\frac{2}{k_2} > \frac{1}{k_1} + \frac{1}{k_3}$. Then

$$\frac{\partial \Lambda_3}{\partial D} \Big|_{D=d} > 0 \quad \text{for } d > 0 \text{ and } q \in [0, \underline{q}].$$

Proof By Lemmas 15 and 20, $u_1^* > u_2^* > u_3^*$. Using $u_2^* > k_2$ (by Lemma 19) and the second equation of (13), we have $du_2^* - (d+q)u_1^* < 0$. Similarly, using $u_3^* > k_3$ (by Lemma 16) and the third equation of (13), we get $du_3^* - (d+q)u_1^* < 0$. Thus the right hand side of (15) is positive. The conclusion follows from Proposition 5.

Lemma 21 Suppose $k_1 > k_2 > k_3$ and $\frac{2}{k_2} > \frac{1}{k_1} + \frac{1}{k_3}$. Then for $d > 0$, $q \in [0, \underline{q}]$,

$$3 - \frac{u_1^*}{k_1} - \frac{u_2^*}{k_2} - \frac{u_3^*}{k_3} < 0 \quad \text{for } d > 0 \text{ and } q \in [0, \underline{q}].$$

Proof To repeat the proof of Lemma 7, we need

$$u_1^* < k_1, \quad u_3^* > k_3, \quad \text{and} \quad u_1^* > u_2^* > u_3^*,$$

which are already proved in Lemmas 13, 16, 15 and 20.

Corollary 4 Suppose $k_1 > k_2 > k_3$ and $\frac{2}{k_2} > \frac{1}{k_1} + \frac{1}{k_3}$. Then for $d > 0$, $q \in [0, \underline{q}]$, the right hand side of (16) is strictly negative.

Proof By Lemmas 15, 20 and the first equation of (13), we get $-2q + 1 - \frac{u_1^*}{k_1} > 0$. Then by Lemmas 16, 19 and 21, the right hand side of (16) is strictly negative.

Proof of Theorem 2-(iii). Since the right hand side of (16) is strictly negative (by Corollary 4), Proposition 6 says that $\Lambda_3(d, D) = 0$ if and only if $D = d$. Therefore, by Corollary 3 and the continuity of Λ_3 , $\Lambda_3(d, D) > 0$ holds for $D > d > 0$ and $\Lambda_3(d, D) < 0$ holds for $0 < D < d$.

5 The large drift case

In this section, our goal is to establish Theorems 3 and 4. We consider three Models (I)-(III) in Subsections 5.1-5.3, respectively.

5.1 Model (I)

In this subsection, we study the sign of the principal eigenvalue Λ_1 in Model (I) when q is large. In order to prove Theorem 3-(i), we first state some estimates on solutions of (3). In this subsection $u^* = (u_1^*, u_2^*, u_3^*)$ denotes the unique positive solution of (3).

Lemma 22 Assume $k_1 > k_2 > k_3$ and $\frac{2}{k_2} < \frac{1}{k_1} + \frac{1}{k_3}$. Then for any $q \geq \frac{k_1 - k_3}{k_1 + k_3}$ and $d > 0$, $u_2^* < k_2$ always holds.

Proof The proof is similar as that of Lemma 19. For fixed $q \geq 0$, we have $u_2^* < k_2$ for sufficiently large d by assumption. Since u_2^* is continuous with respect to d , it is sufficient to prove $u_2^* \neq k_2$ for all $d > 0$. We argue by contradiction and assume that there exists $d > 0$ such that $u_2^* = k_2$. In such a case, the second equation of (3) implies $d(u_3^* - u_2^*) - qu_2^* = 0$, and the first and third equation of (3) is equivalent to (24). As $q \geq \frac{k_1 - k_3}{k_1 + k_3}$, it follows from Lemma 18 that $u_1^* \leq 2k_1k_3/(k_1 + k_3)$. Then by Lemma 3, we know $2k_1k_3/(k_1 + k_3) \geq u_1^* > u_2^* = k_2$, which is impossible since $\frac{2}{k_2} < \frac{1}{k_1} + \frac{1}{k_3}$.

Lemma 23 Assume $k_1 > k_2 > k_3$ and $\frac{2}{k_2} < \frac{1}{k_1} + \frac{1}{k_3}$. Then for $d > 0$ and $q \geq \frac{k_1-k_3}{k_1+k_3}$, $u_3^* > u_1^*$ holds.

