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GLOBAL DYNAMICS FOR TWO-SPECIES COMPETITION IN PATCHY ENVIRONMENT

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Abstract. An ODE system modeling the competition between two species in a two-patch environment is studied. Both species move between the patches with the same dispersal rate. It is shown that the species with larger birth rates in both patches drives the other species to extinction, regardless of the dispersal rate. The more interesting case is when both species have the same average birth rate but each species has larger birth rate in one patch. It has previously been conjectured by Gourley and Kuang that the species that can concentrate its birth in a single patch wins if the diffusion rate is large enough, and two species will coexist if the diffusion rate is small. We solve these two conjectures by applying the monotone dynamics theory, incorporated with a complete characterization of the positive equilibrium and a thorough analysis on the stability of the semi-trivial equilibria with respect to the dispersal rate. Our result on the winning strategy for sufficiently large dispersal rate might explain the group breeding behavior that is observed in some animals under certain ecological conditions.

1. **Introduction.** Gourley and Kuang [3] studied the following two-patch system as a model for two neutrally competing species:

$$\begin{cases} \frac{du_1}{dt} = u_1(\alpha_1 - u_1 - v_1) + d(u_2 - u_1) \\ \frac{du_2}{dt} = u_2(\alpha_2 - u_2 - v_2) + d(u_1 - u_2) \\ \frac{dv_1}{dt} = v_1(\beta_1 - u_1 - v_1) + d(v_2 - v_1) \\ \frac{dv_2}{dt} = v_2(\beta_2 - u_2 - v_2) + d(v_1 - v_2), \end{cases} \tag{1}$$

where u_i (resp., v_i) is the number of species u (resp., v) in patch i, $i = 1, 2$; the linear birth rates $\alpha_1, \alpha_2, \beta_1, \beta_2$ are positive parameters, and there is a diffusion between the two patches with the same diffusivity (dispersal rate) d for both species. Two species differ only in their birth rates.

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We denote

$$\begin{aligned}\mathbb{R}^4_+ &= \left\{(u_1,u_2,v_1,v_2)\in\mathbb{R}^4 | u_1,u_2,v_1,v_2\ge 0\right\},\\ \tilde{\mathbb{R}}^{2\times 0}_+ &= \left\{(u_1,u_2,0,0)\in\mathbb{R}^{2\times 2}_+ | u_1+u_2>0\right\},\\ \tilde{\mathbb{R}}^{0\times 2}_+ &= \left\{(0,0,v_1,v_2)\in\mathbb{R}^{2\times 2}_+ | v_1+v_2>0\right\}.\end{aligned}$$

Each of $\mathbb{R}^4_+$, $\tilde{\mathbb{R}}^{2\times 0}_+$ and $\tilde{\mathbb{R}}^{0\times 2}_+$ is positively invariant under the solution flow generated by system (1). The semi-trivial equilibria (boundary equilibria) $(\overline{u}_1,\overline{u}_2,0,0)$ with $\overline{u}_1,\overline{u}_2>0$, and $(0,0,\overline{v}_1,\overline{v}_2)$ with $\overline{v}_1,\overline{v}_2>0$, for system (1), always exist. By Lyapunov function method [2, 5], it is known that every solution of system (1) initially starting from $\tilde{\mathbb{R}}^{2\times 0}_+$ converges to $(\bar{u}_1,\bar{u}_2,0,0)$ and every solution initially starting from $\tilde{\mathbb{R}}^{0\times 2}_+$ converges to $(0,0,\bar{v}_1,\bar{v}_2)$.

We are interested in the dynamics of system (1) in $\mathbb{R}^4_+$. If $\alpha_1+\alpha_2>\beta_1+\beta_2$, then for sufficiently large d, $(\overline{u}_1,\overline{u}_2,0,0)$ is globally asymptotically stable among the initial data in $\mathbb{R}^4_+$ satisfying $u_1(0)+u_2(0)>0$. Similar result holds for the case $\alpha_1+\alpha_2<\beta_1+\beta_2$. As $\alpha_1+\alpha_2$ and $\beta_1+\beta_2$ measure the average birth rate of the species u and v, these results indicate that the species with larger average birth rate has the competitive advantage in a fast diffusion environment. It is thus natural to inquire which species has the winning strategy when they have the same average birth rate, i.e. $\alpha_1+\alpha_2=\beta_1+\beta_2$. This interesting question was raised and studied in [3]. It will be the focus of this work as well. To facilitate further discussions, without loss of generality, we assume that $\beta_1\le\beta_2$. Following [3], we introduce parameter σ by setting $\alpha_1=\beta_1-\sigma$. Assuming $\alpha_1+\alpha_2=\beta_1+\beta_2$, we have $\alpha_2=\beta_2+\sigma$. If we further require $\alpha_1>0$ and $\alpha_2>0$, σ is then restricted to the domain $(-\beta_2,\beta_1)$. The following results on the stability of the semi-trivial equilibria of system (1) were established in [3]:

Proposition 1.1. ([3]) *If $\beta_2>\beta_1$ and $\alpha_1=\beta_1-\sigma$, $\alpha_2=\beta_2+\sigma$ with $0<\sigma<\beta_1$, and d is sufficiently large, then $(0,0,\overline{v}_1,\overline{v}_2)$ is unstable and $(\overline{u}_1,\overline{u}_2,0,0)$ is linearly stable.*

Proposition 1.2. ([3]) *If $\beta_2>\beta_1$ and $\alpha_1=\beta_1+\sigma$, $\alpha_2=\beta_2-\sigma$ with $\sigma<0$ but $|\sigma|$ not too large and d is sufficiently large, then $(0,0,\overline{v}_1,\overline{v}_2)$ is linearly stable and $(\overline{u}_1,\overline{u}_2,0,0)$ is unstable.*

Proposition 1.3. ([3]) *If $\beta_2=\beta_1=\beta>0$ and $\alpha_1=\beta-\sigma$, $\alpha_2=\beta+\sigma$ with σ of either sign and $|\sigma|<\beta$. If d is sufficiently large, then $(0,0,\overline{v}_1,\overline{v}_2)$ is unstable and $(\overline{u}_1,\overline{u}_2,0,0)$ is linearly stable.*

As $|\alpha_1-\alpha_2|$ and $|\beta_1-\beta_2|$ reflect the spatial variation of the birth rate of the species u and v, these results suggest that in a fast diffusion environment where different species have the same average birth rate, the species that do well are those that have greater spatial variation in their birth rates. These results led Gourley and Kuang to pose the following conjectures on the global dynamics of (1) in [3]:

Conjecture 1. *Assume that in system (1), $\beta_1-\sigma=\alpha_1<\beta_1<\beta_2<\alpha_2=\beta_2+\sigma$ with $0<\sigma<\beta_1$, and d is sufficiently large. If $u_1(0)+u_2(0)>0$, then*

$$\lim_{t\to\infty}(u_1(t),u_2(t),v_1(t),v_2(t))=(\bar{u}_1,\bar{u}_2,0,0).$$

Conjecture 2. *Assume that in system (1), $\beta_1-\sigma=\alpha_1<\beta_1<\beta_2<\alpha_2=\beta_2+\sigma$ with $0<\sigma<\beta_1$, and d is small enough so that (1) has a positive steady state E_*.*

If $u_1(0) + u_2(0) > 0$ *and* $v_1(0) + v_2(0) > 0$*, then*

$$\lim_{t\to\infty}(u_1(t), u_2(t), v_1(t), v_2(t)) = E_*.$$

These conjectures, if true, suggest that the species that can concentrate its birth in a single patch wins, if the diffusion rate is larger than a critical value. In short, the winning strategy is simply to focus as much birth in a single patch as possible. In this paper, we will establish the following result, which includes Conjectures 1 and 2 as special cases:

Theorem 1.4. *Suppose that in system* (1)*,* $\beta_1 - \sigma = \alpha_1 < \beta_1 < \beta_2 < \alpha_2 = \beta_2 + \sigma$ *with* $0 < \sigma < \beta_1$*. Then there exists some positive constant* d^* *so that if* $d \geq d^*$*,* $(\bar{u}_1, \bar{u}_2, 0, 0)$ *is globally asymptotically stable among the initial data in* $\mathbb{R}^4_+$ *satisfying* $u_1(0) + u_2(0) > 0$*; if* $d < d^*$*,* (1) *has a unique positive steady state which is globally asymptotically stable among the initial data in* $\mathbb{R}^4_+$ *satisfying* $u_1(0) + u_2(0) > 0$ *and* $v_1(0) + v_2(0) > 0$*.*

Our result may explain some grouping behaviors in animal populations which may be advantageous under certain ecological conditions. Theorem 1.4 proves that in fast diffusion scenarios a winning strategy is to concentrate the birth in a single patch. More specifically, for any positive birth rates (β_1, β_2) with $\beta_1 < \beta_2$, we compare it with the extreme case $(0, \beta_1 + \beta_2)$; i.e., when $\sigma = \beta_1$ and $(\alpha_1, \alpha_2) = (0, \beta_1 + \beta_2)$. Theorem 1.4 implies that the birth rates $(0, \beta_1 + \beta_2)$ provide a winning strategy in the sense that the population adopting it can drive the other population with the birth rates (β_1, β_2) to extinction. This result suggests that for a two-patch habitat it can be more advantageous for the species to have a single breeding site, provided that the dispersal of the species is suitably fast. We do not know whether a similar conclusion can be drawn for multiple-patch models; see also [1].

Theorem 1.4 will be justified in Section 3. The case for larger birth rates for u-species on both patches, namely, $\beta_1 < \alpha_1, \beta_2 < \alpha_2$, is discussed in Section 2. The case of interlacing birth rates: $\alpha_1 < \beta_1 < \beta_2 < \alpha_2$ is investigated in Section 3. We collect in Subsection 3.1 the monotone dynamical system theory to be applied in later sections. The existence of positive equilibrium is studied in Subsection 3.2. The properties and stability of the semi-trivial equilibria are addressed in Subsections 3.3 and 3.4. With the preparation in Subsections 3.1-3.4, we summarize the main results and solve the conjectures in Subsection 3.5. We present the case $\beta_1 < \alpha_1 < \alpha_2 < \beta_2$ which is symmetric to $\alpha_1 < \beta_1 < \beta_2 < \alpha_2$, in Section 4. Two numerical examples illustrating the present theory are given in Section 5. The paper ends with a conclusion section.

2. Larger birth rates for u-species: $\beta_1 < \alpha_1, \beta_2 < \alpha_2$.

In this section we consider the case that u-species has larger birth rates than v-species in both patches, namely, $\beta_1 < \alpha_1, \beta_2 < \alpha_2$. Intuitively, one would expect the extinction of v-species in this situation. Mathematics indeed justifies this intuition, as illustrated in this section. Let us set

$$\hat{\mathbb{R}}^4_+ := \left\{(u_1, u_2, v_1, v_2) \in \mathbb{R}^4_+ | u_1 + u_2 > 0\right\}.$$

Let $\alpha_1 = \beta_1 + \sigma_1$ and $\alpha_2 = \beta_2 + \sigma_2$ with $\sigma_1, \sigma_2 > 0$. We first present the case without dispersal, i.e., $d = 0$.

Theorem 2.1. *Consider* $\beta_1 < \alpha_1, \beta_2 < \alpha_2$ *and* $d = 0$ *in system* (1)*. Then* $(\alpha_1, \alpha_2, 0, 0)$ *is globally asymptotically stable in* $\hat{\mathbb{R}}^4_+$*.*

Proof. Clearly, $(\alpha_1, \alpha_2, 0, 0)$ is an equilibrium of system (1) with $d = 0$. We denote $\bar{u}_1 = \alpha_1$ and $\bar{u}_2 = \alpha_2$. Define $V : \hat{\mathbb{R}}^4_+ \to \mathbb{R}$ by

$$V(u_1, u_2, v_1, v_2) = \left(u_1 + v_1 - \bar{u}_1 - \bar{u}_1 \ln\left(\frac{u_1}{\bar{u}_1}\right)\right) + \left(u_2 + v_2 - \bar{u}_2 - \bar{u}_2 \ln\left(\frac{u_2}{\bar{u}_2}\right)\right).$$

Then

$$\begin{aligned}
\dot{V} &= u_1(\alpha_1 - u_1 - v_1) + v_1(\beta_1 - u_1 - v_1) - \bar{u}_1(\alpha_1 - u_1 - v_1) \\
&+ u_2(\alpha_2 - u_2 - v_2) + v_2(\beta_2 - u_2 - v_2) - \bar{u}_2(\alpha_2 - u_2 - v_2) \\
&= [(u_1 + v_1) - \bar{u}_1](\alpha_1 - u_1 - v_1) - \sigma_1 v_1 \\
&+ [(u_2 + v_2) - \bar{u}_2](\alpha_2 - u_2 - v_2) - \sigma_2 v_2 \\
&= -[(u_1 + v_1) - \alpha_1]^2 - [(u_2 + v_2) - \alpha_2]^2 - \sigma_1 v_1 - \sigma_2 v_2, \\
&\leq 0.
\end{aligned}$$

The equality holds if and only if $u_1 = \alpha_1$ and $u_2 = \alpha_2$, $v_1 = 0, v_2 = 0$. The assertion follows from the Lyapunov function theorem. □

The following theorem shows that the coexistence state does not exist for any $d > 0$.

