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Research article

Coexistence and extinction for two competing species in patchy environments

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Abstract: A system of two competing species u and v that diffuse over a two-patch environment is investigated. When u-species has smaller birth rate in the first patch and larger birth rate in the second patch than v-species, and the average birth rate for u-species is larger than or equal to v-species, it was shown in a previous publication that two species coexist in a slow diffusion environment, whereas u-species drives v-species into extinction in a fast diffusion environment. In this paper, we analyze global dynamics and bifurcations for the same model with identical order of birth rates, but with opposite order of average birth rates, i.e., the average birth rate of u-species is less than that of v-species. We observe richer dynamics with two scenarios, depending on the relative difference between the variation in the birth rates of v-species on two patches and the variation in the average birth rates of two species. When the variation in average birth rates is relatively large, there is no stability switch for the semitrivial equilibria. On the other hand, such a stability switch takes place when the variation in average birth rates is relatively mild. In both cases, v-species, with larger average birth rate, prevails in a fast diffusion environment, whereas in a slow diffusion environment, the two species can coexist or u-species that has the greatest birth rate among both species and patches will persist and drive v-species to extinction.

Keywords: competing species; dispersal rate; patchy environment; spatial heterogeneity; global dynamics; monotone dynamics

1. Introduction

Dispersal of organisms is a topic of central interest in ecology and evolutionary biology. Its effects on the size, stability, and interactions of populations, as well as biological invasions and the geographical distribution of populations have attracted considerable studies. Investigation on dispersal strategies which are evolutionarily stable has been the fundamental research goal for theoretical ecologists [7, 26]. The relationship between diffusion rates, spatial heterogeneity, and coupling from competition of species is the target of several recent works. To tackle these problems, continuous diffusion models expressed by reaction-diffusion systems have been considered in [1, 2, 3, 6, 9, 13, 14, 19, 20, 23, 25]. On the other hand, discrete diffusion models represented by systems of ODEs have been investigated in [4, 5, 11, 12, 24, 31].

Concerning the interaction between diffusion rates and the heterogeneity of the environment and mutant invasion, the following competitive Lotka-Volterra model was investigated in [18, 19]:

$$\begin{aligned} u_t &= \mu\Delta u + u[\alpha(x) - u - v], \\ v_t &= \mu\Delta v + v[\beta(x) - u - v], \end{aligned} \tag{1.1}$$

under homogeneous Neumann boundary condition, where μ is the diffusion rate and functions $\alpha(x)$ and $\beta(x)$ express the spatially dependent intrinsic growth rates or reproductive rates of u- and v-species, respectively. Therein, to study the effect of spatially heterogeneous growth rates on the competitive dynamics, the difference between intrinsic growth rates of two species was set as

$$\alpha(x) = \beta(x) + \tau g(x),$$

where $g(x)$ is a function describing resource difference between two species from the viewpoint of spatial heterogeneity, and $\tau > 0$ measures the magnitude of the difference. The case $g(x) > 0$ on the considered domain was studied in [18], whereas the situation that $g(x)$ changes sign was investigated in [19]. The assumption in [19],

$$\int_\Omega g(x)dx > 0, \tag{1.2}$$

means that the mutant u-species has better average reproductive rate than v-species, and thus the total population of u-species has higher growth rate than that of v-species when two populations are identical in the whole space Ω. However, under such a circumstance, u-species possibly fails to invade when rare for certain level of diffusion rate. Mathematically, stability of semitrivial solutions $(\tilde{u}, 0)$ and $(0, \tilde{v})$, which depend on the magnitudes of μ and τ, was analyzed in [19]. The stability may switch according to the varying diffusion rate μ. In particular, by measuring the level of mutation with the value of τ, theoretical analysis for the cases of tiny and large mutation was established therein. In the former case ($0 < \tau \ll 1$), multiple switches of global convergence to different equilibria was derived and the relationship between the bifurcation value of the diffusion rate and the value of τ was also established, while in the latter case ($\tau \gg 1$), only once switch of global convergence was observed.

The influence from magnitudes of diffusion rates on the competition outcome has been another topic of interest. It has been shown in [9] that the slower diffuser always prevails if the two species interact identically with the environment, see also [12, 20, 23]. To focus on the effect of diffusion rates, the birth rates for all competing species were set equal to the carrying capacity of the environment, see [2, 5, 6, 13, 15].

Models for competitive species with dispersal expressed by discrete diffusion are also very appealing. Indeed, organisms are distributed in space, often in patches of habitat scattered over a landscape and region, and the distribution is determined by the pattern of movement between these patches. More specifically, it is interesting to see how possible interaction outcome, which can be competitive exclusion and coexistence, depends on the diffusion rates and the birth rates.

As early as in 1934, Gause [10] formulated the competitive exclusion law which in particular states that the species with a larger birth rate will outcompete the other one, if the other properties are the same. Concerning these issues, Gourley and Kuang [11] then asked how does diffusion affect the competition outcomes of two competing species that are identical in all respects other than their strategies on how they spatially distribute their birth rates. They studied the following ODE system as a model for two neutrally competing species on two patches of habitat:

$$\begin{cases} \frac{du_1}{dt} = u_1(\alpha_1 - u_1 - v_1) + d(u_2 - u_1) \\ \frac{du_2}{dt} = u_2(\alpha_2 - u_2 - v_2) + d(u_1 - u_2) \\ \frac{dv_1}{dt} = v_1(\beta_1 - u_1 - v_1) + d(v_2 - v_1) \\ \frac{dv_2}{dt} = v_2(\beta_2 - u_2 - v_2) + d(v_1 - v_2) \end{cases} \tag{1.3}$$

where u_i (resp., v_i) is the population density 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 same diffusivity (dispersal rate) d for both species. The two species differ only in their birth rates. Let $(\bar{u}_1, \bar{u}_2, 0, 0)$ denote the semitrivial equilibrium with extinct v-species. The following conjectures on the global dynamics of system (1.3) were posed in [11]:

Conjecture 1. *Assume that in system* (1.3)*,* $\beta_1 - \sigma = \alpha_1 < \beta_1 < \beta_2 < \alpha_2 = \beta_2 + \sigma$ *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* (1.3)*,* $\beta_1 - \sigma = \alpha_1 < \beta_1 < \beta_2 < \alpha_2 = \beta_2 + \sigma$ *with* $0 < \sigma < \beta_1$*, and d is small enough so that* (1.3) *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. That is, the winning strategy is to focus as much birth in a single patch as possible. In [24], the following global dynamics and bifurcation were established, which include confirmation of Conjectures 1 and 2:

Theorem 1.1. *Suppose that the following condition holds in system* (1.3)*,*

$$(\mathrm{C}') : 0 < \alpha_1 = \beta_1 - \sigma_1 < \beta_1 < \beta_2 < \alpha_2 = \beta_2 + \sigma_2 \ \text{ with } 0 < \sigma_1 \le \sigma_2.$$

Then there is a constant $\tilde{d} > 0$ *which can be expressed or estimated by the birth rates, so that if* $d \ge \tilde{d}$*,* $(\bar{u}_1, \bar{u}_2, 0, 0)$ *is globally asymptotically stable among the initial data in* $\mathbb{R}^4_+$ *satisfying* $u_1(0) + u_2(0) > 0$*; if* $d < \tilde{d}$*,* (1.3) *has a unique positive steady state* $(u_1^*, u_2^*, v_1^*, v_2^*)$ *which is globally asymptotically stable among the initial data in* $\mathbb{R}^4_+$ *satisfying* $u_1(0) + u_2(0) > 0$ *and* $v_1(0) + v_2(0) > 0$*.*

Note that $\alpha_1 + \alpha_2$ and $\beta_1 + \beta_2$ measure the average birth rates of species u and v, respectively. The condition of Theorem 1.1 means $\alpha_1 < \beta_1 < \beta_2 < \alpha_2$ and $\beta_1 + \beta_2 \le \alpha_1 + \alpha_2$, and indicates that the birth rate of u-species is larger than that of v-species in the second patch, and less than that of v-species in the first patch, whereas the average birth rate of u-species is larger than or equal to that of v-species. For the situation with identical average birth rate: $\alpha_1 + \alpha_2 = \beta_1 + \beta_2$, i.e., the case in these conjectures, Theorem 1.1 implicates that the two species coexist in a slow diffusion environment, whereas in a fast diffusion environment, the species that can concentrate its birth in a single patch drives the other species into extinction. Convincingly, the same scenario prevails when u has further competitive advantage that its average birth rate is larger than v-species: $\alpha_1 + \alpha_2 > \beta_1 + \beta_2$. Along with such finding is that the semitrivial equilibrium $(0, 0, \bar{v}_1, \bar{v}_2)$ is always unstable for any diffusion rate d, as was stated in Proposition 3.11 of [24]. It becomes very interesting to see what happens when $\alpha_1 + \alpha_2 < \beta_1 + \beta_2$, i.e., v-species has larger average birth rate.

In this paper we will examine such interesting situation, i.e., system (1.3) under condition

$$(\text{C}) : 0 < \alpha_1 = \beta_1 - \sigma_1 < \beta_1 < \beta_2 < \alpha_2 = \beta_2 + \sigma_2 \text{ with } 0 < \sigma_2 < \sigma_1.$$

This condition means $\alpha_1 < \beta_1 < \beta_2 < \alpha_2$, and $\alpha_1+\alpha_2 < \beta_1+\beta_2$, due to $(\beta_1+\beta_2)-(\alpha_1+\alpha_2) = \sigma_1-\sigma_2 > 0$. That is, the birth rate α_2 of u-species in the second patch is the biggest among all species and patches, but the average birth rate of v-species is larger than that of u-species; one may also regard this as that v-species has more total resources than u-species. Then we ask how the magnitude of the dispersal rate d is related to the species persistence or extinction. With the framework of monotone dynamics, we shall target the global dynamics of system (1.3) and the bifurcation with respect to d, under condition (C).