Proof First, we consider the case $q \geq 1$. By the first equation of (3), we have

$$d(u_3^* - u_1^*) = u_1^* \left(q - 1 + \frac{u_1^*}{k_1} \right) > 0.$$

In view of the continuous dependence of u_i^* ($i = 1, 2, 3$) on q , we only need to show $u_1^* \neq u_3^*$ for $\frac{k_1-k_3}{k_1+k_3} \leq q < 1$. If not, then there exists $\frac{k_1-k_3}{k_1+k_3} \leq q < 1$ such that $u_1^* = u_3^*$. Adding the second and third equation of (3) and using $u_1^* = u_3^*$, we have

$$u_2^* \left(1 - \frac{u_2^*}{k_2} \right) + u_3^* \left(q + 1 - \frac{u_3^*}{k_3} \right) = 0,$$

which together with Lemma 22 implies that $u_3^* > k_3(1+q)$. However, by setting $u_1^* = u_3^*$ in the first equation of (3), we get $u_3^* = k_1(1-q)$. Thus $k_1(1-q) > k_3(1+q)$, i.e. $q < \frac{k_1-k_3}{k_1+k_3}$, which is a contradiction.

Corollary 5 Assume $k_1 > k_2 > k_3$. If $\frac{2}{k_2} < \frac{1}{k_1} + \frac{1}{k_3}$, then for $q \geq \frac{k_1-k_3}{k_1+k_3}$ and $d > 0$, $\frac{\partial \Lambda_1}{\partial D} \big|_{D=d} < 0$.

Proof By Lemmas 3 and 23, we get $u_3^* > u_1^* > u_2^*$. Thus $u_3^* - u_1^* > 0$ and $u_3^* - u_2^* > 0$. Using, respectively, $u_1^* < k_1$ (by Lemma 4) and $u_2^* < k_2$ (by Lemma 22) in the first and second equation of (3), we deduce that

$$u_1^* - \frac{d}{d+q} u_3^* > 0 \quad \text{and} \quad u_2^* - \frac{d}{d+q} u_3^* > 0.$$

Therefore, it follows from (5) that $\frac{\partial \Lambda_1}{\partial D} \big|_{D=d} < 0$.

Lemma 24 Assume $k_1 > k_2 > k_3$ and $\frac{2}{k_2} < \frac{1}{k_1} + \frac{1}{k_3}$. If $q \geq \frac{k_1-k_3}{k_1+k_3}$, then for $d > 0$, $3 - \frac{u_1^*}{k_1} - \frac{u_2^*}{k_2} - \frac{u_3^*}{k_3} > 0$.

Proof Adding the equations of (3), we have

$$u_1^* \left(1 - \frac{u_1^*}{k_1} \right) + u_2^* \left(1 - \frac{u_2^*}{k_2} \right) + u_3^* \left(1 - \frac{u_3^*}{k_3} \right) = 0. \quad (35)$$

From $1 - \frac{u_1^*}{k_1} > 0$ (Lemma 4), $1 - \frac{u_2^*}{k_2} > 0$ (Lemma 22), and $u_3^* > u_1^* > u_2^*$ (Lemmas 3 and 23), we obtain

$$u_3^* \left(1 - \frac{u_1^*}{k_1} \right) > u_1^* \left(1 - \frac{u_1^*}{k_1} \right) \quad \text{and} \quad u_3^* \left(1 - \frac{u_2^*}{k_2} \right) > u_2^* \left(1 - \frac{u_2^*}{k_2} \right).$$

Substituting the above into (35), we obtain

$$u_3^* \left(1 - \frac{u_1^*}{k_1} \right) + u_3^* \left(1 - \frac{u_2^*}{k_2} \right) + u_3^* \left(1 - \frac{u_3^*}{k_3} \right) > 0,$$

which, upon cancelling u_3^* , implies the conclusion.

Lemma 25 Assume $k_1 > k_2 > k_3$, $\frac{2}{k_2} < \frac{1}{k_1} + \frac{1}{k_3}$. Then for $q \geq \frac{k_1-k_3}{k_1+k_3}$ and $d > 0$, we have

$$-q + 1 - \frac{u_1^*}{k_1} < 0 \quad \text{and} \quad -q + 1 - \frac{u_2^*}{k_2} < 0.$$

Proof By Lemmas 3 and 23, we have $u_3^* > u_1^* > u_2^*$. Hence, by the first and second equation of (3), we get

$$(-q + 1 - \frac{u_i^*}{k_i})u_i^* = d(u_i^* - u_3^*) < 0, \quad i = 1, 2.$$

This completes the proof.