Theorem 2.2. *Assume $\beta_1 < \alpha_1, \beta_2 < \alpha_2$ and $d > 0$. Then there does not exist any positive equilibrium in system (1).*

Proof. Suppose otherwise that there exists a positive equilibrium $(u_1^*, u_2^*, v_1^*, v_2^*)$, $u_i^*, v_i^* > 0, i = 1, 2$, so that the following equations are satisfied:

$$\begin{cases}
(\alpha_1 - u_1^* - v_1^*) + d(\frac{u_2^*}{u_1^*} - 1) &= 0 \\
(\alpha_2 - u_2^* - v_2^*) + d(\frac{u_1^*}{u_2^*} - 1) &= 0 \\
(\beta_1 - u_1^* - v_1^*) + d(\frac{v_2^*}{v_1^*} - 1) &= 0 \\
(\beta_2 - u_2^* - v_2^*) + d(\frac{v_1^*}{v_2^*} - 1) &= 0.
\end{cases}$$

Combining the above four equations, we obtain $\sigma_1 + d(a - b) = 0$ and $\sigma_2 + d(\frac{1}{a} - \frac{1}{b}) = 0$, where $a = \frac{u_2^*}{u_1^*}, b = \frac{v_2^*}{v_1^*}$. Subsequently, $\sigma_1 + \sigma_2 ab = 0$. This contradicts to the assumption $\sigma_1, \sigma_2 > 0$ and $u_1^*, u_2^*, v_1^*, v_2^* > 0$. □

Next, we study the global stability of semi-trivial equilibrium $(\bar{u}_1, \bar{u}_2, 0, 0)$ in system (1) with $d > 0$. The scenario remains similar to $d = 0$. Note that $\bar{u}_1$ and $\bar{u}_2$ satisfy

$$(\bar{u}_1 - \alpha_1) = d(\frac{\bar{u}_2}{\bar{u}_1} - 1), \; (\bar{u}_2 - \alpha_2) = d(\frac{\bar{u}_1}{\bar{u}_2} - 1).$$

Theorem 2.3. *Consider $\beta_1 < \alpha_1, \beta_2 < \alpha_2$ and $d > 0$ in system (1). Then $(\bar{u}_1, \bar{u}_2, 0, 0)$ is globally asymptotically stable in $\hat{\mathbb{R}}^4_+$.*

Proof. System (1) can be rewritten as

$$\begin{cases}
\frac{du_1}{dt} &= u_1(\bar{u}_1 - u_1 - v_1) - d\frac{\bar{u}_2}{\bar{u}_1}u_1 + du_2 \\
\frac{du_2}{dt} &= u_2(\bar{u}_2 - u_2 - v_2) - d\frac{\bar{u}_1}{\bar{u}_2}u_2 + du_1 \\
\frac{dv_1}{dt} &= v_1(\bar{u}_1 - u_1 - v_1) - d\frac{\bar{u}_2}{\bar{u}_1}v_1 + dv_2 - \sigma_1 v_1 \\
\frac{dv_2}{dt} &= v_2(\bar{u}_2 - u_2 - v_2) - d\frac{\bar{u}_1}{\bar{u}_2}v_2 + dv_1 - \sigma_2 v_2.
\end{cases}$$

We define $V : \hat{\mathbb{R}}^4_+ \to \mathbb{R}$ by $V = c_1V_1 + c_2V_2 + c_3V_3 + c_4V_4$, where $c_i > 0$, $i = 1, 2, 3, 4$, are to be determined, and

$$\begin{aligned} V_1 &= u_1 - \bar{u}_1 - \bar{u}_1 \ln\left(\frac{u_1}{\bar{u}_1}\right), \\ V_2 &= u_2 - \bar{u}_2 - \bar{u}_2 \ln\left(\frac{u_2}{\bar{u}_2}\right), \\ V_3 &= v_1, \\ V_4 &= v_2. \end{aligned}$$

A direct calculation yields

$$\begin{aligned} \dot{V}_1 &= u_1(\bar{u}_1 - u_1 - v_1) - d\frac{\bar{u}_2}{\bar{u}_1}u_1 + du_2 - \bar{u}_1(\bar{u}_1 - u_1 - v_1) + d\bar{u}_2 - d\bar{u}_1\frac{u_2}{u_1} \\ &= (u_1 - \bar{u}_1)(\bar{u}_1 - u_1 - v_1) + d\bar{u}_2\left(-\frac{u_1}{\bar{u}_1} + \frac{u_2}{\bar{u}_2} + 1 - \frac{\bar{u}_1u_2}{u_1\bar{u}_2}\right). \end{aligned}$$

Similarly, we obtain

$$\begin{aligned} \dot{V}_2 &= (u_2 - \bar{u}_2)(\bar{u}_2 - u_2 - v_2) + d\bar{u}_1\left(-\frac{u_2}{\bar{u}_2} + \frac{u_1}{\bar{u}_1} + 1 - \frac{u_1\bar{u}_2}{\bar{u}_1u_2}\right), \\ \dot{V}_3 &= v_1(\bar{u}_1 - u_1 - v_1) + d\bar{u}_2\left(-\frac{v_1}{\bar{u}_1} + \frac{v_2}{\bar{u}_2}\right) - \sigma_1v_1, \\ \dot{V}_4 &= v_2(\bar{u}_2 - u_2 - v_2) + d\bar{u}_1\left(-\frac{v_2}{\bar{u}_2} + \frac{v_1}{\bar{u}_1}\right) - \sigma_2v_2. \end{aligned}$$

We pick $c_1 = c_3 = \bar{u}_1$ and $c_2 = c_4 = \bar{u}_2$, then

$$\begin{aligned} \dot{V} &= \bar{u}_1(u_1 - \bar{u}_1)(\bar{u}_1 - u_1 - v_1) + \bar{u}_2(u_2 - \bar{u}_2)(\bar{u}_2 - u_2 - v_2) \\ &+ d\bar{u}_1\bar{u}_2\left[2 - \left(\frac{\bar{u}_1u_2}{u_1\bar{u}_2} + \frac{u_1\bar{u}_2}{\bar{u}_1u_2}\right)\right] \\ &+ \bar{u}_1v_1(\bar{u}_1 - u_1 - v_1) + \bar{u}_2v_2(\bar{u}_2 - u_2 - v_2) - \sigma_1\bar{u}_1v_1 - \sigma_2\bar{u}_2v_2 \\ &\le \bar{u}_1(u_1 - \bar{u}_1)(\bar{u}_1 - u_1 - v_1) + \bar{u}_2(u_2 - \bar{u}_2)(\bar{u}_2 - u_2 - v_2) \\ &+ \bar{u}_1v_1(\bar{u}_1 - u_1 - v_1) + \bar{u}_2v_2(\bar{u}_2 - u_2 - v_2) - \sigma_1\bar{u}_1v_1 - \sigma_2\bar{u}_2v_2, \end{aligned}$$

where the equality holds if and only if $u_1\bar{u}_2 = \bar{u}_1u_2$. Subsequently,

$$\begin{aligned} \dot{V} &\le -\bar{u}_1(u_1 + v_1 - \bar{u}_1)^2 - \bar{u}_2(u_2 + v_2 - \bar{u}_2)^2 - \sigma_1\bar{u}_1v_1 - \sigma_2\bar{u}_2v_2 \\ &\le 0. \end{aligned}$$

In addition, $\dot{V}(u_1, u_2, v_1, v_2) = 0$ if and only if $u_1\bar{u}_2 = \bar{u}_1u_2$, $u_1 + v_1 = \bar{u}_1, u_2 + v_2 = \bar{u}_2, v_1 = 0$, and $v_2 = 0$, i.e., $u_1 = \bar{u}_1, u_2 = \bar{u}_2, v_1 = 0$ and $v_2 = 0$. The assertion follows from the Lyapunov function theorem. □

To summarize, for birth rates satisfying $\beta_1 < \alpha_1, \beta_2 < \alpha_2$, globally attractive equilibrium $(\bar{u}_1, \bar{u}_2, 0, 0)$ depicts the global dynamical scenario for system (1), and the consequent extinction of v-species is independent of the dispersal rate d.

3. **Interlacing birth rates: $\alpha_1 < \beta_1 < \beta_2 < \alpha_2$.** In this section, we consider the following parameters

$$\alpha_1 < \beta_1 < \beta_2 < \alpha_2,$$

i.e., u-species has larger birth rate than v-species in the second patch, while v-species has larger birth rate than u-species in the first patch. Then we ask how this distribution of birth rates is related to the species persistence or extinction.

Gourley and Kuang [3] studied the local stability of semi-trivial equilibria under the following assumption:

$$\text{Condition } (A): 0 < \alpha_1 = \beta_1 - \sigma < \beta_1 < \beta_2 < \alpha_2 = \beta_2 + \sigma \text{ with } 0 < \sigma < \beta_1.$$

Two conjectures under this parameter condition were posed therein, as mentioned in Section 1. Herein, we consider more general situation:

$$\begin{aligned} \text{Condition } (H): \quad & 0 < \alpha_1 = \beta_1 - \sigma_1 < \beta_1 < \beta_2 < \alpha_2 = \beta_2 + \sigma_2 \\ & \text{with } 0 < \sigma_1 \le \sigma_2 \text{ and } 0 < \sigma_1 < \beta_1. \end{aligned}$$

When $\sigma_1 = \sigma_2$, condition (H) reduces to condition (A).

We recall the monotone dynamics theory in Subsection 3.1, and discuss the existence of positive equilibrium in Subsection 3.2, properties for the semi-trivial equilibria in Subsection 3.3, the stability of the semi-trivial equilibria in Subsection 3.4, and the coexistence of two species and the extinction of one species in Subsection 3.5.

First, when $d = 0$, i.e. there is no dispersal, the species with larger birth rate prevails in each patch, as shown in the following result.

Theorem 3.1. *Under condition (H) and $d = 0$, $(0, \alpha_2, \beta_1, 0)$ is globally asymptotically stable in system (1), among the initial data in $\mathbb{R}^4_+$ satisfying $u_1(0) + u_2(0) > 0$ and $v_1(0) + v_2(0) > 0$.*

The proof of this theorem resembles that of Theorem 2.1, and is omitted.

3.1. **Monotone dynamics theory.** In this subsection, we recall some monotone dynamical system theories. Denote by $\mathbb{R}^n_+ = \{\mathbf{x} \in \mathbb{R}^n : x_i \ge 0, 1 \le i \le n\}$ the first orthant of $\mathbb{R}^n$. Consider the following cones:

$$K_m = \{\mathbf{x} \in \mathbb{R}^n : x_i \ge 0, 1 \le i \le k, \text{ and } x_j \le 0, k+1 \le j \le n\} = \mathbb{R}^k_+ \times (-\mathbb{R}^{n-k}_+).$$

We write $\mathbf{x} \le_m \mathbf{y}$ if $\mathbf{y} - \mathbf{x} \in K_m$, and $\mathbf{x} \ll_m \mathbf{y}$ whenever $\mathbf{y} - \mathbf{x} \in \text{Int}K_m$. For $\mathbf{x}, \mathbf{y} \in \mathbb{R}^n_+$ and $\mathbf{x} \le_m \mathbf{y}$, we define $[\mathbf{x}, \mathbf{y}]_m = \{\mathbf{z} \in \mathbb{R}^n_+ : \mathbf{x} \le_m \mathbf{z} \le_m \mathbf{y}\}$ and $(\mathbf{x}, \mathbf{y})_m = \{\mathbf{z} \in \mathbb{R}^n_+ : \mathbf{x} \ll_m \mathbf{z} \ll_m \mathbf{y}\}$.

A semiflow ϕ is said to be of type-K monotone with respect to K_m provided

$$\phi_t(\mathbf{x}) \le_m \phi_t(\mathbf{y}) \text{ whenever } \mathbf{x} \le_m \mathbf{y},\ t \ge 0.$$

A system of ODEs

$$\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x})$$

is called a type-K monotone system with respect to K_m if the Jacobian matrix of $\mathbf{f}$ is of the form

$$\begin{bmatrix} A_1 & -A_2 \\ -A_3 & A_4 \end{bmatrix},$$

where A_1 is a $k \times k$ matrix, A_4 is an $(n-k) \times (n-k)$ matrix, A_2 is a $k \times (n-k)$ matrix, A_3 is an $(n-k) \times k$ matrix, every off-diagonal element of A_1 and A_4 is nonnegative, and A_2 and A_3 are nonnegative matrices, for some k with $1 \le k \le n$. Smith [6] showed that the flow $\phi_t(\mathbf{x})$ generated by the type-K monotone system is type-K monotone with respect to the cone K_m; i.e., if $\mathbf{x}, \mathbf{y} \in \mathbb{R}^n_+$ with $x_i \le y_i$ for $1 \le i \le k$ and $x_j \ge y_j$ for $k+1 \le j \le n$, then for any $t > 0$, $(\phi_t(\mathbf{x}))_i \le (\phi_t(\mathbf{y}))_i$ for $1 \le i \le k$ and $(\phi_t(\mathbf{x}))_j \ge (\phi_t(\mathbf{y}))_j$ for $k+1 \le j \le n$.