It turns out that the dynamical scenarios are richer than the case under condition (C′). In particular, equilibrium $(0, 0, \bar{v}_1, \bar{v}_2)$ switches from being unstable to stable, as d increases. On the other hand, there are up to two stability changes for equilibrium $(\bar{u}_1, \bar{u}_2, 0, 0)$, as d increases. That is, the property described as monotone relation between the stability of $(\bar{u}_1, \bar{u}_2, 0, 0)$ and the diffusion rate d no longer holds, cf. [19]. The main results will be summarized in Theorem 4.2. There are two dynamical scenarios (see Figure 1): (i) Under $\sigma_2\beta_2 < \sigma_1\beta_1$, there exists an $d_3^* > 0$, so that the positive steady state $(u_1^*, u_2^*, v_1^*, v_2^*)$ is globally attractive for $d < d_3^*$ and the semitrivial equilibrium $(0, 0, \bar{v}_1, \bar{v}_2)$ becomes globally attractive for $d \geq d_3^*$. (ii) Under $\sigma_2\beta_2 > \sigma_1\beta_1$, there exist d_1^*, d_2^*, d_3^* with $0 < d_1^* < d_2^* < d_3^*$, so that $(u_1^*, u_2^*, v_1^*, v_2^*)$ is globally attractive for $d < d_1^*$ or $d_2^* < d < d_3^*$, $(\bar{u}_1, \bar{u}_2, 0, 0)$ is globally attractive for $d_1^* \leq d \leq d_2^*$, and $(0, 0, \bar{v}_1, \bar{v}_2)$ becomes globally attractive for $d \geq d_3^*$. In addition, d_1^*, d_2^*, d_3^* can be estimated in terms of the system parameters. Our analytical work on the model strongly suggests that, in a fast diffusion (large dispersal) environment, a species will prevail if its average birth rate is larger than the other competing species; in a slow diffusion (small dispersal) environment, the two species can coexist or one species that has the greatest birth rate among both species and patches, even with smaller average birth rate, will be able to persist and drive the other species to extinction.

We note that $\alpha_1 + \alpha_2 > \beta_1 + \beta_2$ in system (1.3) is analogous to condition (1.2) in PDE system (1.1). The present study, with $\alpha_1 + \alpha_2 < \beta_1 + \beta_2$, can be compared to the results in [19] with u and v reversed. Systems with two competing species over two patches with different dispersal rates and more general competition coupling have been considered in [21, 29, 30]. While the effect of competition was studied in [29], herein we aim at investigating the influence of both dispersal rate and birth rates on the population dynamics and assume the same ability of competition for two species in (1.3). Predator-prey dynamics on two-patch environments were investigated in [8, 16, 22].

This presentation is organized as follows. In Section 2, we characterize the existence of positive equilibrium for system (1.3). In Section 3, we analyze the stability of the semitrivial equilibria. In Section 4, we discuss the existence of positive steady state representing coexistence of two species and extinction of one species, depending on the magnitude of dispersal rate. Four numerical examples illustrating the present theory are given in Section 5. We summarize our results with some discussions in Sections 6. For reader's convenience, we review in Appendix I the monotone dynamics theory which is to be applied to obtain our results. Some qualitative properties of the semitrivial equilibria for system (1.3) reported in [24] are recalled in Appendix II.

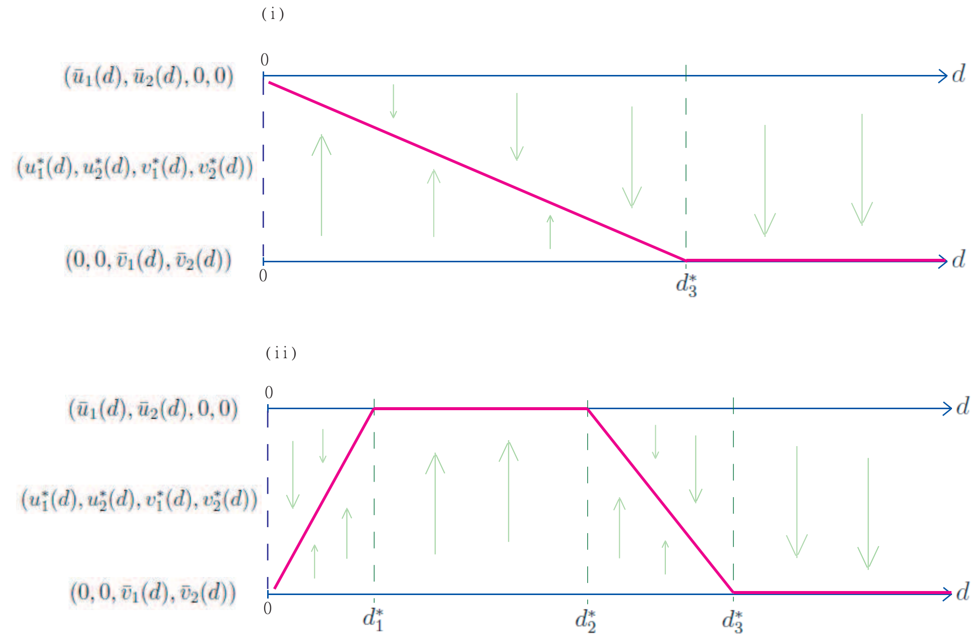

Figure 1. Two dynamical scenarios for system (1.3): the main results, stated in Theorems 2.1 and 4.2.

2. Existence of positive equilibrium

In this section, we characterize the conditions under which the positive equilibrium $(u_1^*, u_2^*, v_1^*, v_2^*)$ of system (1.3) exists. There are five parameters $\alpha_1, \alpha_2, \beta_1, \beta_2, d$ in system (1.3), which generate a complication of analysis for such existence. We first derive the following magnitude relationships which are required in the main result, Theorem 2.1, of this section.

Lemma 2.1. *The following parameter relationships hold under condition* (C).
(i) $\frac{1}{\sigma_1-\sigma_2} < \frac{\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2}$ *if and only if* $(\sigma_2\beta_2^2 - \sigma_1\beta_1^2)(\sigma_1\beta_1 - \sigma_2\beta_2) > 0$.
(ii) $0 < \frac{\alpha_1\alpha_2}{\sigma_2\alpha_2^2-\sigma_1\alpha_1^2} < \frac{\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2}$, *provided* $\sigma_2\beta_2^2 - \sigma_1\beta_1^2 > 0$.
(iii) $\frac{\sigma_1}{\sigma_1-\sigma_2} < \frac{\beta_2}{\sigma_1+\sigma_2}$, *provided* $\sigma_1\beta_1 > \sigma_2\beta_2$ *and* $\beta_2 - \beta_1 \geq \sigma_1 + \sigma_2$.

Proof. Recall that $\sigma_1 > \sigma_2$ in condition (C).
(i) We compute

$$\begin{aligned} & \frac{\beta_1\beta_2}{\sigma_2\beta_2^2 - \sigma_1\beta_1^2} - \frac{1}{\sigma_1 - \sigma_2} \\ = & \frac{\beta_1\beta_2(\sigma_1 - \sigma_2) - (\sigma_2\beta_2^2 - \sigma_1\beta_1^2)}{(\sigma_2\beta_2^2 - \sigma_1\beta_1^2)(\sigma_1 - \sigma_2)} \end{aligned}$$

$$= \frac{(\beta_1+\beta_2)(\sigma_1\beta_1-\sigma_2\beta_2)}{(\sigma_2\beta_2^2-\sigma_1\beta_1^2)(\sigma_1-\sigma_2)}.$$

Thus, $\frac{\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2} - \frac{1}{\sigma_1-\sigma_2} > 0$ if and only if $(\sigma_2\beta_2^2-\sigma_1\beta_1^2)(\sigma_1\beta_1-\sigma_2\beta_2) > 0$.
(ii) Suppose $\sigma_2\beta_2^2-\sigma_1\beta_1^2 > 0$. Then

$$\sigma_2\alpha_2^2-\sigma_1\alpha_1^2 > \sigma_2\beta_2^2-\sigma_1\alpha_1^2 > \sigma_2\beta_2^2-\sigma_1\beta_1^2 > 0.$$

The assertion follows from

$$\frac{\alpha_1\alpha_2}{\sigma_2\alpha_2^2-\sigma_1\alpha_1^2} - \frac{\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2} = \frac{(\sigma_2\alpha_2\beta_2+\sigma_1\alpha_1\beta_1)(\alpha_1\beta_2-\alpha_2\beta_1)}{(\sigma_2\alpha_2^2-\sigma_1\alpha_1^2)(\sigma_2\beta_2^2-\sigma_1\beta_1^2)} < 0,$$

due to $\alpha_1\beta_2-\alpha_2\beta_1 = \alpha_1\beta_2-(\beta_2+\sigma_2)(\alpha_1+\sigma_1) < 0$.
(iii) If $\sigma_1\beta_1 > \sigma_2\beta_2$, then

$$\begin{aligned}\frac{\beta_2}{\sigma_1+\sigma_2} - \frac{\sigma_1}{\sigma_1-\sigma_2} &= \frac{\sigma_1\beta_2-\sigma_2\beta_2-\sigma_1(\sigma_1+\sigma_2)}{\sigma_1^2-\sigma_2^2}\\ &> \frac{\sigma_1\beta_2-\sigma_1\beta_1-\sigma_1(\sigma_1+\sigma_2)}{\sigma_1^2-\sigma_2^2}\\ &= \frac{\sigma_1[(\beta_2-\beta_1)-(\sigma_1+\sigma_2)]}{\sigma_1^2-\sigma_2^2}\\ &\geq 0,\end{aligned}$$

provided $\beta_2-\beta_1 \geq \sigma_1+\sigma_2$. The assertion thus follows. □

The following parameter condition is to be used throughout the discussions:

$$\text{Condition (P)}: \quad \frac{1}{\sigma_1+\sigma_2} < \frac{\sigma_1\beta_1}{\sigma_2\beta_2^2-\sigma_1\beta_1^2}.$$

Certainly condition (P) holds only if $\sigma_2\beta_2^2-\sigma_1\beta_1^2 > 0$. And a direct computation shows that condition (P) is equivalent to $\sigma_2\beta_2^2-\sigma_1\beta_1^2 > 0$ with

$$\sigma_2\beta_2^2 < \sigma_1\beta_1(\beta_1+\sigma_1+\sigma_2). \tag{2.1}$$

Accordingly, if condition (P) holds, Lemma 2.1(i) can be recast as

$$\frac{1}{\sigma_1-\sigma_2} < \frac{\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2} \Leftrightarrow \sigma_2\beta_2 < \sigma_1\beta_1;$$

for convenience of later use, we put this relationship as

$$\frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2} < \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2} \Leftrightarrow \sigma_2\beta_2 < \sigma_1\beta_1. \tag{2.2}$$

The condition of Lemma 2.1(iii): $\sigma_1\beta_1 > \sigma_2\beta_2$ and $\beta_2-\beta_1 \geq \sigma_1+\sigma_2$ implies

$$\frac{\sigma_1}{\sigma_1-\sigma_2} < \frac{\beta_2}{\sigma_1+\sigma_2}.$$

Then, by combining condition (P), we obtain

$$\frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2} < \frac{\sigma_2\beta_2}{\sigma_1+\sigma_2} < \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2}. \tag{2.3}$$

On the other hand, combining $\frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2} > \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2}$, i.e. $\sigma_2\beta_2 > \sigma_1\beta_1$ by (2.2), with condition (P) yields

$$\frac{\sigma_2\beta_2}{\sigma_1+\sigma_2} < \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2} < \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}. \tag{2.4}$$

Therefore, by imposing condition (P) additionally, the following relationships can be concluded.