Corollary 6 *Assume $k_1 > k_2 > k_3$, $\frac{2}{k_2} < \frac{1}{k_1} + \frac{1}{k_3}$. If $q \geq \frac{k_1 - k_3}{k_1 + k_3}$, then for $d > 0$, the right hand side of (9) is strictly negative.*

Proof The conclusion follows from Lemmas 1, 24 and 25.

Proof of Theorem 3-(i). Since the right hand side of (9) is strictly negative (by Corollary 6), Proposition 2 says that $\Lambda_1(d, D) = 0$ if and only if $D = d$. Therefore, by Corollary 5 and the continuity of Λ_1 , $\Lambda_1(d, D) < 0$ holds for $D > d > 0$ and $\Lambda_1(d, D) > 0$ holds for $0 < D < d$.

5.2 Model (II)

In this subsection, we study the sign of the principal eigenvalue Λ_2 in Model (II) when q is large. We first establish a few estimates on solutions of (10). Let $u^* = (u_1^*, u_2^*, u_3^*)$ denote the unique positive solution of (10) throughout this subsection.

Lemma 26 *Suppose $k_1 > k_2 > k_3$. If $q > \max\{1 - \frac{k_2}{k_1}, \frac{k_2}{k_3} - 1\}$, then $u_1^* < u_2^* < u_3^*$ for $d > 0$.*

Proof We first prove that $u_1^* < u_2^*$. If not, there exists some $q > \max\{1 - \frac{k_2}{k_1}, \frac{k_2}{k_3} - 1\}$ such that $u_1^* \geq u_2^*$. By the first equation of (10), $u_1^* \leq k_1(1-q)$, and using $q > 1 - \frac{k_2}{k_1}$, we have $k_2 > u_1^* \geq u_2^*$. Combining this with the equation of u_2^* in (10), we get

$$d(u_3^* - u_2^*) = (d+q)(u_2^* - u_1^*) + u_2^*(\frac{u_2^*}{k_2} - 1) < 0,$$

and obtain $u_2^* > u_3^*$. Hence, $u_1^* \geq u_2^* > u_3^*$. By the third equation of (10), we have $u_3^* > k_3(1+q)$. This, together with $k_2 > u_2^* > u_3^*$, implies $q < \frac{k_2}{k_3} - 1$, which is impossible.

Next, we prove $u_2^* < u_3^*$. We argue by contradiction and assume that there exists some $q > \max\{1 - \frac{k_2}{k_1}, \frac{k_2}{k_3} - 1\}$ such that $u_2^* \geq u_3^*$. By the third equation of (10), we have

$$(q + 1 - \frac{u_3^*}{k_3})u_3^* \leq qu_2^* + u_3^*(1 - \frac{u_3^*}{k_3}) = d(u_3^* - u_2^*) \leq 0,$$

thus $u_3^* \geq k_3(1+q)$. By $q > \frac{k_2}{k_3} - 1$, we have $u_2^* \geq u_3^* > k_2$, which together with the second equation of (10) implies that

$$(d+q)(u_1^* - u_2^*) \geq d(u_1^* + u_3^* - 2u_2^*) + qu_1^* - qu_2^* = u_2^*(\frac{u_2^*}{k_2} - 1) > 0.$$

Therefore, we have $u_1^* > u_2^* \geq u_3^*$. By the first equation of (10), we have $u_1^* < k_1(1-q)$. This together with $u_1^* > u_2^* \geq u_3^* > k_2$ implies that $q < 1 - \frac{k_2}{k_1}$, which is a contradiction.

Lemma 27 *Assume $k_1 > k_2 > k_3$, then $\frac{d+q}{d}u_1^* > u_2^* > \frac{d}{d+q}u_3^*$ holds for $d > 0$ and $q \geq 0$.*

Proof By the first equation of (10) and $u_1^* < k_1$ (Lemma 9), we have $du_2^* < (d+q)u_1^*$. Similarly, by the third equation of (10) and $u_3^* > k_3$ (Lemma 10), we have $(d+q)u_2^* > du_3^*$.