We note that system (1) is a type-K monotone system with respect to

$$K_m = \{(u_1, u_2, v_1, v_2) : u_i \ge 0, v_i \le 0,\ i = 1, 2\},$$

since the Jacobian matrix is given by

$$\begin{bmatrix} \alpha_1 - 2u_1 - v_1 - d & d & -u_1 & 0 \\ d & \alpha_2 - 2u_2 - v_2 - d & 0 & -u_2 \\ -v_1 & 0 & \beta_1 - 2v_1 - u_1 - d & d \\ 0 & -v_2 & d & \beta_2 - 2v_2 - u_2 - d \end{bmatrix}.$$

For system (1), let us denote by $E_{\mathbf{0}} := (0,0,0,0)$ the trivial equilibrium, by $E_{\bar{\mathbf{u}}} := (\bar{u}_1, \bar{u}_2, 0, 0)$, and $E_{\bar{\mathbf{v}}} := (0,0,\bar{v}_1,\bar{v}_2)$, $\bar{u}_i$, $\bar{v}_i > 0$, $i = 1,2$, the semi-trivial equilibria. If $\mathbf{w} = (u_1,u_2,v_1,v_2) \in \mathbb{R}^4_+$, then $(0,0,v_1,v_2) \leq_m (u_1,u_2,v_1,v_2) \leq_m (u_1,u_2,0,0)$, and therefore,

$$\phi_t((0,0,v_1,v_2)) \leq_m \phi_t((u_1,u_2,v_1,v_2)) \leq_m \phi_t((u_1,u_2,0,0)),$$

for all $t \geq 0$. Since $\phi_t((0,0,v_1,v_2)) \to E_{\bar{\mathbf{v}}}$ and $\phi_t((u_1,u_2,0,0)) \to E_{\bar{\mathbf{u}}}$ as $t \to \infty$, for $(u_1,u_2,v_1,v_2) \in \mathbb{R}^{2\times 2}_+$, and $u_1 + u_2 > 0$, $v_1 + v_2 > 0$, it follows that all points in $\mathbb{R}^{2\times 2}_+$ are attracted to the set

$$\Gamma := [0,\bar{u}_1] \times [0,\bar{u}_2] \times [0,\bar{v}_1] \times [0,\bar{v}_2] = [E_{\bar{\mathbf{v}}}, E_{\bar{\mathbf{u}}}]_m = \{\mathbf{w} \in \mathbb{R}^4_+ : E_{\bar{\mathbf{v}}} \leq_m \mathbf{w} \leq_m E_{\bar{\mathbf{u}}}\}.$$

If $\mathbf{w} = (u_1,u_2,v_1,v_2)$ with $u_1,u_2,v_1,v_2 > 0$, then $\phi_t(\mathbf{w}) \gg 0$ for $t > 0$. Define E and E^+ the sets of all nonnegative equilibria and all positive equilibria for ϕ_t, respectively. Obviously, $[E_{\bar{\mathbf{v}}}, E_{\bar{\mathbf{u}}}]_m$ contains E and $E_* \in (E_{\bar{\mathbf{v}}}, E_{\bar{\mathbf{u}}})_m$ for any $E_* \in E^+$. The following theorem restates Corollary 4.4.3 in [7] for system (1); see also [6, 8].

Theorem 3.2. *If $E_{\bar{\mathbf{u}}}$ and $E_{\bar{\mathbf{v}}}$ are both linearly unstable, then system (1) is permanent. More precisely, there exist positive equilibria E_* and E_{**}, not necessarily distinct, satisfying*

$$E_{\bar{\mathbf{v}}} \ll_m E_{**} \leq_m E_* \ll_m E_{\bar{\mathbf{u}}}.$$

The order interval

$$[E_{**}, E_*]_m := \{\mathbf{w} : E_{**} \leq_m \mathbf{w} \leq_m E_*\}$$

attracts all solutions evolved from $\mathbf{w} = (u_1,u_2,v_1,v_2) \in \mathbb{R}^4_+$, with $u_1 + u_2 > 0$ and $v_1 + v_2 > 0$. In particular, if $E_{**} = E_*$, then E_* attracts all such solutions.

Hsu et al. [4] showed that, for two competing-species models, either there is a positive equilibrium representing coexistence of two species, or one species drives the other to extinction. As system (1) satisfies conditions (H1)-(H4) in [4], Theorem B in [4] can be restated as follows.

Theorem 3.3. *For system (1), the ω-limit set of every orbit evolved from $\mathbb{R}^4_+$ is contained in Γ and exactly one of the following holds:*
(a) *There exists a positive equilibrium E_* in Γ;*
(b) *$\phi_t(\mathbf{w}) \to E_{\bar{\mathbf{u}}}$ as $t \to \infty$, for every $\mathbf{w} = (u_1,u_2,v_1,v_2) \in \Gamma$ with $u_1 + u_2 > 0$;*
(c) *$\phi_t(\mathbf{w}) \to E_{\bar{\mathbf{v}}}$ as $t \to \infty$, for every $\mathbf{w} = (u_1,u_2,v_1,v_2) \in \Gamma$ with $v_1 + v_2 > 0$.*
In addition, if (b) *or* (c) *holds, $\mathbf{w} = (u_1,u_2,v_1,v_2) \in \mathbb{R}^4_+ \setminus \Gamma$, then either $\phi_t(\mathbf{w}) \to E_{\bar{\mathbf{u}}}$ or $\phi_t(\mathbf{w}) \to E_{\bar{\mathbf{v}}}$, as $t \to \infty$.*

A system similar to (1) has been studied in Section 4.4 of [7]. Therein, monotone structure was employed to obtain the attracting regions, and global convergence to the semi-trivial equilibrium and the positive equilibrium. However, those results are under conditions on eigenvalues of the Jacobian of the vector field at the semi-trivial equilibria. Those quantities depend on the coordinate values of the semi-trivial equilibria, and thus the theorem does not provide answers to the conjectures mentioned in Section 1. Indeed, to see the complete scenarios, one needs to elucidate on how the dynamics depend on the parameters and especially, the dispersal rate d.

3.2. **Existence of positive equilibrium.** The existence of positive equilibrium for system (1) can be characterized completely, as shown in the following theorem.

Theorem 3.4. *Under condition* (H)*, there exists a* $d^* > 0$ *so that system* (1) *has a unique positive equilibrium* $(u_1^*, u_2^*, v_1^*, v_2^*)$ *if and only if* $d < d^*$*; in addition,*

$$\frac{\alpha_1\alpha_2\sigma_1\sigma_2}{\alpha_2^2\sigma_2 - \alpha_1^2\sigma_1} < d^* < \frac{\beta_1\beta_2\sigma_1\sigma_2}{\beta_2^2\sigma_2 - \beta_1^2\sigma_1}.$$

Proof. System (1) has a positive equilibrium $(u_1^*, u_2^*, v_1^*, v_2^*)$ if and only if

$$\begin{aligned} &(\alpha_1 - u_1^* - v_1^*) + d(\frac{u_2^*}{u_1^*} - 1) = 0, \quad (\alpha_2 - u_2^* - v_2^*) + d(\frac{u_1^*}{u_2^*} - 1) = 0, \\ &(\beta_1 - v_1^* - u_1^*) + d(\frac{v_2^*}{v_1^*} - 1) = 0, \quad (\beta_2 - v_2^* - u_2^*) + d(\frac{v_1^*}{v_2^*} - 1) = 0 \end{aligned} \tag{2}$$

is satisfied for $u_1^*, u_2^*, v_1^*, v_2^* > 0$. Let

$$a = \frac{u_2^*}{u_1^*}, \quad b = \frac{v_2^*}{v_1^*}. \tag{3}$$

Combining each pair of equations (2), we obtain $-\sigma_1 + d(a-b) = 0$ and $\sigma_2 + d(\frac{1}{a} - \frac{1}{b}) = 0$. Thus,

$$ab = \frac{\sigma_1}{\sigma_2} =: k,$$

and $0 < k \le 1$, as $0 < \sigma_1 \le \sigma_2$. Therefore

$$a = \frac{\sigma_1 + \sqrt{\sigma_1^2 + 4kd^2}}{2d}, \quad b = \frac{-\sigma_1 + \sqrt{\sigma_1^2 + 4kd^2}}{2d}. \tag{4}$$

Note that a, b are now expressed in terms of parameters, and $a^2 > k > b^2$. With (3) we substitute them back to (2) and obtain

(i) $(\alpha_1 - u_1^* - v_1^*) + d(a-1) = 0,$ (ii) $a(\alpha_2 - au_1^* - bv_1^*) + d(1-a) = 0,$
(iii) $(\beta_1 - v_1^* - u_1^*) + d(b-1) = 0,$ (iv) $b(\beta_2 - bv_1^* - au_1^*) + d(1-b) = 0.$

Solving (i) and (ii), we have

$$u_1^* = \frac{a\alpha_2 + d - ad - k(\alpha_1 + ad - d)}{a^2 - k}, \quad v_1^* = \alpha_1 + ad - d - u_1^*.$$

On the other hand, solving (iii) and (iv), we have

$$u_1^* = \frac{b\beta_2 + d - bd - b^2(\beta_1 + bd - d)}{k - b^2}, \quad v_1^* = \beta_1 + bd - d - u_1^*.$$

The consistency can be verified: from $d(a-b) = \sigma_1$, we see that $\alpha_1 + ad - d = \beta_1 + bd - d$ and

$$\frac{a\alpha_2 + d - ad - k(\alpha_1 + ad - d)}{a^2 - k} = \frac{b\beta_2 + d - bd - b^2(\beta_1 + bd - d)}{k - b^2}.$$

Hence, the unique positive equilibrium exists for system (1) if and only if

$$\alpha_1 + ad - d > \frac{a\alpha_2 + d - ad - k(\alpha_1 + ad - d)}{a^2 - k} > 0, \tag{5}$$

or equivalently,

$$\beta_1 + bd - d > \frac{b\beta_2 + d - bd - b^2(\beta_1 + bd - d)}{k - b^2} > 0. \tag{6}$$

First, since $b < 1$, we have $\beta_2 - b\beta_1 > 0$, and

$$b\beta_2 + d - bd - b^2(\beta_1 + bd - d) = b(\beta_2 - b\beta_1) + d(1 - b) + b^2 d(1 - b) > 0,$$

for all $d \geq 0$. Next, we shall find the condition under which the left inequalities of (5) and (6) hold. These inequalities are equivalent to $G(d) > 0$ and $F(d) > 0$ respectively, where

$$F(d) := d(1 + a^2)(a - 1) + \alpha_1 a^2 - \alpha_2 a,$$
$$G(d) := k(\beta_1 + bd - d) + bd - d - \beta_2 b.$$

Let us study the property for functions F and G. Note that

$$F(d) = \frac{a^2 - k}{k - b^2} G(d).$$

We claim that $G'(d) < 0$, for all $d > 0$. Indeed, since $b = \frac{-\sigma_1 + \sqrt{\sigma_1^2 + 4kd^2}}{2d}$, $k = \frac{\sigma_1}{\sigma_2}$, we have

$$b' = b'(d) = \frac{\sigma_1 b}{d\sqrt{\sigma_1^2 + 4kd^2}} > 0.$$

We then compute

$$\begin{aligned} G'(d) &= k(b'd + b - 1) + (b'd + b - 1) - \beta_2 b' \\ &= (k + 1)(b'd + b - 1) - \beta_2 b' \\ &= (k + 1)\left(\frac{\sigma_1 b}{\sqrt{\sigma_1^2 + 4kd^2}} + b - 1\right) - \beta_2 b' \\ &= (k + 1)\left(\frac{2kd}{\sqrt{\sigma_1^2 + 4kd^2}} - 1\right) - \beta_2 b' \\ &< 0. \end{aligned}$$

Next, we show that

$$F(d) > 0, \quad \text{for all} \quad d \leq \frac{\alpha_1 \alpha_2 \sigma_1 \sigma_2}{\alpha_2^2 \sigma_2 - \alpha_1^2 \sigma_1},$$
$$G(d) < 0, \quad \text{for all} \quad d \geq \frac{\beta_1 \beta_2 \sigma_1 \sigma_2}{\beta_2^2 \sigma_2 - \beta_1^2 \sigma_1}.$$

We consider $b \leq \frac{\alpha_1 k}{\alpha_2}$, then $a = \frac{k}{b} \geq \frac{\alpha_2}{\alpha_1} > 1$ and

$$\begin{aligned} F(d) &= d(1 + a^2)(a - 1) + \alpha_1 a^2 - \alpha_2 a \\ &= d(1 + a^2)(a - 1) + a(\alpha_1 a - \alpha_2) \\ &> 0. \end{aligned}$$