Lemma 2.2. *Assume that conditions* (C) *and* (P) *hold.*
(i) *If* $\sigma_2\beta_2 < \sigma_1\beta_1$ *and* $\beta_2-\beta_1 \geq \sigma_1+\sigma_2$, *then*

$$\frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2} < \frac{\sigma_2\beta_2}{\sigma_1+\sigma_2} < \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2}.$$

(ii) *If* $\sigma_2\beta_2 > \sigma_1\beta_1$, *then*

$$\frac{\sigma_2\beta_2}{\sigma_1+\sigma_2} < \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2} < \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}.$$

It is obvious that the terms in the inequalities in Lemma 2.2 can be simplified. But it is convenient to keep these forms.

Remark 1. *In Lemma 2.2, with* (2.1)*, the condition in* (ii)*:* $\sigma_2\beta_2 > \sigma_1\beta_1$ *leads to* $\sigma_1\beta_1\beta_2 < \sigma_2\beta_2^2 < \sigma_1\beta_1(\beta_1+\sigma_1+\sigma_2)$*, and thus* $\beta_2-\beta_1 < \sigma_1+\sigma_2$*, which is contrary to the condition* $\beta_2-\beta_1 \geq \sigma_1+\sigma_2$ *in* (i)*. That is, the condition in* (i) *and the condition in* (ii) *are opposite cases under assumption* (P)*. In addition, the condition in Lemma 2.2*(i)*:* $\sigma_2\beta_2 < \sigma_1\beta_1$ *and* $\beta_2-\beta_1 \geq \sigma_1+\sigma_2$ *further indicates*

$$\sigma_2\beta_2^2 < \sigma_1\beta_1(\beta_1+\sigma_1+\sigma_2) \leq \sigma_1\beta_1\beta_2, \tag{2.5}$$

via (2.1).

We characterize the existence of positive equilibrium for system (1.3) in the following theorem.

Theorem 2.1. *Consider system* (1.3) *under conditions* (C) *and* (P).
(i) *Under* $\sigma_2\beta_2 < \sigma_1\beta_1$ *and* $\beta_2-\beta_1 \geq \sigma_1+\sigma_2$*, there exists an* $d_3^* > 0$ *so that the system has a unique positive equilibrium* $(u_1^*, u_2^*, v_1^*, v_2^*)$ *if and only if* $0 < d < d_3^*$.
(ii) *Under* $\sigma_2\beta_2 > \sigma_1\beta_1$*, there exist* $d_1^*, d_2^*, d_3^* > 0$*, with* $d_1^* < d_2^* < d_3^*$*, so that the system has a unique positive equilibrium* $(u_1^*, u_2^*, v_1^*, v_2^*)$ *if and only if* $0 < d < d_1^*$ *or* $d_2^* < d < d_3^*$.
In addition,

$$\frac{\sigma_1\sigma_2\alpha_1\alpha_2}{\sigma_2\alpha_2^2-\sigma_1\alpha_1^2} < d_1^* < \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2}$$
$$\frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2} < d_2^* < \frac{\sigma_1\sqrt{\sigma_1\sigma_2}+\sigma_1\sigma_2}{\sigma_1^2-\sigma_2^2}(\alpha_2-\alpha_1)$$
$$\frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2} < d_3^* < \frac{\sigma_1}{\sigma_1-\sigma_2}(\alpha_2-\alpha_1).$$

Proof. System (1.3) has a positive equilibrium $(u_1^*, u_2^*, v_1^*, v_2^*)$ if and only if

$$\begin{aligned} &(\alpha_1 - u_1^* - v_1^*) + d(\frac{u_2^*}{u_1^*} - 1) = 0, \quad (\alpha_2 - u_2^* - v_2^*) + d(\frac{u_1^*}{u_2^*} - 1) = 0, \\ &(\beta_1 - v_1^* - u_1^*) + d(\frac{v_2^*}{v_1^*} - 1) = 0, \quad (\beta_2 - v_2^* - u_2^*) + d(\frac{v_1^*}{v_2^*} - 1) = 0, \end{aligned} \tag{2.6}$$

are satisfied for $u_1^*, u_2^*, v_1^*, v_2^* > 0$. Let $(u_1^*, u_2^*, v_1^*, v_2^*)$ be a solution of (2.6) and denote

$$a := \frac{u_2^*}{u_1^*}, \quad b := \frac{v_2^*}{v_1^*}. \tag{2.7}$$

Combining each pair of equations in (2.6), we obtain

$$\begin{aligned} &-\sigma_1 + d(a - b) = 0, \\ &\sigma_2 + d(\frac{1}{a} - \frac{1}{b}) = 0. \end{aligned} \tag{2.8}$$

This yields

$$ab = \frac{\sigma_1}{\sigma_2} =: k, \tag{2.9}$$

and $k > 1$, as $0 < \sigma_2 < \sigma_1$. Substituting $b = k/a$ and $a = k/b$ into (2.8) respectively leads to

$$a = \frac{\sigma_1 + \sqrt{\sigma_1^2 + 4kd^2}}{2d}, \ b = \frac{-\sigma_1 + \sqrt{\sigma_1^2 + 4kd^2}}{2d}. \tag{2.10}$$

We thus express a, b in terms of system parameters, and it can be computed that $b^2 < k < a^2$ and $a > 1$. We substitute (2.7) into (2.6) and obtain

$$(\alpha_1 - u_1^* - v_1^*) + d(a - 1) = 0, \ a(\alpha_2 - au_1^* - bv_1^*) + d(1 - a) = 0, \tag{2.11}$$

$$(\beta_1 - v_1^* - u_1^*) + d(b - 1) = 0, \ b(\beta_2 - bv_1^* - au_1^*) + d(1 - b) = 0. \tag{2.12}$$

Solving the two equations in (2.11), we have

$$\begin{cases} u_1^* = \frac{1}{a^2 - k} [(a\alpha_2 - ad + d) - k(\alpha_1 + ad - d)] \\ v_1^* = (\alpha_1 + ad - d) - u_1^*. \end{cases} \tag{2.13}$$

On the other hand, solving the two equations in (2.12), we obtain

$$\begin{cases} u_1^* = \frac{1}{k - b^2} [(b\beta_2 - bd + d) - b^2(\beta_1 + bd - d)] \\ v_1^* = (\beta_1 + bd - d) - u_1^*. \end{cases} \tag{2.14}$$

In fact, (2.13) and (2.14) are equivalent, as it can be seen by (2.8) that $\alpha_1 + ad - d = \beta_1 + bd - d$ and

$$\frac{1}{a^2 - k} [(a\alpha_2 - ad + d) - k(\alpha_1 + ad - d)] = \frac{1}{k - b^2} [(b\beta_2 - bd + d) - b^2(\beta_1 + bd - d)].$$

Herein, $\alpha_1 + ad - d > 0$ since $a > 1$. From (2.13) and (2.14), we obtain

$$v_1^* = \frac{1}{a^2 - k} \left[a^2(\alpha_1 + ad - d) - (a\alpha_2 - ad + d) \right]$$

$$= \frac{1}{k-b^2}[k(\beta_1 + bd - d) - (b\beta_2 - bd + d)].$$

Observe that $u_1^*, v_1^* > 0$ imply $u_2^*, v_2^* > 0$, due to (2.7) and $a, b > 0$. Hence, system (1.3) has a unique positive equilibrium if and only if

$$\begin{aligned} u_1^* &= \frac{1}{a^2-k}[(a\alpha_2 - ad + d) - k(\alpha_1 + ad - d)] \\ &= \frac{1}{k-b^2}[(b\beta_2 - bd + d) - b^2(\beta_1 + bd - d)] > 0, \end{aligned} \tag{2.15}$$

and

$$\begin{aligned} v_1^* &= \frac{1}{a^2-k}\left[a^2(\alpha_1 + ad - d) - (a\alpha_2 - ad + d)\right] \\ &= \frac{1}{k-b^2}[k(\beta_1 + bd - d) - (b\beta_2 - bd + d)] > 0. \end{aligned} \tag{2.16}$$

To explore the range of d where $u_1^*, v_1^* > 0$, we denote $u_1^*(d), v_1^*(d)$ to express the dependence of u_1^*, v_1^* on d. Let us discuss the positivity of v_1^* first. The terms in the brackets of (2.16) can be recast as

$$\begin{cases} a^2(\alpha_1 + ad - d) - (a\alpha_2 - ad + d) = a^2\alpha_1 - a\alpha_2 + d(a^2+1)(a-1) \\ k(\beta_1 + bd - d) - (b\beta_2 - bd + d) = k\beta_1 - b\beta_2 + d(k+1)(b-1). \end{cases} \tag{2.17}$$

We define two functions to discuss the positivity of v_1^*:

$$\begin{aligned} F_{v^*}(d) &:= a^2\alpha_1 - a\alpha_2 + d(a^2+1)(a-1), \\ G_{v^*}(d) &:= k\beta_1 - b\beta_2 + d(k+1)(b-1). \end{aligned}$$

It follows from (2.16) and (2.17) that

$$F_{v^*}(d) = \frac{a^2-k}{k-b^2}G_{v^*}(d).$$

In addition, $v_1^* > 0$ if and only if $F_{v^*}(d) > 0$ if and only if $G_{v^*}(d) > 0$, due to $b^2 < k < a^2$. In the following discussions (a)-(e), we analyze the ranges of d within which $F_{v^*}(d)$ and $G_{v^*}(d)$ take positive or negative values. For some situations, analyzing F_{v^*} is more convenient than G_{v^*}, whereas the convenience is reverse in other cases.

(a) $F_{v^*}(d) > 0$ if $d < \frac{\sigma_1\sigma_2\alpha_1\alpha_2}{\sigma_2\alpha_2^2 - \sigma_1\alpha_1^2}$: It can be seen that $a\alpha_1 > \alpha_2$ implies $F_{v^*}(d) > 0$, due to $a > 1$. On the other hand, $a\alpha_1 > \alpha_2$ is actually

$$a = \frac{\sigma_1 + \sqrt{\sigma_1^2 + 4kd^2}}{2d} > \frac{\alpha_2}{\alpha_1},$$

which is equivalent to $d < \frac{\sigma_1\sigma_2\alpha_1\alpha_2}{\sigma_2\alpha_2^2 - \sigma_1\alpha_1^2}$.