Corollary 7 *Suppose $k_1 > k_2 > k_3$. If $q > \max\{1 - \frac{k_2}{k_1}, \frac{k_2}{k_3} - 1\}$, then $\frac{\partial \Lambda_2}{\partial D}|_{D=d} < 0$ for $d > 0$.*

Proof By Lemma 26, we have $u_1^* < u_2^* < u_3^*$. Note that

$$\begin{aligned} & \frac{d+q}{d}u_1^*(u_2^* - u_1^*) + u_2^*(u_1^* + u_3^* - 2u_2^*) + \frac{d}{d+q}u_3^*(u_2^* - u_3^*) \\ &= (u_2^* - u_1^*)(\frac{d+q}{d}u_1^* - u_2^*) + (u_3^* - u_2^*)(u_2^* - \frac{d}{d+q}u_3^*), \end{aligned}$$

and we can then conclude by Lemma 27, i.e., the right hand side of (12) is negative.

Lemma 28 *Assume $k_1 > k_2 > k_3$. If $q > \max\{1 - \frac{k_2}{k_1}, \frac{k_2}{k_3} - 1\}$, then $3 - \frac{u_1^*}{k_1} - \frac{u_2^*}{k_2} - \frac{u_3^*}{k_3} > 0$ for any $d > 0$.*

Proof Adding the equations of (10), we have

$$u_1^*(1 - \frac{u_1^*}{k_1}) + u_2^*(1 - \frac{u_2^*}{k_2}) + u_3^*(1 - \frac{u_3^*}{k_3}) = 0. \quad (36)$$

From $1 - \frac{u_1^*}{k_1} > 0$ (Lemma 9), $1 - \frac{u_3^*}{k_3} < 0$ (Lemma 10), and $u_1^* < u_2^* < u_3^*$ (Lemma 26), we obtain

$$u_2^*(1 - \frac{u_1^*}{k_1}) > u_1^*(1 - \frac{u_1^*}{k_1}) \quad \text{and} \quad u_2^*(1 - \frac{u_3^*}{k_3}) > u_3^*(1 - \frac{u_3^*}{k_3}).$$

Substituting the above into (36), we obtain

$$u_2^*(1 - \frac{u_1^*}{k_1}) + u_2^*(1 - \frac{u_2^*}{k_2}) + u_2^*(1 - \frac{u_3^*}{k_3}) > 0,$$

which, upon cancelling u_2^* , implies the conclusion.

Lemma 29 *Assume $k_1 > k_2 > k_3$. If $q > \max\{1 - \frac{k_2}{k_1}, \frac{k_2}{k_3} - 1\}$, then $-q + 1 - \frac{u_2^*}{k_2} < 0$ holds for any $d > 0$.*

Proof When $q \geq 1$, the conclusion holds trivially. We only need to consider the case $\max\{1 - \frac{k_2}{k_1}, \frac{k_2}{k_3} - 1\} < q < 1$. By the first equation of (10) and $u_2^* > u_1^*$ (Lemma 26), we have $u_2^* > u_1^* > k_1(1 - q)$. Since $k_1 > k_2$ and $1 - q > 0$, we have $u_2^* > k_2(1 - q)$, which is the same as $-q + 1 - \frac{u_2^*}{k_2} < 0$.

Corollary 8 *Assume $k_1 > k_2 > k_3$. If $q > \max\{1 - \frac{k_2}{k_1}, \frac{k_2}{k_3} - 1\}$, then the right hand side of (9) is strictly negative.*

Proof By Lemma 26, $u_2^* > u_1^*$, which together with the first equation of (10) implies that $-q + 1 - \frac{u_1^*}{k_1} < 0$. This together with Lemmas 10, 28 and 29 shows that the right hand side of (9) is negative.

Proof of Theorem 3-(ii). Since the right hand side of (9) is strictly negative (by Corollary 8), Proposition 4 says that $\Lambda_2(d, D) = 0$ if and only if $D = d$. Therefore, by Corollary 7 and the continuity of Λ_2 , $\Lambda_2(d, D) < 0$ holds for $D > d > 0$ and $\Lambda_2(d, D) > 0$ holds for $0 < D < d$.

5.3 Model (III)

In this subsection, we mainly prove Theorem 4.