Note that

$$b = \frac{-\sigma_1 + \sqrt{\sigma_1^2 + 4kd^2}}{2d} \leq \frac{\alpha_1 k}{\alpha_2}$$

is equivalent to

$$\frac{\sqrt{\sigma_1^2 + 4kd^2}}{2d} \leq \frac{\sigma_1}{2d} + \frac{\alpha_1 k}{\alpha_2},$$

and
$$d \le \frac{\alpha_1\alpha_2\sigma_1\sigma_2}{\alpha_2^2\sigma_2 - \alpha_1^2\sigma_1}.$$
On the other hand, considering $b \ge \frac{\beta_1 k}{\beta_2}$ and using $b < 1$, we have
$$\begin{aligned} G(d) &= k(\beta_1 + bd - d) + bd - d - \beta_2 b \\ &= kd(b-1) + d(b-1) + \beta_1 k - \beta_2 b \\ &< 0. \end{aligned}$$
Note that
$$b = \frac{-\sigma_1 + \sqrt{\sigma_1^2 + 4kd^2}}{2d} \ge \frac{\beta_1 k}{\beta_2}$$
is equivalent to
$$\frac{\sqrt{\sigma_1^2 + 4kd^2}}{2d} \ge \frac{\sigma_1}{2d} + \frac{\beta_1 k}{\beta_2},$$
and
$$d \ge \frac{\beta_1\beta_2\sigma_1\sigma_2}{\beta_2^2\sigma_2 - \beta_1^2\sigma_1}.$$
We thus conclude that the system must have a positive equilibrium when
$$d \le \frac{\alpha_1\alpha_2\sigma_1\sigma_2}{\alpha_2^2\sigma_2 - \alpha_1^2\sigma_1},$$
and has no positive equilibrium when
$$d \ge \frac{\beta_1\beta_2\sigma_1\sigma_2}{\beta_2^2\sigma_2 - \beta_1^2\sigma_1}.$$
Since $G'(d) < 0$ for all $d > 0$, we can deduce that there is a unique point d^* with
$$\frac{\alpha_1\alpha_2\sigma_1\sigma_2}{\alpha_2^2\sigma_2 - \alpha_1^2\sigma_1} < d^* < \frac{\beta_1\beta_2\sigma_1\sigma_2}{\beta_2^2\sigma_2 - \beta_1^2\sigma_1}$$
such that $F(d^*) = G(d^*) = 0$. This completes the proof. □

Corollary 3.5. *If $\sigma_1 = \sigma_2 = \sigma$ in condition* (H)*, then d^* can be computed exactly as*
$$d^* = \frac{(\alpha_2^2 - \alpha_1^2) - \sqrt{(\alpha_2^2 - \alpha_1^2)^2 - 16\beta_1\beta_2\sigma(\beta_2 - \alpha_1)}}{8(\beta_2 - \alpha_1)}.$$

Proof. If $\sigma_1 = \sigma_2 = \sigma$, then $ab = 1, a > 1 > b$, and
$$a = \frac{\sigma + \sqrt{\sigma^2 + 4d^2}}{2d}\ , b = \frac{-\sigma + \sqrt{\sigma^2 + 4d^2}}{2d}.$$
By argument similar to above, we have
$$u_1^* = \frac{a\alpha_2 + 2d - 2ad - \alpha_1}{a^2 - 1},\ v_1^* = \alpha_1 + ad - d - u_1^*.$$
or
$$u_1^* = \frac{b\beta_2 + d - bd - b^2(\beta_1 + bd - d)}{1 - b^2},\ v_1^* = \beta_1 + bd - d - u_1^*.$$
The consistency can be verified as
$$\frac{a\alpha_2 + 2d - 2ad - \alpha_1}{a^2 - 1} = \frac{b\beta_2 + d - bd - b^2(\beta_1 + bd - d)}{1 - b^2},$$

and $\alpha_1 + ad - d = \beta_1 + bd - d$. Hence, the unique positive equilibrium exists for system (1) if and only if

$$\alpha_1 + ad - d > \frac{a\alpha_2 + 2d - 2ad - \alpha_1}{a^2 - 1} > 0, \tag{7}$$

or equivalently

$$\beta_1 + bd - d > \frac{b\beta_2 + d - bd - b^2(\beta_1 + bd - d)}{1 - b^2} > 0. \tag{8}$$

The left inequalities of (7) and (8) are equivalent to $G(d) > 0$ and $F(d) > 0$, where

$$F(d) := d(1 + a^2)(a - 1) + \alpha_1 a^2 - \alpha_2 a \quad \text{and} \quad G(d) := 2bd - 2d - \beta_2 b + \beta_1.$$

Notice that

$$F(d) = \frac{a^2 - 1}{1 - b^2} G(d).$$

We claim that $G'(d) < 0$, for all $d > 0$. With $b = \frac{-\sigma + \sqrt{\sigma^2 + 4d^2}}{2d}$, we compute

$$b' = b'(d) = \frac{b\sigma}{d\sqrt{\sigma^2 + 4d^2}} > 0,$$

and

$$\begin{aligned} G'(d) &= 2(b'd + b - 1) - \beta_2 b' \\ &= 2\Big(\frac{\sigma b}{\sqrt{\sigma^2 + 4d^2}} + b - 1\Big) - \beta_2 b' \\ &= 2\Big(\frac{2d}{\sqrt{\sigma^2 + 4d^2}} - 1\Big) - \beta_2 b' \\ &< 0. \end{aligned}$$

Now, let us solve $G(d) = 0$, i.e.,

$$\begin{aligned} 0 &= 2bd - 2d - b\beta_2 + \beta_1 \\ &= \frac{2d(-\sigma + \sqrt{\sigma^2 + 4d^2}) - 4d^2 - \beta_2(-\sigma + \sqrt{\sigma^2 + 4d^2}) + 2\beta_1 d}{2d}. \end{aligned}$$

Since $d > 0$, we consider

$$2d(-\sigma + \sqrt{\sigma^2 + 4d^2}) - 4d^2 - \beta_2(-\sigma + \sqrt{\sigma^2 + 4d^2}) + 2\beta_1 d = 0,$$

i.e.,

$$(-2d\sigma - 4d^2 + \beta_2\sigma + 2\beta_1 d)^2 = (\beta_2 - 2d)^2(\sigma^2 + 4d^2),$$

and

$$4(\beta_2 - \alpha_1)d^2 + (\alpha_1^2 - \alpha_2^2)d + \beta_1\beta_2\sigma = 0.$$

Therefore, there are two roots

$$d_{\pm} = \frac{(\alpha_2^2 - \alpha_1^2) \pm \sqrt{(\alpha_2^2 - \alpha_1^2)^2 - 16\beta_1\beta_2\sigma(\beta_2 - \alpha_1)}}{8(\beta_2 - \alpha_1)}.$$

Actually, the graph of $G(d)$ only intersects d-axis at one point. Hence, the only solution to equation $G(d) = 0$ is

$$d^* := d_- = \frac{(\alpha_2^2 - \alpha_1^2) - \sqrt{(\alpha_2^2 - \alpha_1^2)^2 - 16\beta_1\beta_2\sigma(\beta_2 - \alpha_1)}}{8(\beta_2 - \alpha_1)}.$$

This completes the proof. □

Note that $(u_1^*, u_2^*, v_1^*, v_2^*)$ is a positive equilibrium of system (1) if and only if $(u_1^*, u_2^*, v_1^*, v_2^*)$ satisfies

$$\begin{aligned} \alpha_1 - u_1^* - v_1^* &= -d\left(\frac{u_2^*}{u_1^*} - 1\right), \quad \alpha_2 - u_2^* - v_2^* = -d\left(\frac{u_1^*}{u_2^*} - 1\right), \\ \beta_1 - u_1^* - v_1^* &= -d\left(\frac{v_2^*}{v_1^*} - 1\right), \quad \beta_2 - u_2^* - v_2^* = -d\left(\frac{v_1^*}{v_2^*} - 1\right). \end{aligned} \tag{9}$$

Remark 1. From the proof of Theorem 3.4, Corollary 3.5, and (9), we have actually obtained the following results.
(i) $a > 1$, and $u_2^* > u_1^*$.
(ii) $b < 1$, so $v_2^* < v_1^*$.
(iii) $u_2^* v_2^* \leq u_1^* v_1^*$. If $\sigma_1 = \sigma_2$, then $u_2^* v_2^* = u_1^* v_1^*$.
(iv) $d(u_2^* v_1^* - u_1^* v_2^*) = \sigma_2 u_2^* v_2^* = \sigma_1 u_1^* v_1^*$.
(v) $v_1^*, v_2^* \to 0$, as $d \to (d^*)^-$. That is, the positive equilibrium $(u_1^*, u_2^*, v_1^*, v_2^*)$ degenerates and merges into the semi-trivial equilibrium $(\overline{u}_1, \overline{u}_2, 0, 0)$ at $d = d^*$.

Corollary 3.6. *Under condition* (H)*, if $d < d^*$, then*

$$\alpha_1 < u_1^* + v_1^* < \beta_1 < \beta_2 < u_2^* + v_2^* < \alpha_2.$$

Proof. By Theorem 3.4, we have $u_2^* > u_1^*$ and $v_2^* < v_1^*$. From (9), we see that $\alpha_1 < u_1^* + v_1^* < \beta_1 < \beta_2 < u_2^* + v_2^* < \alpha_2$, if $d < d^*$. □

3.3. **Qualitative properties for semi-trivial equilibria.** The following two propositions provide some qualitative properties of the semi-trivial equilibria.

Proposition 3.7. *If $\alpha_1 < \alpha_2$, the following hold for all $d > 0$:*
(i) $\alpha_1 < \bar{u}_1 < \bar{u}_2 < \alpha_2$;
(ii) $(\alpha_1 - \bar{u}_1) - (\alpha_2 - \bar{u}_2) = \frac{d(\bar{u}_1^2 - \bar{u}_2^2)}{\bar{u}_1 \bar{u}_2} < 0$, $(\alpha_1 - \bar{u}_1) + (\alpha_2 - \bar{u}_2) = d\left[2 - \left(\frac{\bar{u}_2}{\bar{u}_1} + \frac{\bar{u}_1}{\bar{u}_2}\right)\right] < 0$;
(iii) $\alpha_1 < \bar{u}_1 < \frac{\alpha_1 + \alpha_2}{2} < \bar{u}_2 < \alpha_2$.

Proof. (i) We argue by contradiction. Suppose that $\bar{u}_1 \geq \bar{u}_2$. By the equations for $\bar{u}_i$, $i = 1, 2$, we have

$$\begin{cases} \bar{u}_1(\alpha_1 - \bar{u}_1) + d(\bar{u}_2 - \bar{u}_1) = 0 \\ \bar{u}_2(\alpha_2 - \bar{u}_2) + d(\bar{u}_1 - \bar{u}_2) = 0. \end{cases}$$

Hence, $\bar{u}_1 \leq \alpha_1$, as $\bar{u}_1(\alpha_1 - \bar{u}_1) = d(\bar{u}_1 - \bar{u}_2) \geq 0$, and $\bar{u}_2 \geq \alpha_2$, as $\bar{u}_2(\alpha_2 - \bar{u}_2) = d(\bar{u}_2 - \bar{u}_1) \leq 0$. Therefore, $\alpha_1 \geq \bar{u}_1 \geq \bar{u}_2 \geq \alpha_2$, which contradicts the assumption $\alpha_1 < \alpha_2$. Thus $\bar{u}_1 < \bar{u}_2$. Furthermore, $\alpha_1 < \bar{u}_1$ and $\bar{u}_2 < \alpha_2$. Therefore, $\alpha_1 < \bar{u}_1 < \bar{u}_2 < \alpha_2$.
(ii) By the equations of $\bar{u}_i$, $i = 1, 2$, we have

$$\begin{cases} \alpha_1 - \bar{u}_1 = d\left(1 - \frac{\bar{u}_2}{\bar{u}_1}\right) \\ \alpha_2 - \bar{u}_2 = d\left(1 - \frac{\bar{u}_1}{\bar{u}_2}\right). \end{cases}$$

Then

$$(\alpha_1 - \bar{u}_1) - (\alpha_2 - \bar{u}_2) = \frac{d(\bar{u}_1^2 - \bar{u}_2^2)}{\bar{u}_1 \bar{u}_2} < 0,$$

where the last inequality follows from $\bar{u}_1 < \bar{u}_2$. By the equations of $\bar{u}_i$ we also have

$$(\alpha_1 - \bar{u}_1) + (\alpha_2 - \bar{u}_2) = d\left[2 - \left(\frac{\bar{u}_2}{\bar{u}_1} + \frac{\bar{u}_1}{\bar{u}_2}\right)\right] < 0.$$

(iii) From (i), we only need to prove $\bar{u}_1 < \frac{\alpha_1+\alpha_2}{2}$ and $\frac{\alpha_1+\alpha_2}{2} < \bar{u}_2$. By (i) and (ii), $\alpha_1 + \alpha_2 < \bar{u}_1 + \bar{u}_2 < 2\bar{u}_2$. Hence $\frac{\alpha_1+\alpha_2}{2} < \bar{u}_2$. To prove $\bar{u}_1 < \frac{\alpha_1+\alpha_2}{2}$, we argue by contradiction. Suppose that $\bar{u}_1 \geq \frac{\alpha_1+\alpha_2}{2}$. Then, since function $z(z-\alpha_1)$ is monotone increasing for $z > \alpha_1/2$,

$$\bar{u}_1(\bar{u}_1 - \alpha_1) \geq \frac{\alpha_2^2 - \alpha_1^2}{4}. \tag{10}$$

Similarly, since $z(\alpha_2 - z)$ is monotone decreasing for $z > \alpha_2/2$,

$$\bar{u}_2(\alpha_2 - \bar{u}_2) < \frac{\alpha_2^2 - \alpha_1^2}{4}. \tag{11}$$

From the equations for $\bar{u}_i$ we have

$$\bar{u}_1(\alpha_1 - \bar{u}_1) + \bar{u}_2(\alpha_2 - \bar{u}_2) = 0,$$

which contradicts (10) and (11). □

The following proposition can be obtained by arguments similar to those for Proposition 3.7 .