(b) $F_{v^*}(d) > 0$ if $d > \frac{\sigma_1\sqrt{\sigma_1\sigma_2} + \sigma_1\sigma_2}{\sigma_1^2 - \sigma_2^2}(\alpha_2 - \alpha_1)$: If $b > 1$, i.e. $d > \frac{\sigma_1\sigma_2}{\sigma_1 - \sigma_2}$ by (2.10), then $a < k$ since $ab = k$. From $b^2 < k < a^2$, we have $1 < b < \sqrt{k} < a < k$. Then

$$F_{v^*}(d) = a^2\alpha_1 - a\alpha_2 + d(a^2+1)(a-1)$$

$$> \quad k\alpha_1 - k\alpha_2 + d(k+1)(\sqrt{k}-1)$$
$$> \quad 0,$$

if $d > \frac{k}{(k+1)(\sqrt{k}-1)}(\alpha_2 - \alpha_1) = \frac{\sigma_1\sqrt{\sigma_1\sigma_2}+\sigma_1\sigma_2}{\sigma_1^2-\sigma_2^2}(\alpha_2 - \alpha_1)$. It is clear that

$$\begin{aligned} & \frac{\sigma_1\sqrt{\sigma_1\sigma_2}+\sigma_1\sigma_2}{\sigma_1^2-\sigma_2^2}(\alpha_2-\alpha_1) \\ = & \frac{\sigma_1\sqrt{\sigma_1\sigma_2}+\sigma_1\sigma_2}{\sigma_1^2-\sigma_2^2}(\beta_2-\beta_1) + \frac{\sigma_1\sqrt{\sigma_1\sigma_2}+\sigma_1\sigma_2}{\sigma_1-\sigma_2} \\ > & \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}. \end{aligned}$$

(c) $G_{v^*}(d) > 0$ if $\frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2} < d < \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2}$: Obviously, $G_{v^*}(d) > 0$ if $k\beta_1 - b\beta_2 > 0$ and $b > 1$, which is

$$k\frac{\beta_1}{\beta_2} > b = \frac{-\sigma_1 + \sqrt{\sigma_1^2 + 4kd^2}}{2d} > 1.$$

This is equivalent to

$$\frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2} < d < \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2},$$

by (2.10). Such value of d exists provided $\frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2} < \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2}$.

(d) $G_{v^*}(d) < 0$ if $\frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2} < d < \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}$: $G_{v^*}(d) < 0$ provided $k\beta_1 - b\beta_2 < 0$ and $b < 1$, which is

$$k\frac{\beta_1}{\beta_2} < b = \frac{-\sigma_1 + \sqrt{\sigma_1^2 + 4kd^2}}{2d} < 1,$$

and equivalent to $\frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2} < d < \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}$, provided $\frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2} < \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}$.

(e) $G'_{v^*}(d) < 0$ if $d < \min\left\{\frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}, \frac{\sigma_2\beta_2}{\sigma_1+\sigma_2}\right\}$ and $G'_{v^*}(d) > 0$ if $d > \max\left\{\frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}, \frac{\sigma_2\beta_2}{\sigma_1+\sigma_2}\right\}$: From (2.10), we compute

$$b' = b'(d) = \frac{\sigma_1 b}{d\sqrt{\sigma_1^2 + 4kd^2}} > 0, \tag{2.18}$$

and $G'_{v^*}(d) = (k+1)(b-1) + b'(kd - \beta_2 + d)$. It can be seen that $G'_{v^*}(d) < 0$, provided $b < 1$ and $kd - \beta_2 + d < 0$, which are equivalent to $d < \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}$ and $d < \frac{\sigma_2\beta_2}{\sigma_1+\sigma_2}$. On the contrary, $G'_{v^*}(d) > 0$, if $b > 1$ and $kd - \beta_2 + d > 0$, which are equivalent to $d > \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}$ and $d > \frac{\sigma_2\beta_2}{\sigma_1+\sigma_2}$.

For case (i), we will show that $v_1^*(d) > 0$ for all $d > 0$ if $\sigma_2\beta_2 < \sigma_1\beta_1$ and $\beta_2 - \beta_1 \geq \sigma_1 + \sigma_2$. Recall Lemma 2.2(i): $\frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2} < \frac{\sigma_2\beta_2}{\sigma_1+\sigma_2} < \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2}$. From the above (c), (e), we summarize

$$\begin{cases} G_{v^*}(d) > 0 \text{ if } \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2} < d < \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2} \\ G'_{v^*}(d) < 0 \text{ if } d < \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2} \\ G'_{v^*}(d) > 0 \text{ if } d > \frac{\sigma_2\beta_2}{\sigma_1+\sigma_2}. \end{cases} \tag{2.19}$$

In addition, at $d = \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}$, i.e., $b = 1$, we have $G_{v^*}(\frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}) = k\beta_1 - \beta_2 > 0$, thanks to $\sigma_2\beta_2 < \sigma_1\beta_1$. Therefore, from (2.19), we see that $G_{v^*}(d) > 0$ for all $d > 0$, namely, $v_1^*(d) > 0$ for all $d > 0$, under $\sigma_2\beta_2 < \sigma_1\beta_1, \beta_2 - \beta_1 \geq \sigma_1 + \sigma_2$, and condition (P).

For case (ii), if $\sigma_2\beta_2 > \sigma_1\beta_1$, we will show that $G_{v^*}(d) > 0$, and hence $v_1^*(d) > 0$, for d in certain range. Recall Lemma 2.2(ii): $\frac{\sigma_2\beta_2}{\sigma_1+\sigma_2} < \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2} < \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}$. With the above (a), (b), (d), (e), we obtain

$$\begin{cases} F_{v^*}(d) > 0 \text{ if } d < \frac{\sigma_1\sigma_2\alpha_1\alpha_2}{\sigma_2\alpha_2^2-\sigma_1\alpha_1^2} \\ G_{v^*}(d) < 0 \text{ if } \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2} < d < \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2} \\ F_{v^*}(d) > 0 \text{ if } d > \frac{\sigma_1\sqrt{\sigma_1\sigma_2}+\sigma_1\sigma_2}{\sigma_1^2-\sigma_2^2}(\alpha_2-\alpha_1) \end{cases} \tag{2.20}$$

and

$$\begin{cases} G'_{v^*}(d) < 0 \text{ if } d < \frac{\sigma_2\beta_2}{\sigma_1+\sigma_2} \\ G'_{v^*}(d) > 0 \text{ if } d > \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}. \end{cases} \tag{2.21}$$

Furthermore, if $d \geq \frac{\sigma_2\beta_2}{\sigma_1+\sigma_2}$, i.e. $d(k+1) \geq \beta_2$, and $d \leq \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}$, i.e. $b \leq 1$, we have

$$G_{v^*}(d) = k\beta_1 - b\beta_2 - d(k+1)(1-b) \leq k\beta_1 - b\beta_2 - \beta_2(1-b) = k\beta_1 - \beta_2 < 0,$$

by $\sigma_2\beta_2 > \sigma_1\beta_1$. To summarize, $G_{v^*}(d) < 0$ if $\frac{\sigma_2\beta_2}{\sigma_1+\sigma_2} \leq d \leq \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}$. Therefore, from (2.20) and (2.21), there exists a unique $d_1^* > 0$ so that $G_{v^*}(d) > 0$ if $d < d_1^*$ and $G_{v^*}(d_1^*) = 0$, where

$$\frac{\sigma_1\sigma_2\alpha_1\alpha_2}{\sigma_2\alpha_2^2 - \sigma_1\alpha_1^2} < d_1^* < \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2 - \sigma_1\beta_1^2},$$

and there exists a unique $d_2^* > 0$ so that $G_{v^*}(d) > 0$ if $d > d_2^*$, where

$$\frac{\sigma_1\sigma_2}{\sigma_1 - \sigma_2} < d_2^* < \frac{\sigma_1\sqrt{\sigma_1\sigma_2} + \sigma_1\sigma_2}{\sigma_1^2 - \sigma_2^2}(\alpha_2 - \alpha_1).$$

The two cases for the assertion of $v_1^*(d) > 0$ are thus concluded. Now let us discuss the positivity of $u_1^*(d)$. From (2.15), we have

$$\begin{cases} (a\alpha_2 - ad + d) - k(\alpha_1 + ad - d) = a\alpha_2 - k\alpha_1 - d(k+1)(a-1), \\ (b\beta_2 - bd + d) - b^2(\beta_1 + bd - d) = b(\beta_2 - b\beta_1) + d(b^2+1)(1-b). \end{cases} \tag{2.22}$$

Let

$$\begin{aligned} F_{u^*}(d) &:= a\alpha_2 - k\alpha_1 - d(k+1)(a-1), \\ G_{u^*}(d) &:= b(\beta_2 - b\beta_1) + d(b^2+1)(1-b). \end{aligned}$$

Then

$$F_{u^*}(d) = \frac{a^2-k}{k-b^2}G_{u^*}(d).$$

In addition, $u_1^* > 0$ if and only if $F_{u^*}(d) > 0$ if and only if $G_{u^*}(d) > 0$, due to $b^2 < k < a^2$. Let us discuss the signs of $F_{u^*}(d)$ and $G_{u^*}(d)$ in the following (a')-(d').

(a') $G_{u^*}(d) > 0$ if $d \leq \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}$: It is clear that $b \leq 1$ implies $G_{u^*}(d) > 0$, and $b \leq 1$ is equivalent to $d \leq \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}$. Thus, $G_{u^*}(d) > 0$ if $d \leq \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}$.

(b') $F_{u^*}(d) < 0$ if $d > \frac{\sigma_1}{\sigma_1-\sigma_2}(\alpha_2 - \alpha_1)$: If $b > 1$, then from $1 < b < \sqrt{k} < a < k$, we have

$$\begin{aligned} F_{u^*}(d) &= a\alpha_2 - k\alpha_1 - d(k+1)(a-1) \\ &< a\alpha_2 - a\alpha_1 - d(a+1)(a-1) \\ &= a(\alpha_2 - \alpha_1) - d(a^2 - 1) \\ &< k(\alpha_2 - \alpha_1) - d(k-1) \\ &< 0, \end{aligned}$$

if $d > \frac{k}{k-1}(\alpha_2 - \alpha_1) = \frac{\sigma_1}{\sigma_1-\sigma_2}(\alpha_2 - \alpha_1)$.