Proof of Theorem 4. Step 1. We show that if $q > \frac{1}{2}$, then for sufficiently small $d > 0$,

$$\frac{\partial A_3}{\partial D} \Big|_{D=d} = -\frac{\frac{1}{2(2q-1)}(k_2+k_3)^2 - \frac{1}{2}(k_2-k_3)^2}{o(1) + k_2^2 + k_3^3}. \quad (37)$$

In particular, if $q > \underline{p}$, then $\frac{\partial A_3}{\partial D} \Big|_{D=d} > 0$ holds for sufficiently small d .

Fix $q > 0$ and let $d \rightarrow 0$, we have $(u_1^*, u_2^*, u_3^*) \rightarrow (\bar{u}_1, \bar{u}_2, \bar{u}_3)$, for some $\bar{u}_i \geq 0$, $i = 1, 2, 3$. In fact, \bar{u}_i can be determined by $\bar{u}_1 = k_1(1-2q)_+$ and

$$k_1q(1-2q)_+ + \bar{u}_i(1 - \frac{\bar{u}_i}{k_i}) = 0 \quad \text{for } i = 2, 3. \quad (38)$$

Hence, if $q > 1/2$ and $d \rightarrow 0$, we have $u_1^* \rightarrow 0$ and $u_i^* \rightarrow k_i$ for $i = 2, 3$. Since the first equation of (13) can be written as $d(k_2+k_3+o(1)) = u_1^*(2q-1+o(1))$, we get

$$u_1^* = \frac{k_2+k_3}{2q-1}d + o(d) \quad \text{as } d \rightarrow 0.$$

Similarly, by the second and third equation of (13) we have

$$\begin{aligned} \frac{u_2^*}{k_2} &= 1 - d + \frac{q}{2q-1}(1 + \frac{k_3}{k_2})d + o(d), \\ \frac{u_3^*}{k_3} &= 1 - d + \frac{q}{2q-1}(1 + \frac{k_2}{k_3})d + o(d). \end{aligned}$$

So as $d \rightarrow 0$, by (15) we have

$$\begin{aligned} \frac{\partial A_3}{\partial D} \Big|_{D=d} &= -\frac{[k_2 - \frac{q}{2q-1}(k_2+k_3) + o(1)](o(1)-k_2) + [k_3 - \frac{q}{2q-1}(k_2+k_3) + o(1)](o(1)-k_3)}{o(1) + k_2^2 + k_3^3} \\ &= -\frac{\frac{q}{2q-1}(k_2+k_3)^2 - k_2^2 - k_3^2 + o(1)}{o(1) + k_2^2 + k_3^3} \\ &= -\frac{\frac{1}{2(2q-1)}(k_2+k_3)^2 - \frac{1}{2}(k_2-k_3)^2}{o(1) + k_2^2 + k_3^3}. \end{aligned}$$

In particular, we need to take $\underline{p} := \frac{1}{2} \left(\frac{k_2+k_3}{k_2-k_3} \right)^2 + \frac{1}{2} = \frac{k_2^2+k_3^2}{(k_2-k_3)^2}$. This proves (37) and completes Step 1.

Step 2. We claim that $\lim_{d \rightarrow \infty} \frac{\partial A_3}{\partial D} \Big|_{D=d} < 0$ when $q > \bar{p}$.

Fix $q > 0$ and let $d \rightarrow +\infty$, we have $u_1^*, u_2^*, u_3^* \rightarrow u_\infty = 3/(\frac{1}{k_1} + \frac{1}{k_2} + \frac{1}{k_3})$. By (13) and (15), we have

$$\lim_{d \rightarrow \infty} d^2 \frac{\partial A_3}{\partial D} \Big|_{D=d} = \frac{1}{3} \left[q(2 - \frac{u_\infty}{k_2} - \frac{u_\infty}{k_3}) + (1 - \frac{u_\infty}{k_2})^2 + (1 - \frac{u_\infty}{k_3})^2 \right].$$

This completes Step 2.

Step 3. From Steps 1 and 2 we can conclude that when $q > \max\{\underline{p}, \bar{p}\}$,

$$\frac{\partial A_3}{\partial D} \Big|_{D=d} = \begin{cases} + & 0 < d \ll 1; \\ - & d \gg 1. \end{cases}$$

Therefore, by the analytic dependence of Λ_3 on parameter d (see end of Sect. 3), there exists at least one $d^* = d^*(q) > 0$ such that

$$\frac{\partial \Lambda_3}{\partial D} \Big|_{D=d} = \begin{cases} + & d < d^*, \text{ } d \text{ close to } d^*; \\ 0 & d = d^*; \\ - & d > d^*, \text{ } d \text{ close to } d^*. \end{cases}$$

This completes the proof of Theorem 4.