Proposition 3.8. *If $\beta_1 < \beta_2$, the following hold for all $d > 0$:*
(i) $\beta_1 < \bar{v}_1 < \bar{v}_2 < \beta_2$;
(ii) $(\beta_1-\bar{v}_1)-(\beta_2-\bar{v}_2) = \frac{d(\bar{v}_1^2-\bar{v}_2^2)}{\bar{v}_1\bar{v}_2} < 0$, $(\beta_1-\bar{v}_1)+(\beta_2-\bar{v}_2) = d\left[2 - \left(\frac{\bar{v}_2}{\bar{v}_1} + \frac{\bar{v}_1}{\bar{v}_2}\right)\right] < 0$;
(iii) $\beta_1 < \bar{v}_1 < \frac{\beta_1+\beta_2}{2} < \bar{v}_2 < \beta_2$.

Note that for the special case $d = 0$, we have $\bar{u}_1 = \alpha_1$, $\bar{u}_2 = \alpha_2$, $\bar{v}_1 = \beta_1$ and $\bar{v}_2 = \beta_2$. The next two propositions are dependent of the size of dispersal rate d.

Proposition 3.9. *If $\alpha_1 < \alpha_2$, the following hold:*
(i) $\bar{u}_1, \bar{u}_2 \to \frac{\alpha_1+\alpha_2}{2}$ *as* $d \to \infty$;
(ii) *d is strictly decreasing with respect to $\bar{u}_2$ on $(\frac{\alpha_1+\alpha_2}{2}, \alpha_2)$, and d is strictly increasing with respect to $\bar{u}_1$ on $(\alpha_1, \frac{\alpha_1+\alpha_2}{2})$.*

Proof. (i) By the equations for $\bar{u}_i$, $i = 1, 2$, we have

$$\begin{aligned} \bar{u}_1(\alpha_1 - \bar{u}_1) + d(\bar{u}_2 - \bar{u}_1) = 0 \\ \bar{u}_2(\alpha_2 - \bar{u}_2) + d(\bar{u}_1 - \bar{u}_2) = 0. \end{aligned} \tag{12}$$

From (12), $\bar{u}_1$ and $\bar{u}_2$ satisfy

$$\bar{u}_2^2 - \alpha_2\bar{u}_2 - \alpha_1\bar{u}_1 + \bar{u}_1^2 = 0,$$

regardless of the value of d. It can be seen from (12) that $(\bar{u}_1 - \bar{u}_2) \to 0$ as $d \to \infty$. Thus $\bar{u}_1, \bar{u}_2 \to \frac{\alpha_1+\alpha_2}{2}$ as $d \to \infty$.
(ii) From Proposition 3.7, we have $\bar{u}_1 \in (\alpha_1, \frac{\alpha_1+\alpha_2}{2})$ and $\bar{u}_2 \in (\frac{\alpha_1+\alpha_2}{2}, \alpha_2)$. From (12), $\bar{u}_1$ and $\bar{u}_2$ satisfy

$$\bar{u}_1^2 - \alpha_1\bar{u}_1 + \bar{u}_2^2 - \alpha_2\bar{u}_2 = 0.$$

Let us solve for $\bar{u}_1$ as a function of $\bar{u}_2$:

$$\bar{u}_1 = \frac{\alpha_1 + \sqrt{\alpha_1^2 - 4\bar{u}_2^2 + 4\alpha_2\bar{u}_2}}{2}$$

since $0 < \alpha_1 < \bar{u}_1$ and $\bar{u}_2 < \alpha_2$. From (12), we can express d as a function of $\bar{u}_2$:

$$d = \frac{\bar{u}_2(\alpha_2 - \bar{u}_2)}{\bar{u}_2 - \bar{u}_1} = \frac{-\bar{u}_2^2 + \alpha_2\bar{u}_2}{\bar{u}_2 - \frac{\alpha_1+\sqrt{\alpha_1^2-4\bar{u}_2^2+4\alpha_2\bar{u}_2}}{2}} =: h(\bar{u}_2).$$

We claim that d is strictly decreasing with respect to $\bar{u}_2$ on $(\frac{\alpha_1+\alpha_2}{2}, \alpha_2)$. Direct calculation yields

$$\begin{aligned}
&h'(\bar{u}_2)\\
&= \Big[(-2\bar{u}_2+\alpha_2)\left(\bar{u}_2 - \left(\alpha_1 + \sqrt{\alpha_1^2 - 4\bar{u}_2^2 + 4\alpha_2\bar{u}_2}\right)/2\right) - \left(-\bar{u}_2^2 + \alpha_2\bar{u}_2\right)\cdot\\
&\left(1 - \frac{1}{4}\left(\alpha_1^2 - 4\bar{u}_2^2 + 4\alpha_2\bar{u}_2\right)^{-\frac{1}{2}}(-8\bar{u}_2 + 4\alpha_2)\right)\Big] / \left(\bar{u}_2 - \left(\alpha_1 + \sqrt{\alpha_1^2 - 4\bar{u}_2^2 + 4\alpha_2\bar{u}_2}\right)/2\right)^2\\
&= \Big[(-2\bar{u}_2+\alpha_2)\left(\bar{u}_2 - \left(\alpha_1 + \sqrt{\alpha_1^2 - 4\bar{u}_2^2 + 4\alpha_2\bar{u}_2}\right)/2\right) + \bar{u}_2(\bar{u}_2 - \alpha_2)\\
&+\bar{u}_2(-\bar{u}_2+\alpha_2)(-2\bar{u}_2+\alpha_2)\left(\alpha_1^2 - 4\bar{u}_2^2 + 4\alpha_2\bar{u}_2\right)^{-\frac{1}{2}}\Big] / \left(\bar{u}_2 - \left(\alpha_1 + \sqrt{\alpha_1^2 - 4\bar{u}_2^2 + 4\alpha_2\bar{u}_2}\right)/2\right)^2
\end{aligned}$$

Let us focus on the numerator. For the first term, we see that

$$(-2\bar{u}_2+\alpha_2)\left(\bar{u}_2 - \frac{\alpha_1+\sqrt{\alpha_1^2-4\bar{u}_2^2+4\alpha_2\bar{u}_2}}{2}\right) < 0,$$

on $(\frac{\alpha_1+\alpha_2}{2}, \alpha_2)$ since $\bar{u}_1 < \bar{u}_2$; for the second term,

$$\bar{u}_2(\bar{u}_2 - \alpha_2) < 0,$$

on $(\frac{\alpha_1+\alpha_2}{2}, \alpha_2)$; for the third term,

$$\bar{u}_2(-\bar{u}_2+\alpha_2)(-2\bar{u}_2+\alpha_2)\left(\alpha_1^2 - 4\bar{u}_2^2 + 4\alpha_2\bar{u}_2\right)^{-\frac{1}{2}} < 0,$$

on $(\frac{\alpha_1+\alpha_2}{2}, \alpha_2)$. Therefore, we obtain $h'(\bar{u}_2) < 0$ on $(\frac{\alpha_1+\alpha_2}{2}, \alpha_2)$. Namely, d is strictly decreasing with respect to $\bar{u}_2$ on $(\frac{\alpha_1+\alpha_2}{2}, \alpha_2)$. Next, we prove that d is strictly increasing with respect to $\bar{u}_1$ on $(\alpha_1, \frac{\alpha_1+\alpha_2}{2})$. From (12), $\bar{u}_1$ and $\bar{u}_2$ satisfy

$$\bar{u}_2^2 - \alpha_2\bar{u}_2 + \bar{u}_1^2 - \alpha_1\bar{u}_1 = 0.$$

Let us solve for $\bar{u}_2$ as a function of $\bar{u}_1$:

$$\bar{u}_2 = \frac{\alpha_2 + \sqrt{\alpha_2^2 - 4\bar{u}_1^2 + 4\alpha_1\bar{u}_1}}{2}$$

since $\alpha_1 < \bar{u}_1 < \bar{u}_2 < \alpha_2$. From (12), we can express d as a function of $\bar{u}_1$:

$$d = \frac{-\bar{u}_1^2 + \alpha_1\bar{u}_1}{\bar{u}_1 - \frac{\alpha_2+\sqrt{\alpha_2^2-4\bar{u}_1^2+4\alpha_1\bar{u}_1}}{2}} =: \tilde{g}(\bar{u}_1).$$

A direct calculation yields

$$\begin{aligned}
\tilde{g}'(\bar{u}_1) &= \frac{(-2\bar{u}_1+\alpha_1)\left(\bar{u}_1 - \frac{\alpha_2+\sqrt{\alpha_2^2-4\bar{u}_1^2+4\alpha_1\bar{u}_1}}{2}\right) - \left(-\bar{u}_1^2+\alpha_1\bar{u}_1\right)\left[1-\frac{1}{4}\left(\alpha_2^2-4\bar{u}_1^2+4\alpha_1\bar{u}_1\right)^{-\frac{1}{2}}(-8\bar{u}_1+4\alpha_1)\right]}{\left(\bar{u}_1 - \frac{\alpha_2+\sqrt{\alpha_2^2-4\bar{u}_1^2+4\alpha_1\bar{u}_1}}{2}\right)^2}\\
&= \frac{(-2\bar{u}_1+\alpha_1)\left(\bar{u}_1 - \frac{\alpha_2+\sqrt{\alpha_2^2-4\bar{u}_1^2+4\alpha_1\bar{u}_1}}{2}\right) + \bar{u}_1(\bar{u}_1-\alpha_1) + \left(-\bar{u}_1^2+\alpha_1\bar{u}_1\right)(-2\bar{u}_1+\alpha_1)\left(\alpha_2^2-4\bar{u}_1^2+4\alpha_1\bar{u}_1\right)^{-\frac{1}{2}}}{\left(\bar{u}_1 - \frac{\alpha_2+\sqrt{\alpha_2^2-4\bar{u}_1^2+4\alpha_1\bar{u}_1}}{2}\right)^2}.
\end{aligned}$$

Let us focus on the numerator. Every term is positive for $\bar{u}_1$ between α_1 and $\frac{\alpha_1+\alpha_2}{2}$. Thus we obtain $\tilde{g}'(\bar{u}_1) > 0$ on $(\alpha_1, \frac{\alpha_1+\alpha_2}{2})$. Namely, d is strictly increasing with respect to $\bar{u}_1$ on $(\alpha_1, \frac{\alpha_1+\alpha_2}{2})$. □

The following proposition can be obtained by arguments similar to those for Proposition 3.9.

Proposition 3.10. *If $\beta_1 < \beta_2$, the following hold:*
(i) $\bar{v}_1, \bar{v}_2 \to \frac{\beta_1+\beta_2}{2}$ *as* $d \to \infty$*;*
(ii) d *is strictly decreasing with respect to* $\bar{v}_2$ *on* $(\frac{\beta_1+\beta_2}{2}, \beta_2)$*, and* d *is strictly increasing with respect to* $\bar{v}_1$ *on* $(\beta_1, \frac{\beta_1+\beta_2}{2})$*.*

3.4. **Stability analysis of the semi-trivial equilibria.** In Subsection 3.1, we have derived the Jacobian matrix for system (1). At $(\bar{u}_1, \bar{u}_2, 0, 0)$, the Jacobian matrix is

$$\begin{bmatrix} \alpha_1 - 2\bar{u}_1 - d & d & -\bar{u}_1 & 0 \\ d & \alpha_2 - 2\bar{u}_2 - d & 0 & -\bar{u}_2 \\ 0 & 0 & \beta_1 - \bar{u}_1 - d & d \\ 0 & 0 & d & \beta_2 - \bar{u}_2 - d \end{bmatrix}, \tag{13}$$

and at $(0, 0, \bar{v}_1, \bar{v}_2)$, the Jacobian matrix is

$$\begin{bmatrix} \alpha_1 - \bar{v}_1 - d & d & 0 & 0 \\ d & \alpha_2 - \bar{v}_2 - d & 0 & 0 \\ -\bar{v}_1 & 0 & \beta_1 - 2\bar{v}_1 - d & d \\ 0 & -\bar{v}_2 & d & \beta_2 - 2\bar{v}_2 - d \end{bmatrix}.$$

First, let us focus on the semi-trivial equilibrium $(0, 0, \bar{v}_1, \bar{v}_2)$.