(c') Case (i): $\sigma_2\beta_2 < \sigma_1\beta_1$, i.e., $\frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2} < \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2}$ by (2.2). We claim that $F'_{u^*}(d) < 0$ for $d \le \frac{\sigma_2\beta_2}{\sigma_1+\sigma_2}$ and $G'_{u^*}(d) < 0$ for $d > \frac{\sigma_2\beta_2}{\sigma_1+\sigma_2}$. Notably,

$$F'_{u^*}(d) = [\beta_2 + \sigma_2 - d(k+1)]a' - (k+1)(a-1) \tag{2.23}$$

and

$$G'_{u^*}(d) = -(b^2+1)(b-1) - 2bb'd(b-1) - b'[d(b^2+1) + 2b\beta_1 - \beta_2], \tag{2.24}$$

by direct computations, where $a' = a'(d), b' = b'(d)$. For the first term of (2.23), we see that

$$\beta_2 + \sigma_2 - d(k+1) \ge \sigma_2 > 0 \ \text{ if } d \le \frac{\sigma_2\beta_2}{\sigma_1+\sigma_2}.$$

In addition, from (2.10), we compute

$$a' = -\frac{\sigma_1 a}{d\sqrt{\sigma_1^2 + 4kd^2}} < 0. \tag{2.25}$$

Hence, in (2.23), we confirm $F'_{u^*}(d) < 0$ for $d \le \frac{\sigma_2\beta_2}{\sigma_1+\sigma_2}$, due to $a > 1$ and $a' < 0$. Next, we discuss the third term of $G'_{u^*}(d)$ in (2.24), and claim that

$$d(b^2+1) + 2b\beta_1 - \beta_2 > 0 \ \text{ if } d > \frac{\sigma_2\beta_2}{\sigma_1+\sigma_2}.$$

From (2.10) and $b' > 0$ shown in (2.18), a direct computation shows

$$b > \frac{-\sigma_1(\sigma_1+\sigma_2) + \sqrt{\sigma_1^2(\sigma_1+\sigma_2)^2 + 4\sigma_1\sigma_2\beta_2^2}}{2\sigma_2\beta_2} \ \text{ if } d > \frac{\sigma_2\beta_2}{\sigma_1+\sigma_2}.$$

For $d > \frac{\sigma_2\beta_2}{\sigma_1+\sigma_2}$, we compute directly

$$\begin{aligned} & d(b^2+1) + 2b\beta_1 - \beta_2 \\ > \ & \frac{1}{2\sigma_2\beta_2(\sigma_1+\sigma_2)}[\sigma_1^2(\sigma_1+\sigma_2)^2 + 2\sigma_1\sigma_2\beta_2^2 + 2\sigma_2^2\beta_2^2] - \frac{\sigma_1\beta_1(\sigma_1+\sigma_2)}{\sigma_2\beta_2} - \beta_2 \\ + \ & \frac{1}{2\sigma_2\beta_2(\sigma_1+\sigma_2)}\left[(2\beta_1 - \sigma_1)(\sigma_1+\sigma_2)\sqrt{\sigma_1^2(\sigma_1+\sigma_2)^2 + 4\sigma_1\sigma_2\beta_2^2}\right] \end{aligned}$$

$$
\begin{aligned}
&= \frac{2\beta_1-\sigma_1}{2\sigma_2\beta_2}\left[\sqrt{\sigma_1^2(\sigma_1+\sigma_2)^2+4\sigma_1\sigma_2\beta_2^2}-\sigma_1(\sigma_1+\sigma_2)\right] \\
&> 0. \qquad (2.26)
\end{aligned}
$$

Note that $\frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2} < \frac{\sigma_2\beta_2}{\sigma_1+\sigma_2}$, according to Lemma 2.2(i). As seen in (b) above, $b > 1$ is equivalent to $d > \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}$. Thus, we see from (2.24) that $G'_{u^*}(d) < 0$ for $d > \frac{\sigma_2\beta_2}{\sigma_1+\sigma_2}$, due to (2.26), $b > 1$, and $b' > 0$.

(d') Case (ii): $\sigma_2\beta_2 > \sigma_1\beta_1$, i.e. $\frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2} > \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2}$ by (2.2). We claim that the third term of (2.24): $d(b^2+1)+2b\beta_1-\beta_2 > 0$ for $d \geq \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}$. If so, then it can be seen from (2.24) and $b' > 0$, that $G'_{u^*}(d) < 0$ for $d \geq \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}$ which is equivalent to $b \geq 1$. For $d \geq \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}$, we obtain

$$
\begin{aligned}
& d(b^2+1)+2b\beta_1-\beta_2 \\
\geq\ & 2\frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}+2\beta_1-\beta_2 \\
=\ & \frac{1}{\sigma_1-\sigma_2}[2\sigma_1\sigma_2+2\sigma_1\beta_1-2\sigma_2\beta_1-\sigma_1\beta_2+\sigma_2\beta_2] \\
>\ & \frac{1}{\sigma_1-\sigma_2}[2\sigma_1\sigma_2+3\sigma_1\beta_1-2\sigma_2\beta_1-\sigma_1\beta_2] \\
>\ & \frac{1}{\sigma_1-\sigma_2}[2\sigma_1\sigma_2+3\sigma_1\beta_1-2\sigma_2\beta_1-\sigma_1(\beta_1+\sigma_1+\sigma_2)] \\
=\ & 2\beta_1-\sigma_1 \\
>\ & 0,
\end{aligned}
$$

due to $\beta_1 > \sigma_1 > 0$ and $\beta_2-\beta_1 < \sigma_1+\sigma_2$, mentioned in Remark 1.

For case (i), we summarize properties (a')-(c'):

$$
\begin{cases}
G_{u^*}(d) > 0 \text{ if } d \leq \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2} \\
F_{u^*}(d) < 0 \text{ if } d > \frac{\sigma_1}{\sigma_1-\sigma_2}(\alpha_2-\alpha_1) \\
F'_{u^*}(d) < 0 \ \text{ for } d \leq \frac{\sigma_2\beta_2}{\sigma_1+\sigma_2} \\
G'_{u^*}(d) < 0 \ \text{ for } d > \frac{\sigma_2\beta_2}{\sigma_1+\sigma_2}.
\end{cases}
$$

Recall Lemma 2.2(i): $\frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2} < \frac{\sigma_2\beta_2}{\sigma_1+\sigma_2} < \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2}$, and that $G_{u^*}(d)$ and $F_{u^*}(d)$ have identical sign. There are two possibilities:

(I) $F_{u^*}(\frac{\sigma_2\beta_2}{\sigma_1+\sigma_2}) \geq 0$, i.e., $G_{u^*}(\frac{\sigma_2\beta_2}{\sigma_1+\sigma_2}) \geq 0$: As $G'_{u^*}(d) < 0$ for $d > \frac{\sigma_2\beta_2}{\sigma_1+\sigma_2}$ and $F_{u^*}(d) < 0$ if $d > \frac{\sigma_1}{\sigma_1-\sigma_2}(\alpha_2-\alpha_1)$, there exists a unique $d_3^* > 0$ such that $G_{u^*}(d_3^*) = 0$, where

$$
\frac{\sigma_2\beta_2}{\sigma_1+\sigma_2} \leq d_3^* < \frac{\sigma_1}{\sigma_1-\sigma_2}(\alpha_2-\alpha_1).
$$

(II) $F_{u^*}(\frac{\sigma_2\beta_2}{\sigma_1+\sigma_2}) < 0$, i.e., $G_{u^*}(\frac{\sigma_2\beta_2}{\sigma_1+\sigma_2}) < 0$: As $F_{u^*}(d) > 0$ for $d \leq \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}$, $F'_{u^*}(d) < 0$ for $d \leq \frac{\sigma_2\beta_2}{\sigma_1+\sigma_2}$, and $G'_{u^*}(d) < 0$ for $d > \frac{\sigma_2\beta_2}{\sigma_1+\sigma_2}$, we confirm that there exists a unique $d_3^* > 0$ such that $G_{u^*}(d_3^*) = 0$, where

$$
\frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2} < d_3^* < \min\left\{\frac{\sigma_2\beta_2}{\sigma_1+\sigma_2}, \frac{\sigma_1}{\sigma_1-\sigma_2}(\alpha_2-\alpha_1)\right\}.
$$

Both (I) and (II) indicate that there exists a unique $d_3^* > 0$ such that $G_{u^*}(d_3^*) = 0$, $G_{u^*}(d) > 0$ if $d < d_3^*$, and $G_{u^*}(d) < 0$ if $d > d_3^*$, where

$$\frac{\sigma_1\sigma_2}{\sigma_1 - \sigma_2} < d_3^* < \frac{\sigma_1}{\sigma_1 - \sigma_2}(\alpha_2 - \alpha_1).$$

For case (ii), from the above (a'), (b'), and (d'), we summarize

$$\begin{cases} G_{u^*}(d) > 0 \text{ if } d \le \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2} \\ F_{u^*}(d) < 0 \text{ if } d > \frac{\sigma_1}{\sigma_1-\sigma_2}(\alpha_2 - \alpha_1) \\ G'_{u^*}(d) < 0 \text{ if } d \ge \frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}. \end{cases}$$

We thus conclude that there exists a unique $d_3^* > 0$ such that $G_{u^*}(d_3^*) = 0$, $G_{u^*}(d) > 0$ if $d < d_3^*$, and $G_{u^*}(d) < 0$ if $d > d_3^*$, where

$$\frac{\sigma_1\sigma_2}{\sigma_1 - \sigma_2} < d_3^* < \frac{\sigma_1}{\sigma_1 - \sigma_2}(\alpha_2 - \alpha_1).$$

From (2.13), we see that $v_1^* \to \alpha_1 + ad - d > 0$ as $u_1^* \to 0^+$, i.e., u_1^* and v_1^* can not be zero simultaneously. From the above discussions, we confirm that $d_2^* < d_3^*$.

Combining the above discussions of two scenarios for $v_1^*(d) > 0$, and one single scenario for $u_1^*(d) > 0$, the assertions are thus justified, see Figure 2. □

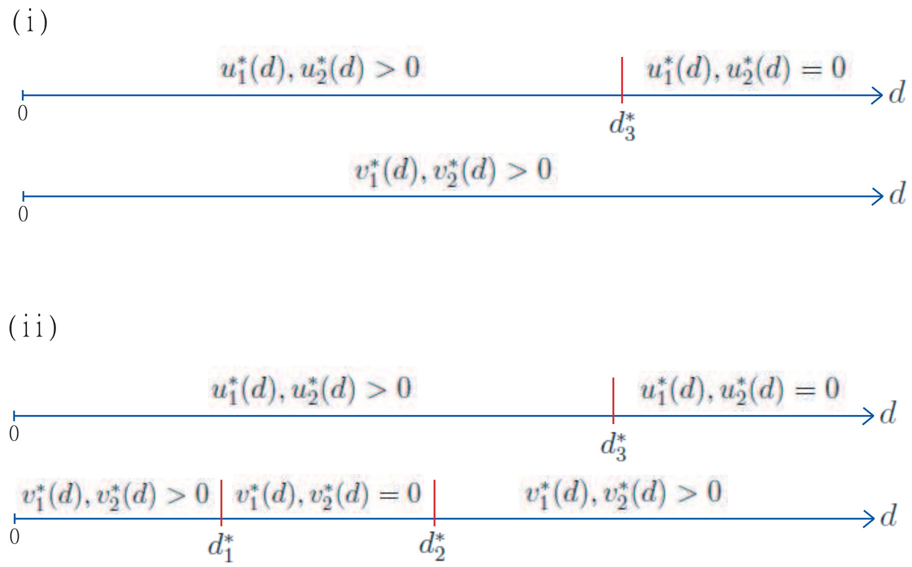

Figure 2. The existence of $u_1^*(d), u_2^*(d), v_1^*(d), v_2^*(d)$ with respect to d, in cases (i) and (ii) of Theorem 2.1 respectively.