Next, we show that under large advection, a species with dispersal rate d behaves approximately as a random disperser in the two downstream patches with dispersal rate $d/2$.

Lemma 30 *Let (u_1^*, u_2^*, u_3^*) be the unique steady state of (13) for some fixed $d \geq 0$. Then*

$$\lim_{q \rightarrow \infty} (u_1^*, u_2^*, u_3^*) = (0, \tilde{u}_2, \tilde{u}_3),$$

where $(\tilde{u}_2, \tilde{u}_3)$ is the unique positive solution of the following two-patch system with dispersal rate $d/2$ and zero drift:

$$\begin{cases} \frac{d}{2}(\tilde{u}_3 - \tilde{u}_2) + \tilde{u}_2 \left(1 - \frac{\tilde{u}_2}{k_2}\right) = 0, \\ \frac{d}{2}(\tilde{u}_2 - \tilde{u}_3) + \tilde{u}_3 \left(1 - \frac{\tilde{u}_3}{k_3}\right) = 0. \end{cases} \quad (39)$$

Proof From the first equation of (13), we see that for $q > 1/2$,

$$u_1^* = \frac{d(u_2^* + u_3^*)}{2q - 1 + \frac{u_1^*}{k_1}} = \frac{d + o(1)}{2q} (u_2^* + u_3^*).$$

Substitute the above into the second equation of (13), we have

$$d(o(1) - u_2^*) + \frac{d + o(1)}{2} (u_2^* + u_3^*) + u_2^* \left(1 - \frac{u_2^*}{k_2}\right) = 0.$$

Thus we obtain the first equation of (39) upon letting $q \rightarrow \infty$. The second equation of (39) can be similarly proved.

Next, we prove Theorem 6.

Proof of Theorem 6. First, we show assertion (i). First, let $\tilde{\Lambda}_3$ be the principal eigenvalue of

$$\tilde{\Lambda}_3 := \begin{pmatrix} -2D - 2q + 1 & D & D \\ D + q & -D & 0 \\ D + q & 0 & -D \end{pmatrix},$$

with a positive eigenvector $\tilde{\Phi} = (\tilde{\varphi}_1, \tilde{\varphi}_2, \tilde{\varphi}_3)^T$. Then by adding the rows of $\tilde{\Lambda}_3 \tilde{\Phi} + \tilde{\Lambda}_3 \tilde{\Phi} = \mathbf{0}$, we can show that $\tilde{\varphi}_1 + \tilde{\Lambda}_3 \sum_{i=1}^3 \tilde{\varphi}_i = 0$, i.e. $\tilde{\Lambda}_3 < 0$ for any $D > 0$. Moreover, as $D \rightarrow \infty$, $\tilde{\varphi}_i / \tilde{\varphi}_j \rightarrow 1$, so that $\tilde{\Lambda}_3 \rightarrow -1/3$. Hence, we deduce that for each $\underline{D} > 0$, $\sup_{D > \underline{D}} \tilde{\Lambda}_3 < 0$.

To prove assertion (i) of Theorem 6, we take $d \geq 0$, and let (u_1^*, u_2^*, u_3^*) be the unique steady state of (13). By Lemma 30,

$$\lim_{d \rightarrow 0, q \rightarrow \infty} (u_1^*, u_2^*, u_3^*) = (0, k_2, k_3).$$

Hence, $\lim_{d \rightarrow 0, q \rightarrow \infty} A_3 = \tilde{\Lambda}_3$. Thus for each $\underline{D} > 0$, there exist $\hat{d}_1, \hat{q}_1 > 0$ such that

$$\sup_{D > \underline{D}} \Lambda_3(d, D) < 0 \quad \text{whenever } 0 \leq d < \hat{d}_1 \text{ and } q \geq \hat{q}_1.$$

This proves assertion (i).