Proposition 3.11. *Under condition* (H)*, the semi-trivial equilibrium* $(0, 0, \bar{v}_1, \bar{v}_2)$ *is unstable in system* (1) *for any* $d > 0$*.*

Proof. It can be computed that the two eigenvalues of matrix

$$\begin{bmatrix} \beta_1 - 2\bar{v}_1 - d & d \\ d & \beta_2 - 2\bar{v}_2 - d \end{bmatrix}$$

are negative, under condition (H). The instability of $(0, 0, \bar{v}_1, \bar{v}_2)$ is determined by the sign of the larger eigenvalue (denoted by λ_+) of

$$d(\varphi_2 - \varphi_1) + \varphi_1(\alpha_1 - \bar{v}_1) = \lambda\varphi_1,$$
$$d(\varphi_1 - \varphi_2) + \varphi_2(\alpha_2 - \bar{v}_2) = \lambda\varphi_2.$$

By a direct calculation,

$$\lambda_+ = \frac{1}{2}\left[(\alpha_1 - \bar{v}_1 + \alpha_2 - \bar{v}_2 - 2d) + \sqrt{(\alpha_1 - \bar{v}_1 - \alpha_2 + \bar{v}_2)^2 + 4d^2}\right].$$

If $\alpha_1 - \bar{v}_1 + \alpha_2 - \bar{v}_2 - 2d \geq 0$, then λ_+ is already positive for all $d > 0$. If $\alpha_1 - \bar{v}_1 + \alpha_2 - \bar{v}_2 - 2d < 0$, then we claim that $\lambda_+ > 0$ for all $d > 0$. If not,

$$-(\alpha_1 - \bar{v}_1 + \alpha_2 - \bar{v}_2 - 2d) \geq \sqrt{(\alpha_1 - \bar{v}_1 - \alpha_2 + \bar{v}_2)^2 + 4d^2}$$

for some $d > 0$. A direct calculation yields

$$(\alpha_1 - \bar{v}_1)(\alpha_2 - \bar{v}_2) - d(\alpha_1 - \bar{v}_1 + \alpha_2 - \bar{v}_2) \geq 0.$$

Since $\alpha_1 = \beta_1 - \sigma_1$ and $\alpha_2 = \beta_2 + \sigma_2$, we have

$$(\beta_1 - \bar{v}_1 - \sigma_1)(\beta_2 - \bar{v}_2 + \sigma_2) - d(\beta_1 - \bar{v}_1 + \beta_2 - \bar{v}_2 + \sigma_2 - \sigma_1) \geq 0.$$

Then

$$\left[d\left(1 - \frac{\bar{v}_2}{\bar{v}_1}\right) - \sigma_1\right]\left[d\left(1 - \frac{\bar{v}_1}{\bar{v}_2}\right) + \sigma_2\right] - d^2\left[2 - \left(\frac{\bar{v}_2}{\bar{v}_1} + \frac{\bar{v}_1}{\bar{v}_2}\right)\right] - d(\sigma_2 - \sigma_1) \geq 0,$$

by the equations for $\bar{v}_i$, $i = 1, 2$ and Proposition 3.8(ii). But then

$$\sigma_2 d\left(1 - \frac{\bar{v}_2}{\bar{v}_1}\right) - \sigma_1 d\left(1 - \frac{\bar{v}_1}{\bar{v}_2}\right) - \sigma_2\sigma_1 - d(\sigma_2 - \sigma_1) \geq 0$$

is a contradiction, as the left-hand side of the inequality is negative, due to $\bar{v}_1 < \bar{v}_2$ and $0 < \sigma_1 \le \sigma_2$. Therefore, $\lambda_+ > 0$ for all $d > 0$.

For the special case $\sigma_1 = \sigma_2 = \sigma$, we can provide another argument. Since $\alpha_1 = \beta_1 - \sigma$ and $\alpha_2 = \beta_2 + \sigma$, we have

$$\lambda_+ = \frac{1}{2}\left[(\beta_1 - \bar{v}_1 + \beta_2 - \bar{v}_2 - 2d) + \sqrt{(\beta_1 - \bar{v}_1 - \beta_2 + \bar{v}_2 - 2\sigma)^2 + 4d^2}\right].$$

Hence, for any $\sigma \ge 0$,

$$\frac{\partial \lambda_+}{\partial \sigma} = \frac{2\sigma - \beta_1 + \beta_2 + \bar{v}_1 - \bar{v}_2}{\sqrt{(\beta_1 - \bar{v}_1 - \beta_2 + \bar{v}_2 - 2\sigma)^2 + 4d^2}} \ge \frac{-\beta_1 + \beta_2 + \bar{v}_1 - \bar{v}_2}{\sqrt{(\beta_1 - \bar{v}_1 - \beta_2 + \bar{v}_2 - 2\sigma)^2 + 4d^2}}.$$

Hence, by Proposition 3.8(ii), we have

$$\frac{\partial \lambda_+}{\partial \sigma} \ge 0, \text{ for all } \sigma \ge 0.$$

By the equation for $\bar{v}_i$, $i = 1, 2$, we know $\lambda_+ = 0$ at $\sigma = 0$. Hence, $\lambda_+ > 0$ for any $\sigma > 0$.

As for the other eigenvalue

$$\lambda_- = \frac{1}{2}\left[(\alpha_1 - \bar{v}_1 + \alpha_2 - \bar{v}_2 - 2d) - \sqrt{(\alpha_1 - \bar{v}_1 - \alpha_2 + \bar{v}_2)^2 + 4d^2}\right],$$

similar computation shows that $\lambda_- < 0$ for any $d > 0$. This completes the proof. ☐

Next, we study the stability of $(\bar{u}_1, \bar{u}_2, 0, 0)$, by calculating the eigenvalues of the two 2×2 Jacobian matrices obtained from (13):

$$\begin{bmatrix} \alpha_1 - 2\bar{u}_1 - d & d \\ d & \alpha_2 - 2\bar{u}_2 - d \end{bmatrix} \text{ and } \begin{bmatrix} \beta_1 - \bar{u}_1 - d & d \\ d & \beta_2 - \bar{u}_2 - d \end{bmatrix}. \tag{14}$$

Proposition 3.12. *Under condition* (H)*, there exists a $\bar{d} > 0$ so that the semi-trivial equilibrium $(\bar{u}_1, \bar{u}_2, 0, 0)$ is asymptotically stable if $d > \bar{d}$, and unstable if $d < \bar{d}$, in system* (1)*; in addition,*

$$\frac{\alpha_1\alpha_2\sigma_1\sigma_2}{\alpha_2^2\sigma_2 - \alpha_1^2\sigma_1} < \bar{d} < \frac{\beta_1\beta_2\sigma_1\sigma_2}{\beta_2^2\sigma_2 - \beta_1^2\sigma_1}.$$

Proof. First, we calculate the eigenvalues of the first matrix in (14), i.e., we solve for λ in

$$d(\varphi_2 - \varphi_1) + \varphi_1(\alpha_1 - 2\bar{u}_1) = \lambda\varphi_1,$$
$$d(\varphi_1 - \varphi_2) + \varphi_2(\alpha_2 - 2\bar{u}_2) = \lambda\varphi_2.$$

By a direct calculation, the two roots are

$$\lambda_{1,2} = \frac{1}{2}\left[(\alpha_1 - 2\bar{u}_1 + \alpha_2 - 2\bar{u}_2 - 2d) \mp \sqrt{(\alpha_1 - 2\bar{u}_1 - \alpha_2 + 2\bar{u}_2)^2 + 4d^2}\right].$$

Note that $\alpha_1 - 2\bar{u}_1 + \alpha_2 - 2\bar{u}_2 - 2d < 0$, by Proposition 3.7(ii). Thus,

$$\lambda_1 = \frac{1}{2}\left[(\alpha_1 - 2\bar{u}_1 + \alpha_2 - 2\bar{u}_2 - 2d) - \sqrt{(\alpha_1 - 2\bar{u}_1 - \alpha_2 + 2\bar{u}_2)^2 + 4d^2}\right] < 0.$$

On the other hand,

$$\begin{aligned}
&(\alpha_1 - 2\bar{u}_1 + \alpha_2 - 2\bar{u}_2 - 2d) + \sqrt{(\alpha_1 - 2\bar{u}_1 - \alpha_2 + 2\bar{u}_2)^2 + 4d^2} \\
&\le (\alpha_1 - 2\bar{u}_1 + \alpha_2 - 2\bar{u}_2 - 2d) + |\alpha_1 - 2\bar{u}_1 - \alpha_2 + 2\bar{u}_2| + 2d \\
&\le 2(\alpha_1 - 2\bar{u}_1) \\
&= 2(\alpha_1 - \bar{u}_1) - 2\bar{u}_1 \\
&< 0,
\end{aligned}$$

if $\alpha_1 - 2\bar{u}_1 - \alpha_2 + 2\bar{u}_2 \geq 0$, by Proposition 3.7(i). If $\alpha_1 - 2\bar{u}_1 - \alpha_2 + 2\bar{u}_2 < 0$, then

$$\begin{aligned}&(\alpha_1 - 2\bar{u}_1 + \alpha_2 - 2\bar{u}_2 - 2d) + \sqrt{(\alpha_1 - 2\bar{u}_1 - \alpha_2 + 2\bar{u}_2)^2 + 4d^2}\\ &\leq 2(\alpha_2 - 2\bar{u}_2)\\ &< 0,\end{aligned}$$

by Proposition 3.7(iii). Thus, $\lambda_2 < 0$. Notably, the signs of eigenvalues $\lambda_{1,2}$ are independent of the size of dispersal rate d. Therefore, we obtain $\lambda_{1,2} < 0$ for $d > 0$.

Next, we calculate the eigenvalues of the second matrix in (14), which satisfy

$$\begin{aligned}d(\varphi_2 - \varphi_1) + \varphi_1(\beta_1 - \bar{u}_1) = \lambda\varphi_1,\\ d(\varphi_1 - \varphi_2) + \varphi_2(\beta_2 - \bar{u}_2) = \lambda\varphi_2.\end{aligned}$$

By a direct calculation, the two eigenvalues are

$$\lambda_{3,4} = \frac{1}{2}\left[(\beta_1 - \bar{u}_1 + \beta_2 - \bar{u}_2 - 2d) \mp \sqrt{(\beta_1 - \bar{u}_1 - \beta_2 + \bar{u}_2)^2 + 4d^2}\right].$$

Since $\alpha_1 = \beta_1 - \sigma_1$ and $\alpha_2 = \beta_2 + \sigma_2$, we have

$$\beta_1 - \bar{u}_1 + \beta_2 - \bar{u}_2 - 2d = \alpha_1 - \bar{u}_1 + \alpha_2 - \bar{u}_2 - (\sigma_2 - \sigma_1) - 2d < 0,$$

by Proposition 3.7(ii). Hence,

$$\lambda_3 = \frac{1}{2}\left[(\beta_1 - \bar{u}_1 + \beta_2 - \bar{u}_2 - 2d) - \sqrt{(\beta_1 - \bar{u}_1 - \beta_2 + \bar{u}_2)^2 + 4d^2}\right] < 0,$$

for $d > 0$. The following calculation focuses on the sign of the eigenvalue λ_4. Consider

$$\lambda_4 = \lambda_4(d) := (\beta_1 - \bar{u}_1 + \beta_2 - \bar{u}_2 - 2d) + \sqrt{(\beta_1 - \bar{u}_1 - \beta_2 + \bar{u}_2)^2 + 4d^2}.$$

Note that $(\beta_1 - \bar{u}_1 + \beta_2 - \bar{u}_2 - 2d) < 0$, and $\lambda_4(d) \geq 0$ if and only if

$$(\beta_1 - \bar{u}_1)(\beta_2 - \bar{u}_2) - d(\beta_1 - \bar{u}_1 + \beta_2 - \bar{u}_2) \leq 0. \tag{15}$$

Since $\alpha_1 = \beta_1 - \sigma_1$ and $\alpha_2 = \beta_2 + \sigma_2$, (15) is equivalent to

$$(\alpha_1 - \bar{u}_1 + \sigma_1)(\alpha_2 - \bar{u}_2 - \sigma_2) - d(\alpha_1 - \bar{u}_1 + \alpha_2 - \bar{u}_2 - (\sigma_2 - \sigma_1)) \leq 0;$$

i.e.,

$$\left[d\left(1 - \frac{\bar{u}_2}{\bar{u}_1}\right) + \sigma_1\right]\left[d\left(1 - \frac{\bar{u}_1}{\bar{u}_2}\right) - \sigma_2\right] - d^2\left[2 - \left(\frac{\bar{u}_2}{\bar{u}_1} + \frac{\bar{u}_1}{\bar{u}_2}\right)\right] + d(\sigma_2 - \sigma_1) \leq 0,$$

by Proposition 3.7(ii). This inequality is simplified to

$$d\left(\sigma_2\frac{\bar{u}_2}{\bar{u}_1} - \sigma_1\frac{\bar{u}_1}{\bar{u}_2}\right) \leq \sigma_1\sigma_2. \tag{16}$$

Now from (16) and the equations for $\bar{u}_i$:

$$\begin{aligned}\bar{u}_1(\alpha_1 - \bar{u}_1) + d(\bar{u}_2 - \bar{u}_1) = 0\\ \bar{u}_2(\alpha_2 - \bar{u}_2) + d(\bar{u}_1 - \bar{u}_2) = 0,\end{aligned} \tag{17}$$

we have

$$\sigma_1\bar{u}_2 - \sigma_2\bar{u}_1 - d(\sigma_2 - \sigma_1) \geq \sigma_1\alpha_2 - \sigma_2\alpha_1 - \sigma_1\sigma_2. \tag{18}$$