Remark 2. (I) *Under conditions* (C) *and* (P)*, the proof of Theorem 2.1 actually indicate:*
(i) *If* $\sigma_2\beta_2 < \sigma_1\beta_1$ *and* $\beta_2 - \beta_1 \ge \sigma_1 + \sigma_2$*, then* $(u_1^*, u_2^*, v_1^*, v_2^*) \to (0, 0, \bar{v}_1, \bar{v}_2)$*, as* $d \to (d_3^*)^-$*, i.e., the positive equilibrium* $(u_1^*, u_2^*, v_1^*, v_2^*)$ *degenerates and merges into the semitrivial equilibrium* $(0, 0, \bar{v}_1, \bar{v}_2)$ *at* $d = d_3^*$.
(ii) *If* $\sigma_2\beta_2 > \sigma_1\beta_1$*, then* $(u_1^*, u_2^*, v_1^*, v_2^*) \to (\bar{u}_1, \bar{u}_2, 0, 0)$*, as* $d \to (d_1^*)^-$*, i.e., the positive equilibrium* $(u_1^*, u_2^*, v_1^*, v_2^*)$ *degenerates and merges into the semitrivial equilibrium* $(\bar{u}_1, \bar{u}_2, 0, 0)$ *at* $d = d_1^*$*;*

$(\bar{u}_1, \bar{u}_2, 0, 0) \to (u_1^*, u_2^*, v_1^*, v_2^*)$, *as* $d \to (d_2^*)^+$, *i.e., the semitrivial equilibrium* $(\bar{u}_1, \bar{u}_2, 0, 0)$ *becomes the positive equilibrium* $(u_1^*, u_2^*, v_1^*, v_2^*)$ *as the value of d increases through* d_2^*; $(u_1^*, u_2^*, v_1^*, v_2^*) \to (0, 0, \bar{v}_1, \bar{v}_2)$, *as* $d \to (d_3^*)^-$, *i.e., the positive equilibrium* $(u_1^*, u_2^*, v_1^*, v_2^*)$ *again degenerates and merges into the semitrivial equilibrium* $(0, 0, \bar{v}_1, \bar{v}_2)$ *at* $d = d_3^*$.

(II) *In Theorem 2.1*(ii)*, combining* $\sigma_2\beta_2 > \sigma_1\beta_1$ *and condition* (P) *yields* $\beta_2 - \beta_1 < \sigma_1 + \sigma_2$*, which is contrary to condition* $\beta_2 - \beta_1 \geq \sigma_1 + \sigma_2$ *in case* (i)*, as mentioned in Remark 1.*

(III) *Although the same symbol* d_3^* *is used in Theorem 2.1* (i) *and* (ii)*, they represent different values under assumptions in* (i) *and* (ii)*, respectively.*

(IV) *With the setting* $a := \frac{u_2^*}{u_1^*}, b := \frac{v_2^*}{v_1^*}$*, and subsequently* $ab = \frac{\sigma_1}{\sigma_2} =: k$*, we always have* $b^2 < k < a^2$*. Notably, in [24],* $0 < k \leq 1$ *under assumption* $\sigma_1 \leq \sigma_2$*, and hence* $b < 1$*. This is disparate from the situation in Theorem 2.1 that* $k > 1$*, and hence* $a > 1$*, due to* $\sigma_1 > \sigma_2$*.*

3. Stability analysis of semitrivial equilibria

In this section, we analyze the stability of the semitrivial equilibria for system (1.3). We denote by $(\bar{u}_1, \bar{u}_2, 0, 0)$ and $(0, 0, \bar{v}_1, \bar{v}_2)$ the semitrivial (boundary) equilibria for system (1.3), and by $\bar{u}_i(d)$ and $\bar{v}_i(d), i = 1, 2$, to express the dependence of $\bar{u}_i$ and $\bar{v}_i$ on d. In Appendix II, we recall some properties of semitrivial equilibria of system (1.3) in Propositions 3.7-3.10 of [24], which are independent of the order between σ_1 and σ_2. Herein, we add the following additional properties for the semitrivial equilibria, which shall be employed to discuss the stability of semitrivial equilibria.

Proposition 3.1. (i) *If* $\alpha_1 < \alpha_2$*, then* $\bar{u}_1'(d) > 0, \bar{u}_2'(d) < 0$*,* $\bar{u}_1''(d) < 0$*, and* $\bar{u}_2''(d) > 0$*, for all* $d > 0$*.*
(ii) *If* $\beta_1 < \beta_2$*, then* $\bar{v}_1'(d) > 0, \bar{v}_2'(d) < 0$*,* $\bar{v}_1''(d) < 0$*, and* $\bar{v}_2''(d) > 0$*, for all* $d > 0$*.*

Proof. (i) $(\bar{u}_1, \bar{u}_2, 0, 0)$ is an equilibrium of (1.3) if and only if $\bar{u}_1$ and $\bar{u}_2$ satisfy

$$\begin{aligned} \bar{u}_1(\alpha_1 - \bar{u}_1) + d(\bar{u}_2 - \bar{u}_1) = 0 \\ \bar{u}_2(\alpha_2 - \bar{u}_2) + d(\bar{u}_1 - \bar{u}_2) = 0. \end{aligned} \tag{3.1}$$

Differentiating (3.1) with respect to d, we obtain

$$\begin{aligned} (\alpha_1 - 2\bar{u}_1 - d)\bar{u}_1' + d\bar{u}_2' + \bar{u}_2 - \bar{u}_1 = 0 \\ (\alpha_2 - 2\bar{u}_2 - d)\bar{u}_2' + d\bar{u}_1' + \bar{u}_1 - \bar{u}_2 = 0, \end{aligned} \tag{3.2}$$

where $\bar{u}_i', i = 1, 2$, represent the derivatives of $\bar{u}_i$ with respect to d. Thus,

$$\bar{u}_1' = \frac{(\alpha_2 - 2\bar{u}_2)(\bar{u}_1 - \bar{u}_2)}{(\alpha_1 - 2\bar{u}_1 - d)(\alpha_2 - 2\bar{u}_2 - d) - d^2}, \tag{3.3}$$

$$\bar{u}_2' = \frac{(\alpha_1 - 2\bar{u}_1)(\bar{u}_2 - \bar{u}_1)}{(\alpha_1 - 2\bar{u}_1 - d)(\alpha_2 - 2\bar{u}_2 - d) - d^2}. \tag{3.4}$$

Note that

$$\begin{aligned} & (\alpha_1 - 2\bar{u}_1 - d)(\alpha_2 - 2\bar{u}_2 - d) - d^2 \\ = \; & (\alpha_1 - 2\bar{u}_1)(\alpha_2 - 2\bar{u}_2) - d(\alpha_1 - 2\bar{u}_1) - d(\alpha_2 - 2\bar{u}_2) \\ > \; & 0, \end{aligned}$$

by Proposition A.3 (in Appendix II). Thus $\bar{u}_1' > 0$ and $\bar{u}_2' < 0$. More detailed descriptions for $\bar{u}_1$ and $\bar{u}_2$ can be found in Proposition A.5. We further differentiate (3.2) with respect to d, and obtain

$$(\alpha_1 - 2\bar{u}_1 - d)\bar{u}_1'' + d\bar{u}_2'' = 2\bar{u}_1' - 2\bar{u}_2' + 2(\bar{u}_1')^2$$
$$(\alpha_2 - 2\bar{u}_2 - d)\bar{u}_2'' + d\bar{u}_1'' = 2\bar{u}_2' - 2\bar{u}_1' + 2(\bar{u}_2')^2.$$

Thus,

$$\bar{u}_1'' = 2\frac{(\alpha_2 - 2\bar{u}_2 - d)[\bar{u}_1' - \bar{u}_2' + (\bar{u}_1')^2] - d[\bar{u}_2' - \bar{u}_1' + (\bar{u}_2')^2]}{(\alpha_1 - 2\bar{u}_1 - d)(\alpha_2 - 2\bar{u}_2 - d) - d^2}$$
$$\bar{u}_2'' = 2\frac{(\alpha_1 - 2\bar{u}_1 - d)[\bar{u}_2' - \bar{u}_1' + (\bar{u}_2')^2] - d[\bar{u}_1' - \bar{u}_2' + (\bar{u}_1')^2]}{(\alpha_1 - 2\bar{u}_1 - d)(\alpha_2 - 2\bar{u}_2 - d) - d^2}.$$

Let us focus on the numerators. For $\bar{u}_1''$, we have

$$\begin{aligned} & (\alpha_2 - 2\bar{u}_2 - d)[\bar{u}_1' - \bar{u}_2' + (\bar{u}_1')^2] - d[\bar{u}_2' - \bar{u}_1' + (\bar{u}_2')^2] \\ = \; & (\alpha_2 - 2\bar{u}_2 - d)(\bar{u}_1')^2 + (\alpha_2 - 2\bar{u}_2)(\bar{u}_1' - \bar{u}_2') - d(\bar{u}_2')^2 \\ < \; & 0, \end{aligned}$$

due to $\bar{u}_1' > 0$, $\bar{u}_2' < 0$ for all $d > 0$, and Proposition A.3. Thus, $\bar{u}_1'' < 0$. For $\bar{u}_2''$, with (3.3) and (3.4), we have

$$\begin{aligned} & (\alpha_1 - 2\bar{u}_1 - d)[\bar{u}_2' - \bar{u}_1' + (\bar{u}_2')^2] - d[\bar{u}_1' - \bar{u}_2' + (\bar{u}_1')^2] \\ = \; & (\alpha_1 - 2\bar{u}_1 - d)(\bar{u}_2')^2 + (\alpha_1 - 2\bar{u}_1)(\bar{u}_2' - \bar{u}_1') - d(\bar{u}_1')^2 \\ = \; & (\alpha_1 - 2\bar{u}_1 - d)\left[\frac{(\alpha_1 - 2\bar{u}_1)(\bar{u}_2 - \bar{u}_1)}{(\alpha_1 - 2\bar{u}_1 - d)(\alpha_2 - 2\bar{u}_2 - d) - d^2}\right]^2 \\ + \; & (\alpha_1 - 2\bar{u}_1)\left[\frac{(\alpha_1 - 2\bar{u}_1)(\bar{u}_2 - \bar{u}_1)}{(\alpha_1 - 2\bar{u}_1 - d)(\alpha_2 - 2\bar{u}_2 - d) - d^2} - \frac{(\alpha_2 - 2\bar{u}_2)(\bar{u}_1 - \bar{u}_2)}{(\alpha_1 - 2\bar{u}_1 - d)(\alpha_2 - 2\bar{u}_2 - d) - d^2}\right] \\ - \; & d\left[\frac{(\alpha_2 - 2\bar{u}_2)(\bar{u}_1 - \bar{u}_2)}{(\alpha_1 - 2\bar{u}_1 - d)(\alpha_2 - 2\bar{u}_2 - d) - d^2}\right]^2 \\ = \; & \frac{(\bar{u}_2 - \bar{u}_1)}{[(\alpha_1 - 2\bar{u}_1 - d)(\alpha_2 - 2\bar{u}_2 - d) - d^2]^2} \cdot \\ & \Big\{(\alpha_1 - 2\bar{u}_1 - d)(\alpha_2 - \bar{u}_1 - \bar{u}_2)(\alpha_1 - 2\bar{u}_1)^2 - d(\alpha_1 - 2\bar{u}_1)^3 \\ & +(\alpha_2 - 2\bar{u}_2)^2[(\alpha_1 - 2\bar{u}_1 - d)(\alpha_1 - 2\bar{u}_1) - d(\bar{u}_2 - \bar{u}_1)]\Big\}. \end{aligned}$$