Next, we prove assertions (ii) and (iii). Now, for each fixed q ,

$$\lim_{d \rightarrow \infty} (u_1^*, u_2^*, u_3^*) = (u_\infty, u_\infty, u_\infty), \quad \text{where } u_\infty = \frac{3}{\frac{1}{k_1} + \frac{1}{k_2} + \frac{1}{k_3}}.$$

Hence, it suffices to show that the principal eigenvalue \hat{A}_3 of

$$\hat{A}_3 := \begin{pmatrix} -2D - 2q + 1 - \frac{u_\infty}{k_1} & D & D \\ D + q & -D + 1 - \frac{u_\infty}{k_2} & 0 \\ D + q & 0 & -D + 1 - \frac{u_\infty}{k_3} \end{pmatrix}$$

satisfies $\lim_{D \rightarrow 0} \hat{A}_3 > 0$. Now, by continuous dependence of \hat{A}_3 on $D \geq 0$, for large q we have

$$\lim_{D \rightarrow 0} \hat{A}_3 = \hat{A}_3 \Big|_{D=0} = \frac{u_\infty}{k_2} - 1.$$

On the one hand, if $\frac{2}{k_2} > \frac{1}{k_1} + \frac{1}{k_3}$, then for q large,

$$\lim_{d \rightarrow \infty, D \rightarrow 0} A_3(d, D) = \lim_{D \rightarrow 0} \hat{A}_3 = \frac{u_\infty}{k_2} - 1 > 0. \quad (40)$$

This proves assertion (ii). On the other hand, if $\frac{2}{k_2} < \frac{1}{k_1} + \frac{1}{k_3}$, then the last inequality in (40) is reversed. This proves assertion (iii).

6 The intermediate drift

In this section, we mainly study Models (I) and (II) for q in some intermediate range.

Proof of Theorem 5. We first establish Theorem 5-(i). Set

$$\Omega := (u_1^* - \frac{d}{d+q} u_3^*)(u_3^* - u_1^*) + (u_2^* - \frac{d}{d+q} u_3^*)(u_3^* - u_2^*). \quad (41)$$

By (3) we can rewrite Ω as

$$\Omega = \frac{1}{d(d+q)} [(u_1^*)^2 (\frac{u_1^*}{k_1} - 1 + q)(1 - \frac{u_1^*}{k_1}) + (u_2^*)^2 (\frac{u_2^*}{k_2} - 1 + q)(1 - \frac{u_2^*}{k_2})]. \quad (42)$$

Note that $u_1^*, u_2^*, u_3^* \rightarrow u_\infty$ as $d \rightarrow +\infty$. Therefore, as $d \rightarrow \infty$,

$$d(d+q)\Omega \rightarrow u_\infty^2 [q(2 - \frac{u_\infty}{k_1} - \frac{u_\infty}{k_2}) - (1 - \frac{u_\infty}{k_1})^2 - (1 - \frac{u_\infty}{k_2})^2]. \quad (43)$$

Hence, by Proposition 1 we have, for sufficiently large d ,

$$\frac{\partial \Lambda_1}{\partial D} \Big|_{D=d} = \begin{cases} + & q < \bar{q}, \\ - & q > \bar{q}, \end{cases}$$

where \bar{q} is as given by Theorem 5-(i).

When $d \rightarrow 0$, we have $u_i^* \rightarrow k_i(1-q)_+$ for $i = 1, 2$, and $u_3^* \rightarrow \bar{u}_3$, where \bar{u}_3 is determined by

$$\bar{u}_3 \left(\frac{\bar{u}_3}{k_3} - 1 \right) = q(1-q)_+(k_1 + k_2). \quad (44)$$

Hence, by applying (41) we have

$$\lim_{d \rightarrow 0} \Omega = \bar{u}_3(k_1 + k_2)(1-q)_+ - (k_1^2 + k_2^2)(1-q)_+^2. \quad (45)$$

Therefore, solving (44) and substituting the result into (45) we find that for small d ,

$$\frac{\partial \Lambda_1}{\partial D} \Big|_{D=d} = \begin{cases} + & q < \underline{q}, \\ - & \underline{q} < q < 1, \end{cases}$$

where \underline{q} is as given by Theorem 5-(i).

If $\underline{q} < \bar{q}$, since Λ_1 is analytic in d , there exists some $d^* = d^*(q)$ such that for $q \in (\underline{q}, \bar{q})$,

$$\frac{\partial \Lambda_1}{\partial D} \Big|_{D=d} = \begin{cases} - & d < d^*, \text{ } d \text{ close to } d^*; \\ 0 & d = d^*; \\ + & d > d^*, \text{ } d \text{ close to } d^*. \end{cases}$$

The case $\underline{q} > \bar{q}$ can be similarly treated.

The proof of Theorem 5-(ii) is similar and we omit the details.

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