When the equality in (18) holds, the solution $(\bar{u}_1, \bar{u}_2)$ of (17) satisfies

$$\bar{u}_1 = \frac{\sigma_1\alpha_1 + d(\sigma_2 - \sigma_1) \pm \sqrt{[\sigma_1\alpha_1 + d(\sigma_2 - \sigma_1)]^2 + 4\sigma_1 d[\sigma_1\alpha_2 - \sigma_2\alpha_1 + d(\sigma_2 - \sigma_1) - \sigma_1\sigma_2]}}{2\sigma_1},$$

$$\bar{u}_2 = \frac{\sigma_2\alpha_2 - d(\sigma_2 - \sigma_1) \pm \sqrt{[\sigma_2\alpha_2 - d(\sigma_2 - \sigma_1)]^2 - 4\sigma_2 d[\sigma_1\alpha_2 - \sigma_2\alpha_1 + d(\sigma_2 - \sigma_1) - \sigma_1\sigma_2]}}{2\sigma_2}.$$

Since $0 < \alpha_1 < \bar{u}_1$ and $\frac{\alpha_1+\alpha_2}{2} < \bar{u}_2 < \alpha_2$, we choose

$$\bar{u}_1 = \frac{\sigma_1\alpha_1 + d(\sigma_2-\sigma_1) + \sqrt{[\sigma_1\alpha_1 + d(\sigma_2-\sigma_1)]^2 + 4\sigma_1 d[\sigma_1\alpha_2 - \sigma_2\alpha_1 + d(\sigma_2-\sigma_1) - \sigma_1\sigma_2]}}{2\sigma_1},$$

$$\bar{u}_2 = \frac{\sigma_2\alpha_2 - d(\sigma_2-\sigma_1) + \sqrt{[\sigma_2\alpha_2 - d(\sigma_2-\sigma_1)]^2 - 4\sigma_2 d[\sigma_1\alpha_2 - \sigma_2\alpha_1 + d(\sigma_2-\sigma_1) - \sigma_1\sigma_2]}}{2\sigma_2}.$$

From (18), we define

$$g(d) := [\sigma_1\bar{u}_2(d) - \sigma_2\bar{u}_1(d) - d(\sigma_2-\sigma_1)] - [\sigma_1\alpha_2 - \sigma_2\alpha_1 - \sigma_1\sigma_2]. \tag{19}$$

If $d = 0$, then $\bar{u}_1 = \alpha_1$ and $\bar{u}_2 = \alpha_2$, and $g(d) = \sigma_1\sigma_2 > 0$. Recall that $\alpha_1 < \bar{u}_1 < \frac{\alpha_1+\alpha_2}{2} < \bar{u}_2 < \alpha_2$ in Proposition 3.7(iii), and d is strictly decreasing with respect to $\bar{u}_2$ on $(\frac{\alpha_1+\alpha_2}{2}, \alpha_2)$, and d is strictly increasing with respect to $\bar{u}_1$ on $(\alpha_1, \frac{\alpha_1+\alpha_2}{2})$, by Proposition 3.9. Thus, $\sigma_1\bar{u}_2(d) - \sigma_2\bar{u}_1(d)$ is a strictly decreasing function of d. Accordingly, $g(d)$ is a strictly decreasing function of d and there is a unique $\bar{d} > 0$ such that $g(\bar{d}) = 0$. More precisely,

$$\begin{cases} g(d) > 0, & \text{if } d < \bar{d} \\ g(d) = 0, & \text{if } d = \bar{d} \\ g(d) < 0, & \text{if } d > \bar{d}, \end{cases}$$

correspondingly,

$$\begin{cases} \lambda_4 > 0, & \text{if } d < \bar{d} \\ \lambda_4 = 0, & \text{if } d = \bar{d} \\ \lambda_4 < 0, & \text{if } d > \bar{d}. \end{cases}$$

Unfortunately, it is very difficult to find the exact value of $\bar{d}$. Here, we shall estimate the range of $\bar{d}$. From Proposition 3.7(iii) and Proposition 3.9, we know $\frac{\bar{u}_2(d)}{\bar{u}_1(d)} < \frac{\alpha_2}{\alpha_1}$, and $\frac{\bar{u}_2(d)}{\bar{u}_1(d)}$ is a strictly decreasing function of d. Moreover, $g(d) < -\sigma_1\sigma_2 - d(\sigma_2 - \sigma_1) < 0$ when $\bar{u}_1(d) = \beta_1$ and $\bar{u}_2(d) = \beta_2$. We consider $\frac{\beta_2}{\beta_1} < \frac{\bar{u}_2(d)}{\bar{u}_1(d)} < \frac{\alpha_2}{\alpha_1}$. By (16),

$$d = \frac{\alpha_1\alpha_2\sigma_1\sigma_2}{\alpha_2^2\sigma_2 - \alpha_1^2\sigma_1}, \text{ when } \frac{\bar{u}_2(d)}{\bar{u}_1(d)} = \frac{\alpha_2}{\alpha_1},$$
$$d = \frac{\beta_1\beta_2\sigma_1\sigma_2}{\beta_2^2\sigma_2 - \beta_1^2\sigma_1}, \text{ when } \frac{\bar{u}_2(d)}{\bar{u}_1(d)} = \frac{\beta_2}{\beta_1}.$$

Hence,

$$\frac{\alpha_1\alpha_2\sigma_1\sigma_2}{\alpha_2^2\sigma_2 - \alpha_1^2\sigma_1} < \bar{d} < \frac{\beta_1\beta_2\sigma_1\sigma_2}{\beta_2^2\sigma_2 - \beta_1^2\sigma_1}.$$

Therefore, we obtain $\lambda_4 > 0$ if $d < \bar{d}$, and $\lambda_4 \leq 0$ if $d \geq \bar{d}$, where

$$\frac{\alpha_1\alpha_2\sigma_1\sigma_2}{\alpha_2^2\sigma_2 - \alpha_1^2\sigma_1} < \bar{d} < \frac{\beta_1\beta_2\sigma_1\sigma_2}{\beta_2^2\sigma_2 - \beta_1^2\sigma_1}.$$

Therefore, we conclude that at the semi-trivial equilibrium $(\bar{u}_1, \bar{u}_2, 0, 0)$, the four eigenvalues of the Jacobian matrix are $\lambda_1, \lambda_2, \lambda_3 < 0$ for all $d > 0$, and $\lambda_4 > 0$ if $d < \bar{d}$, $\lambda_4 = 0$ if $d = \bar{d}$, and $\lambda_4 < 0$ if $d > \bar{d}$. □

Corollary 3.13. *If* $\sigma_1 = \sigma_2 = \sigma$ *in condition* (H), *then* $\bar{d}$ *can be computed exactly as*

$$\bar{d} = \frac{(\alpha_2^2 - \alpha_1^2) - \sqrt{(\alpha_2^2 - \alpha_1^2)^2 - 16\beta_1\beta_2\sigma(\beta_2 - \alpha_1)}}{8(\beta_2 - \alpha_1)}.$$

Proof. As $\sigma_1 = \sigma_2 = \sigma$, (16) reduces to

$$d\left(\frac{\bar{u}_2}{\bar{u}_1} - \frac{\bar{u}_1}{\bar{u}_2}\right) \le \sigma,$$

and (18) reduces to

$$\bar{u}_2 - \bar{u}_1 \ge \beta_2 - \alpha_1. \tag{20}$$

In addition, $\bar{u}_1$ and $\bar{u}_2$ reduce to

$$\bar{u}_1 = \frac{\alpha_1 + \sqrt{\alpha_1^2 + 4d(\beta_2 - \alpha_1)}}{2}, \; \bar{u}_2 = \frac{\alpha_2 + \sqrt{\alpha_2^2 - 4d(\beta_2 - \alpha_1)}}{2}. \tag{21}$$

From (20), we define

$$h(d) := (\bar{u}_2(d) - \bar{u}_1(d)) - (\beta_2 - \alpha_1).$$

In particular, if $d = 0$, then $\bar{u}_1 = \alpha_1$, $\bar{u}_2 = \alpha_2$, and $h(d) = \sigma > 0$. Observe that h is a strictly decreasing function of d, by Proposition 3.7(iii) and Proposition 3.9. Under condition (H), there exists a unique $\bar{d} > 0$ such that $h(\bar{d}) = 0$; in addition, $h(d) > 0$ if $d < \bar{d}$, and $h(d) < 0$ if $d > \bar{d}$. This corresponds to $\lambda_4 = 0$ if $d = \bar{d}$, $\lambda_4 > 0$, if $d < \bar{d}$, and $\lambda_4 < 0$ if $d > \bar{d}$ respectively. Now, let us find $\bar{d} > 0$. When the equality in (20) holds, by (21), we have

$$\frac{\alpha_2 + \sqrt{\alpha_2^2 - 4d(\beta_2 - \alpha_1)}}{2} - \frac{\alpha_1 + \sqrt{\alpha_1^2 + 4d(\beta_2 - \alpha_1)}}{2} = \beta_2 - \alpha_1.$$

By a direct calculation, this is equivalent to

$$2(\beta_2-\alpha_1)^2-2(\beta_2-\alpha_1)(\alpha_2-\alpha_1)-\alpha_1\alpha_2 = -\sqrt{(\alpha_1^2 + 4d(\beta_2 - \alpha_1))(\alpha_2^2 - 4d(\beta_2 - \alpha_1))},$$

and hence

$$4(\beta_2 - \alpha_1)d^2 - (\alpha_2^2 - \alpha_1^2)d + \beta_1\beta_2\sigma = 0.$$

Therefore,

$$d_\pm = \frac{(\alpha_2^2 - \alpha_1^2) \pm \sqrt{(\alpha_2^2 - \alpha_1^2)^2 - 16\beta_1\beta_2\sigma(\beta_2 - \alpha_1)}}{8(\beta_2 - \alpha_1)}.$$

We choose $\bar{d} = d_-$, i.e.,

$$\bar{d} = \frac{(\alpha_2^2 - \alpha_1^2) - \sqrt{(\alpha_2^2 - \alpha_1^2)^2 - 16\beta_1\beta_2\sigma(\beta_2 - \alpha_1)}}{8(\beta_2 - \alpha_1)}.$$

This completes the proof. □

3.5. **Coexistence of two species and extinction of one species.** Recall Theorem 3.4 that the positive equilibrium $(u_1^*, u_2^*, v_1^*, v_2^*)$ exists if and only if $d < d^*$, and Proposition 3.12 that the semi-trivial equilibrium $(\bar{u}_1, \bar{u}_2, 0, 0)$ is unstable if $d < \bar{d}$, and asymptotically stable if $d > \bar{d}$. The range we estimated for d^* in Theorem 3.4 coincides with the one for $\bar{d}$ in Proposition 3.12, when $\sigma_2 \ge \sigma_1$. Moreover, $d^* = \bar{d}$, when $\sigma_2 = \sigma_1$, by Corollary 3.5 and Corollary 3.13. The following theorem asserts that d^* coincides with $\bar{d}$ exactly, and the dynamical scenario for system (1) becomes completely transparent.

Theorem 3.14. *$d^* = \bar{d}$, for any σ_1, σ_2 with $0 < \sigma_1 \le \sigma_2$.*

Proof. From (16) and (19), we see that $g(d) = 0$ if and only if

$$d\left(\sigma_2 \frac{\bar{u}_2}{\bar{u}_1}(d) - \sigma_1 \frac{\bar{u}_1}{\bar{u}_2}(d)\right) = \sigma_1\sigma_2,$$

i.e., $\bar{d}$ satisfies

$$\bar{d}\left(\sigma_2 \frac{\bar{u}_2}{\bar{u}_1}(\bar{d}) - \sigma_1 \frac{\bar{u}_1}{\bar{u}_2}(\bar{d})\right) = \sigma_1\sigma_2.$$

Let $\bar{a} := \frac{\bar{u}_2}{\bar{u}_1}(\bar{d})$. Then

$$\bar{d}\left(\sigma_2\bar{a} - \sigma_1\frac{1}{\bar{a}}\right) = \sigma_1\sigma_2.$$

Thus,

$$\bar{a} = \frac{\sigma_1 + \sqrt{\sigma_1^2 + 4k\bar{d}^{\ 2}}}{2\bar{d}}, \tag{22}$$

where $k = \sigma_1/\sigma_2$, as $\bar{u}_2/\bar{u}_1 > 1$. When considering $\bar{u}_2/\bar{u}_1$ as a function of d, $d = \bar{d}$ is the only value such that the expression (22) holds. From Remark 1, we see that $v_1^*, v_2^* \to 0$, and $u_1^* \to \bar{u}_1, u_2^* \to \bar{u}_2$, as $d \to (d^*)^-$. Therefore,

$$\lim_{d\to(d^*)^-} a(d) = \lim_{d\to(d^*)^-} \frac{u_2^*}{u_1^*}(d) = \frac{\bar{u}_2}{\bar{u}_1}(d^*) = \frac{\sigma_1 + \sqrt{\sigma_1^2 + 4k(d^*)^{\ 2}}}{2d^*},$$

as seen in (4) in the proof of Theorem 3.4. We thus conclude that $d^* = \bar{d}$. □

Combining the discussions in Subsections 3.1-3.4, we obtain the following coexistence of two species when d is relatively small.