For the first two terms in the bracket,

$$(\alpha_1 - 2\bar{u}_1 - d)(\alpha_2 - \bar{u}_1 - \bar{u}_2)(\alpha_1 - 2\bar{u}_1)^2 - d(\alpha_1 - 2\bar{u}_1)^3 > 0,$$

by Proposition A.3. For the third term, using (3.1), we have

$$\begin{aligned} & (\alpha_2 - 2\bar{u}_2)^2[(\alpha_1 - 2\bar{u}_1 - d)(\alpha_1 - 2\bar{u}_1) - d(\bar{u}_2 - \bar{u}_1)] \\ = \; & (\alpha_2 - 2\bar{u}_2)^2[(\alpha_1 - 2\bar{u}_1)^2 - d(\alpha_1 - 2\bar{u}_1) - d(\bar{u}_2 - \bar{u}_1)] \end{aligned}$$

$$
\begin{aligned}
&= (\alpha_2 - 2\bar{u}_2)^2 \left\{ \left[d\left(1 - \frac{\bar{u}_2}{\bar{u}_1}\right) - \bar{u}_1 \right]^2 - d\left[d\left(1 - \frac{\bar{u}_2}{\bar{u}_1}\right) - \bar{u}_1 \right] - d(\bar{u}_2 - \bar{u}_1) \right\} \\
&= (\alpha_2 - 2\bar{u}_2)^2 \left\{ d^2\left(1 - \frac{\bar{u}_2}{\bar{u}_1}\right)^2 - d^2\left(1 - \frac{\bar{u}_2}{\bar{u}_1}\right) + d\bar{u}_2 + \bar{u}_1^2 \right\} \\
&> 0,
\end{aligned}
$$

since $\bar{u}_1 < \bar{u}_2$. Thus, $\bar{u}_2'' > 0$.

Part (ii) can be obtained by arguments similar to those for (i), using

$$
\begin{aligned}
&\bar{v}_1(\beta_1 - \bar{v}_1) + d(\bar{v}_2 - \bar{v}_1) = 0 \\
&\bar{v}_2(\beta_2 - \bar{v}_2) + d(\bar{v}_1 - \bar{v}_2) = 0.
\end{aligned} \tag{3.5}
$$

This completes the proof. □

Propositions A.3-A.6, in Appendix II, and Proposition 3.1 are independent of the order between σ_1 and σ_2. Some of the following properties for the semitrivial equilibria hold under $\sigma_2 < \sigma_1$. The following notations will be helpful to recognize various related quantities:

$$
\begin{aligned}
d_1 &:= \frac{\sigma_1\sigma_2(\sigma_1^2 + \sigma_2^2 + \sigma_2\beta_2 - \sigma_1\beta_1)}{(\sigma_1 - \sigma_2)(\sigma_1^2 + \sigma_2^2)}, \\
d_2 &:= \frac{\sigma_1\sigma_2}{\sigma_1 - \sigma_2}, \\
d_3 &:= \frac{\beta_1\beta_2(\sigma_2\beta_1 + \sigma_1\beta_2)}{(\beta_2 - \beta_1)(\beta_1^2 + \beta_2^2)}, \\
d_4 &:= \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2 - \sigma_1\beta_1^2}, \\
d_5 &:= \frac{\sqrt{\sigma_1\sigma_2}(\sqrt{\sigma_2}\alpha_2 - \sqrt{\sigma_1}\alpha_1)}{(\sigma_1 + \sigma_2)(\sqrt{\sigma_1} - \sqrt{\sigma_2})}.
\end{aligned}
$$

Proposition 3.2. *Under conditions* (C) *and* (P)*, the following relationships among parameters hold:*
(I) $\frac{\bar{u}_2}{\bar{u}_1}(d)$ *is strictly decreasing with respect to d.*
(II) *If* $\frac{\bar{u}_2}{\bar{u}_1} = \frac{\sigma_1}{\sigma_2}$, *then* $d = d_1$.
(III) *If* $\frac{\bar{u}_2}{\bar{u}_1} = \frac{\beta_2}{\beta_1}$, *then* $d = d_3$.
(IV) *If* $\frac{\bar{u}_2}{\bar{u}_1} = \frac{\sqrt{\sigma_1}}{\sqrt{\sigma_2}}$, *then* $d = d_5$.
(V) (i) *If* $\sigma_2\beta_2 < \sigma_1\beta_1$, *then* $\frac{\sigma_1}{\sigma_2} > \frac{\beta_2}{\beta_1}$ *and* $d_1 < d_2 < d_3 < d_4$.
(ii) *If* $\sigma_2\beta_2 > \sigma_1\beta_1$, *then* $\frac{\sigma_1}{\sigma_2} < \frac{\beta_2}{\beta_1}$ *and* $d_1 > d_2 > d_3 > d_4$.
(iii) *If* $\sigma_2\beta_2 = \sigma_1\beta_1$, *then* $\frac{\sigma_1}{\sigma_2} = \frac{\beta_2}{\beta_1}$ *and* $d_1 = d_2 = d_3 = d_4$.

Proof. (I) The assertion follows from $\bar{u}_1'(d) > 0, \bar{u}_2'(d) < 0$, as in the proof of Proposition 3.1.

(II) If $\frac{\bar{u}_2}{\bar{u}_1} = \frac{\sigma_1}{\sigma_2}$, with $\bar{u}_1$ and $\bar{u}_2$ satisfying (3.1), we have

$$
\begin{aligned}
&\alpha_1 - \bar{u}_1 + d(\frac{\sigma_1}{\sigma_2} - 1) = 0 \\
&\alpha_2 - \frac{\sigma_1}{\sigma_2}\bar{u}_1 + d(\frac{\sigma_2}{\sigma_1} - 1) = 0.
\end{aligned}
$$

By eliminating $\bar{u}_1$, we have

$$d\left(\frac{\sigma_1^3 - \sigma_1^2\sigma_2 - \sigma_2^3 + \sigma_1\sigma_2^2}{\sigma_1^2\sigma_2}\right) = \frac{\sigma_2\alpha_2 - \sigma_1\alpha_1}{\sigma_1}.$$

Then

$$d = \frac{\sigma_1\sigma_2(\sigma_1^2 + \sigma_2^2 + \sigma_2\beta_2 - \sigma_1\beta_1)}{(\sigma_1 - \sigma_2)(\sigma_1^2 + \sigma_2^2)} = d_1,$$

due to $\alpha_2 = \beta_2 + \sigma_2$ and $\alpha_1 = \beta_1 - \sigma_1$.

Cases (III) and (IV) can be obtained by arguments similar to those for (II). Now let us prove (V), and the assertions will be justified by the following (a)-(c):

(a) It is clear that

$$d_2 - d_1 \begin{cases} > 0 & \text{if } \sigma_2\beta_2 < \sigma_1\beta_1 \\ = 0 & \text{if } \sigma_2\beta_2 = \sigma_1\beta_1 \\ < 0 & \text{if } \sigma_2\beta_2 > \sigma_1\beta_1. \end{cases}$$

(b) We see that

$$d_3 - d_2 \begin{cases} > 0 & \text{if } \sigma_2\beta_2 < \sigma_1\beta_1 \\ = 0 & \text{if } \sigma_2\beta_2 = \sigma_1\beta_1 \\ < 0 & \text{if } \sigma_2\beta_2 > \sigma_1\beta_1. \end{cases}$$

as, by a direct calculation,

$$d_3 - d_2 = \frac{(\sigma_1\beta_2^2 + \sigma_2\beta_1^2)(\sigma_1\beta_1 - \sigma_2\beta_2)}{(\sigma_1 - \sigma_2)(\beta_2 - \beta_1)(\beta_1^2 + \beta_2^2)}.$$

(c) It holds that

$$d_4 - d_3 \begin{cases} > 0 & \text{if } \sigma_2\beta_2 < \sigma_1\beta_1 \\ = 0 & \text{if } \sigma_2\beta_2 = \sigma_1\beta_1 \\ < 0 & \text{if } \sigma_2\beta_2 > \sigma_1\beta_1 \end{cases}$$

due to

$$d_4 - d_3 = \frac{(\sigma_1 + \sigma_2)\beta_1^2\beta_2^2(\sigma_1\beta_1 - \sigma_2\beta_2)}{(\sigma_2\beta_2^2 - \sigma_1\beta_1^2)(\beta_2 - \beta_1)(\beta_1^2 + \beta_2^2)}.$$

This completes the proof. □

In Appendix I, we compute the Jacobian matrix for system (1.3). At $(\bar{u}_1, \bar{u}_2, 0, 0)$, the Jacobian matrix is

$$\begin{bmatrix} \alpha_1 - 2\bar{u}_1 - d & d & -\bar{u}_1 & 0 \\ d & \alpha_2 - 2\bar{u}_2 - d & 0 & -\bar{u}_2 \\ 0 & 0 & \beta_1 - \bar{u}_1 - d & d \\ 0 & 0 & d & \beta_2 - \bar{u}_2 - d \end{bmatrix}, \tag{3.6}$$

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

$$\begin{bmatrix} \alpha_1-\bar{v}_1-d & d & 0 & 0 \\ d & \alpha_2-\bar{v}_2-d & 0 & 0 \\ -\bar{v}_1 & 0 & \beta_1-2\bar{v}_1-d & d \\ 0 & -\bar{v}_2 & d & \beta_2-2\bar{v}_2-d \end{bmatrix}. \tag{3.7}$$

First, let us focus on the stability of semitrivial equilibrium $(\bar{u}_1,\bar{u}_2,0,0)$, by calculating the eigenvalues of the following submatrices in (3.6):

$$\begin{bmatrix} \alpha_1-2\bar{u}_1-d & d \\ d & \alpha_2-2\bar{u}_2-d \end{bmatrix} \text{ and } \begin{bmatrix} \beta_1-\bar{u}_1-d & d \\ d & \beta_2-\bar{u}_2-d \end{bmatrix}. \tag{3.8}$$