Theorem 3.15. *Assume that condition* (H) *holds for system* (1). *If $d < d^*$, then the unique positive steady state $(u_1^*, u_2^*, v_1^*, v_2^*)$ is stable, and $\lim_{t\to\infty}(u_1(t), u_2(t), v_1(t), v_2(t)) = (u_1^*, u_2^*, v_1^*, v_2^*)$, for all $(u_1(0), u_2(0), v_1(0), v_2(0)) \in \mathbb{R}_+^4$ with $u_1(0) + u_2(0) > 0$ and $v_1(0) + v_2(0) > 0$.*

Proof. That the positive steady state $(u_1^*, u_2^*, v_1^*, v_2^*)$ uniquely exists if and only if $d < d^*$ was proved in Theorem 3.4. The instability of the two semi-trivial equilibria was indicated in Propositions 3.11 and 3.12. Therefore, the assertions follow from Theorem 4.4.2 and Corollary 4.4.3 in [7], or Theorem 3.2. □

The following theorem indicates that the v-species is driven to extinction when d is relatively large.

Theorem 3.16. *Assume that condition* (H) *holds for system* (1). *If $d \geq d^*$, then $\lim_{t\to\infty}(u_1(t), u_2(t), v_1(t), v_2(t)) = (\bar{u}_1, \bar{u}_2, 0, 0)$, for all $(u_1(0), u_2(0), v_1(0), v_2(0)) \in \mathbb{R}_+^4$ with $u_1(0) + u_2(0) > 0$.*

Proof. If $d \geq d^*$, then case (a) of the trichotomy in Theorem 3.3 does not hold, as the positive equilibrium does not exist, by Theorem 3.4. Case (c) does not hold since $(0, 0, \bar{v}_1, \bar{v}_2)$ is unstable, by Proposition 3.11. Therefore, case (b) holds. The assertion now follows from Theorem 4.4.2 in [7] or Theorem 3.3. □

That the equilibrium $(\bar{u}_1, \bar{u}_2, 0, 0)$ is globally asymptotically stable for $d > d^*$ now follows from Proposition 3.12 and Theorem 3.16. At $d = d^*$, the local stability for $(\bar{u}_1, \bar{u}_2, 0, 0)$ can be concluded by some comparison argument. We have therefore established Theorem 1.4 from Theorem 3.15 and Theorem 3.16.

4. **Other case.** Propositions 3.11 and 3.12 actually improve and extend Propositions 1.1, 1.3 in Section 1, reported in [3]. Proposition 1.2 can also be generalized in a similar fashion.

Consider $\beta_1 < \alpha_1 < \alpha_2 < \beta_2$ (compared to $\alpha_1 < \beta_1 < \beta_2 < \alpha_2$ in Section 3). More precisely, we consider

$$\text{Condition } (H_1): \qquad 0 < \beta_1 < \alpha_1 = \beta_1 + \sigma_1 < \alpha_2 = \beta_2 - \sigma_2 < \beta_2,$$
$$\text{with } 0 < \sigma_1 \le \sigma_2 \text{ and } 0 < \sigma_1 < \frac{\beta_2 - \beta_1}{2}.$$

We need $\sigma_1 < \frac{\beta_2-\beta_1}{2}$ to ensure $\alpha_1 < \alpha_2$. When $\sigma_1 = \sigma_2$, condition (H_1) reduces to the consideration in [3]. The following theorem can be obtained by arguments similar to those in Theorem 3.4 and Corollary 3.5.

Theorem 4.1. *Assume that condition* (H_1) *holds. There exists a* $d^* > 0$*, so that system* (1) *has a unique positive equilibrium* $(u_1^*, u_2^*, v_1^*, v_2^*)$ *if and only if* $d < d^*$*. In addition,*

$$\frac{\beta_1\beta_2\sigma_1\sigma_2}{\beta_2^2\sigma_2 - \beta_1^2\sigma_1} < d^* < \frac{\alpha_1\alpha_2\sigma_1\sigma_2}{\alpha_2^2\sigma_2 - \alpha_1^2\sigma_1}.$$

In particular, if $\sigma_1 = \sigma_2 = \sigma$*, then*

$$d^* = \frac{(\beta_2^2 - \beta_1^2) - \sqrt{(\beta_2^2 - \beta_1^2)^2 - 16\alpha_1\alpha_2\sigma(\alpha_2 - \beta_1)}}{8(\alpha_2 - \beta_1)}.$$

The following propositions improve and extend Proposition 1.2 in Section 1, reported in [3]. They are obtained by arguments similar to those for Propositions 3.11, 3.12, and Corollary 3.13.

Proposition 4.2. *Under condition* (H_1)*, the semi-trivial equilibrium* $(\bar{u}_1, \bar{u}_2, 0, 0)$ *is unstable in system* (1) *for any* $d > 0$.

Proposition 4.3. *Under condition* (H_1)*, there exists a* $\bar{d} > 0$ *so that the semi-trivial equilibrium* $(0, 0, \bar{v}_1, \bar{v}_2)$ *is unstable in system* (1) *if* $d < \bar{d}$*, and asymptotically stable if* $d > \bar{d}$*, where*

$$\frac{\beta_1\beta_2\sigma_1\sigma_2}{\beta_2^2\sigma_2 - \beta_1^2\sigma_1} < \bar{d} < \frac{\alpha_1\alpha_2\sigma_1\sigma_2}{\alpha_2^2\sigma_2 - \alpha_1^2\sigma_1}.$$

In particular, if $\sigma_1 = \sigma_2 = \sigma$*, then*

$$\bar{d} = \frac{(\beta_2^2 - \beta_1^2) - \sqrt{(\beta_2^2 - \beta_1^2)^2 - 16\alpha_1\alpha_2\sigma(\alpha_2 - \beta_1)}}{8(\alpha_2 - \beta_1)}.$$

It can be further shown that $d^* = \bar{d}$. Assertions similar to those in Theorems 3.15, 3.16 can thus be concluded.

5. **Numerical illustrations.** We provide two examples to illustrate the bifurcation of dynamics for system (1) with respect to the dispersal rate d, which is concluded by the present theorems.

Example 1. Consider system (1) with $\alpha_1 = 1, \alpha_2 = 3$, $\beta_1 = 1.5, \beta_2 = 2.5$, i.e., $\sigma_1 = \sigma_2 = \sigma = 0.5$. Then $d^* = 0.3$, according to Theorem 3.4. Figure 1 demonstrates the bifurcation diagram with respect to the dispersal rate d. The globally stable positive equilibrium $(u_1^*, u_2^*, v_1^*, v_2^*)$ exists for $d < d^* = 0.3$ and collides with the semi-trivial equilibrium $(\bar{u}_1, \bar{u}_2, 0, 0)$ at $d = d^* = 0.3$. For $d \ge \bar{d} = 0.3$, $(\bar{u}_1, \bar{u}_2, 0, 0)$ becomes globally attractive.

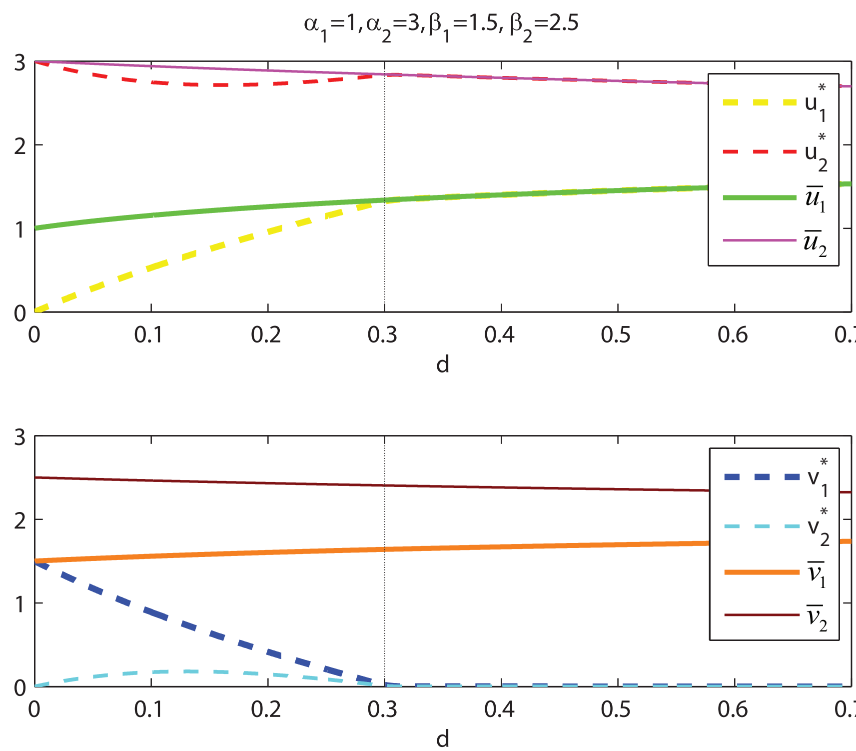

FIGURE 1. Bifurcation diagram for the equilibria of system (1) with $\beta_1 = 1.5, \beta_2 = 2.5, \sigma_1 = \sigma_2 = 0.5$, with respect to d.

Example 2. Consider system (1) with $\beta_1 = 1.5, \beta_2 = 2.5$, same as Example 1, but with $\alpha_1 = 1.2, \alpha_2 = 3.1$, i.e., $\sigma_1 = 0.3, \sigma_2 = 0.6$. Then $0.13 < d^* < 0.22$, according to Theorem 3.4, as marked by two vertical pale lines in Figure 2. The bifurcation scenario, depicted in Figure 2, is similar to Example 1.

6. **Conclusion.** We have characterized the global dynamics for a system modeling competition of two-species living in a two-patchy environment. The coexistence state exists for smaller dispersal rate $d < d^*$ where d^* can be expressed or estimated by the birth rates. The stability of two semi-trivial equilibria $(\bar{u}_1, \bar{u}_2, 0, 0)$ and $(0, 0, \bar{v}_1, \bar{v}_2)$ can also be analyzed completely. For the most interesting case $\alpha_1 < \beta_1 < \beta_2 < \alpha_2$, where u-species has larger birth rate than v-species in the second patch, while v-species has larger birth rate than u-species in the first patch, $(0, 0, \bar{v}_1, \bar{v}_2)$ is unstable for any $d > 0$. On the other hand, one of the eigenvalues of the linearized system at $(\bar{u}_1, \bar{u}_2, 0, 0)$ changes from positive to negative as d increases from 0 to d^*, and $(\bar{u}_1, \bar{u}_2, 0, 0)$ becomes globally attractive for $d \geq d^*$. Thus, for a sufficiently small dispersal rate, the two species can coexist. For a sufficiently large dispersal rate, the two species cannot coexist and the winning strategy is for a species to concentrate its birth on a single patch. This winning strategy might explain the group breeding behavior that is observed in some animals under certain

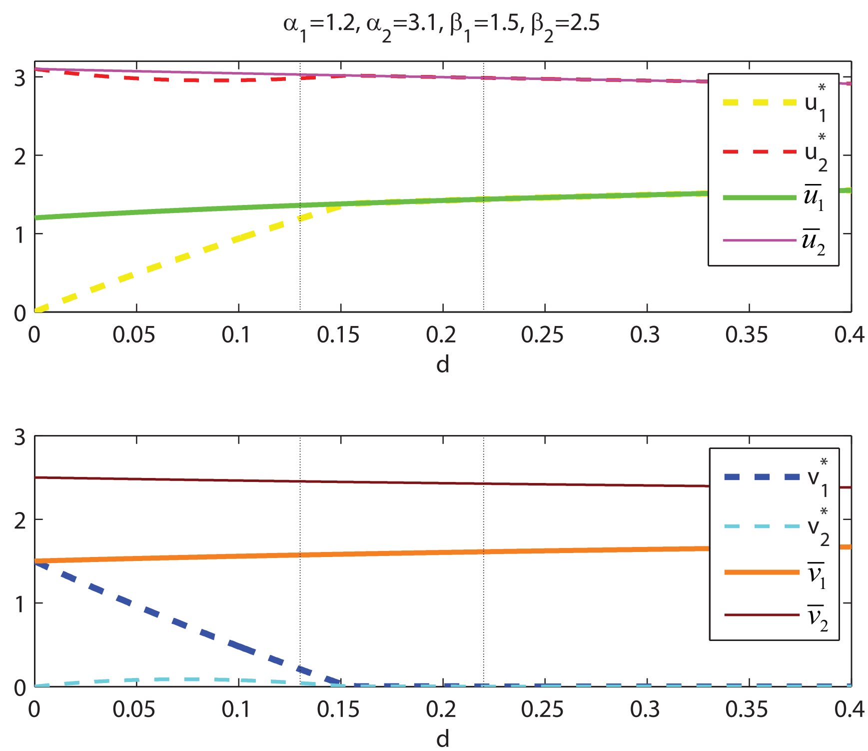

FIGURE 2. Bifurcation diagram for the equilibria of system (1) with $\beta_1 = 1.5, \beta_1 = 2.5, \sigma_1 = 0.3, \sigma_2 = 0.6$, with respect to d.

ecological conditions. Theorem 3.15 and Theorem 3.16 have resolved the conjectures by Gourley and Kuang, stated in Section 1.

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