Theorem 3.3. *Assume that conditions* (C) *and* (P) *hold for system* (1.3).
(i) *If $\sigma_2\beta_2<\sigma_1\beta_1$ and $\beta_2-\beta_1\geq\sigma_1+\sigma_2$, the semitrivial equilibrium $(\bar{u}_1,\bar{u}_2,0,0)$ is unstable for all $d>0$.*
(ii) *If $\sigma_2\beta_2>\sigma_1\beta_1$, there exist $\bar{d}_1,\bar{d}_2>0$, with $\bar{d}_1<\bar{d}_2$, so that the semitrivial equilibrium $(\bar{u}_1,\bar{u}_2,0,0)$ is unstable when $d<\bar{d}_1$ or $d>\bar{d}_2$ and is asymptotically stable when $\bar{d}_1<d<\bar{d}_2$.*
In addition,

$$\frac{\sigma_1\sigma_2\alpha_1\alpha_2}{\sigma_2\alpha_2^2-\sigma_1\alpha_1^2}<\bar{d}_1<\frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2},$$
$$\frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2}<\bar{d}_2<\frac{\sigma_1\sqrt{\sigma_1\sigma_2}+\sigma_1\sigma_2}{\sigma_1^2-\sigma_2^2}(\alpha_2-\alpha_1).$$

Proof. Under condition (C), the two eigenvalues of the first matrix in (3.8) are negative by Gerschgorin's Theorem and Proposition A.3. Thus, the stability of $(\bar{u}_1,\bar{u}_2,0,0)$ is determined by the two eigenvalues, denoted by $\lambda_\mp$, of the second matrix in (3.8). By a direct calculation, the two eigenvalues are

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

First, we consider $\lambda_-=\lambda_-(d)$ and claim $\lambda_-(d)<0$ for all $d>0$. From condition (C) and Proposition A.3, we have

$$\beta_1-\bar{u}_1+\beta_2-\bar{u}_2=(\sigma_1-\sigma_2)+d\left[2-\left(\frac{\bar{u}_2}{\bar{u}_1}+\frac{\bar{u}_1}{\bar{u}_2}\right)\right],$$

and

$$\beta_1-\bar{u}_1-\beta_2+\bar{u}_2=(\sigma_1+\sigma_2)+d\left(\frac{\bar{u}_1}{\bar{u}_2}-\frac{\bar{u}_2}{\bar{u}_1}\right).$$

Then

$$\begin{aligned} \lambda_- &= \frac{1}{2}\left[(\beta_1-\bar{u}_1+\beta_2-\bar{u}_2-2d)-\sqrt{(\beta_1-\bar{u}_1-\beta_2+\bar{u}_2)^2+4d^2}\right] \\ &= \frac{1}{2}\left[(\sigma_1-\sigma_2)-d\left(\frac{\bar{u}_2}{\bar{u}_1}+\frac{\bar{u}_1}{\bar{u}_2}\right)-\sqrt{\left[(\sigma_1+\sigma_2)+d\left(\frac{\bar{u}_1}{\bar{u}_2}-\frac{\bar{u}_2}{\bar{u}_1}\right)\right]^2+4d^2}\right] \end{aligned}$$

$$< \frac{1}{2}\left[(\sigma_1-\sigma_2)-d\left(\frac{\bar u_2}{\bar u_1}+\frac{\bar u_1}{\bar u_2}\right)-\left|(\sigma_1+\sigma_2)+d\left(\frac{\bar u_1}{\bar u_2}-\frac{\bar u_2}{\bar u_1}\right)\right|\right].$$

We obtain

$$\lambda_- < -\sigma_2 - d\frac{\bar u_1}{\bar u_2} < 0,$$

if $(\sigma_1+\sigma_2)+d\left(\frac{\bar u_1}{\bar u_2}-\frac{\bar u_2}{\bar u_1}\right)\geq 0$, and

$$\lambda_- < \sigma_1 - d\frac{\bar u_2}{\bar u_1} < 0,$$

if $(\sigma_1+\sigma_2)+d\left(\frac{\bar u_1}{\bar u_2}-\frac{\bar u_2}{\bar u_1}\right)< 0$. Consequently, $\lambda_-(d)<0$ for all $d>0$.

Next, we identify the sign of $\lambda_+=\lambda_+(d)$. Note that $\lambda_+(d)\geq 0$ if and only if

$$|\beta_1-\bar u_1+\beta_2-\bar u_2-2d| \leq \sqrt{(\beta_1-\bar u_1-\beta_2+\bar u_2)^2+4d^2},$$

equivalently,

$$(\beta_1-\bar u_1)(\beta_2-\bar u_2)-d(\beta_1-\bar u_1+\beta_2-\bar u_2)\leq 0. \tag{3.9}$$

As $\beta_1=\alpha_1+\sigma_1$ and $\beta_2=\alpha_2-\sigma_2$, (3.9) can be expressed by

$$(\alpha_1-\bar u_1+\sigma_1)(\alpha_2-\bar u_2-\sigma_2)-d[\alpha_1-\bar u_1+\alpha_2-\bar u_2+(\sigma_1-\sigma_2)]\leq 0,$$

i.e.,

$$\left[d\left(1-\frac{\bar u_2}{\bar u_1}\right)+\sigma_1\right]\left[d\left(1-\frac{\bar u_1}{\bar u_2}\right)-\sigma_2\right]-d^2\left[2-\left(\frac{\bar u_2}{\bar u_1}+\frac{\bar u_1}{\bar u_2}\right)\right]-d(\sigma_1-\sigma_2)\leq 0,$$

using (3.1). This inequality can be simplified to

$$d\left(\sigma_2\frac{\bar u_2}{\bar u_1}-\sigma_1\frac{\bar u_1}{\bar u_2}\right)-\sigma_1\sigma_2\leq 0. \tag{3.10}$$

From (3.10), we define

$$g(d):=d\left(\sigma_2\frac{\bar u_2(d)}{\bar u_1(d)}-\sigma_1\frac{\bar u_1(d)}{\bar u_2(d)}\right)-\sigma_1\sigma_2. \tag{3.11}$$

Then $\lambda_+(d)\geq 0$ if and only if $g(d)\leq 0$. According to Propositions A.3 and A.5, we have that $1<\frac{\bar u_2(d)}{\bar u_1(d)}<\frac{\alpha_2}{\alpha_1}$ and $\frac{\bar u_2(d)}{\bar u_1(d)}$ decreases from $\frac{\alpha_2}{\alpha_1}$ to 1 as d increases from 0 to ∞. Thus, $g(0)=-\sigma_1\sigma_2$ and $g(d)\to-\infty$ as $d\to\infty$, because of $\sigma_1>\sigma_2$. More precisely,

$$\begin{aligned} g(d) &= d\left(\sigma_2\frac{\bar u_2}{\bar u_1}-\sigma_1\frac{\bar u_1}{\bar u_2}\right)-\sigma_1\sigma_2 \\ &< d\left(\sigma_2\frac{\alpha_2}{\alpha_1}-\sigma_1\frac{\alpha_1}{\alpha_2}\right)-\sigma_1\sigma_2 \\ &= d\left(\frac{\sigma_2\alpha_2^2-\sigma_1\alpha_1^2}{\alpha_1\alpha_2}\right)-\sigma_1\sigma_2 \\ &\leq 0,\quad \text{if } d\leq\frac{\sigma_1\sigma_2\alpha_1\alpha_2}{\sigma_2\alpha_2^2-\sigma_1\alpha_1^2}. \end{aligned} \tag{3.12}$$

Note that $\frac{\bar{u}_2(d)}{\bar{u}_1(d)} \le \frac{\sqrt{\sigma_1}}{\sqrt{\sigma_2}}$ is equivalent to $d \ge d_5$, by Proposition 3.2. Hence,

$$\begin{aligned} g(d) &= d\left(\sigma_2\frac{\bar{u}_2}{\bar{u}_1} - \sigma_1\frac{\bar{u}_1}{\bar{u}_2}\right) - \sigma_1\sigma_2 \\ &\le d\left(\sigma_2\frac{\sqrt{\sigma_1}}{\sqrt{\sigma_2}} - \sigma_1\frac{\sqrt{\sigma_2}}{\sqrt{\sigma_1}}\right) - \sigma_1\sigma_2 \\ &= -\sigma_1\sigma_2 \\ &< 0, \text{ if } \frac{\bar{u}_2(d)}{\bar{u}_1(d)} \le \frac{\sqrt{\sigma_1}}{\sqrt{\sigma_2}}. \end{aligned}$$

Thus,

$$g(d) < 0 \text{ if } d \ge d_5. \tag{3.13}$$

A direct calculation yields

$$g'(d) = \left(\sigma_2\frac{\bar{u}_2}{\bar{u}_1} - \sigma_1\frac{\bar{u}_1}{\bar{u}_2}\right) + d\left[\sigma_2(\frac{\bar{u}_2}{\bar{u}_1})' - \sigma_1(\frac{\bar{u}_1}{\bar{u}_2})'\right]. \tag{3.14}$$

We know $\sigma_2(\frac{\bar{u}_2}{\bar{u}_1})' - \sigma_1(\frac{\bar{u}_1}{\bar{u}_2})' < 0$ for all $d > 0$, due to $\bar{u}_1' > 0$ and $\bar{u}_2' < 0$, as in the proof of Proposition 3.1 or by Proposition A.5; $\sigma_2\frac{\bar{u}_2}{\bar{u}_1} - \sigma_1\frac{\bar{u}_1}{\bar{u}_2} = \frac{\sigma_2\alpha_2^2 - \sigma_1\alpha_1^2}{\alpha_1\alpha_2} > 0$ when $d = 0$, by Lemma 2.1(ii); $\sigma_2\frac{\bar{u}_2}{\bar{u}_1} - \sigma_1\frac{\bar{u}_1}{\bar{u}_2} \to \sigma_2 - \sigma_1 < 0$ as $d \to +\infty$, due to Propositions A.3 and A.5. That is, $\sigma_2\frac{\bar{u}_2}{\bar{u}_1} - \sigma_1\frac{\bar{u}_1}{\bar{u}_2}$ decreases from $\frac{\sigma_2\alpha_2^2 - \sigma_1\alpha_1^2}{\alpha_1\alpha_2}$ to $-(\sigma_1 - \sigma_2)$ as d increases from 0 to $+\infty$. On the other hand, by (3.1), we have

$$\begin{cases} d\left(\frac{\bar{u}_2}{\bar{u}_1}\right)' = 1 - \frac{\bar{u}_2}{\bar{u}_1} + \bar{u}_1' \\ d\left(\frac{\bar{u}_1}{\bar{u}_2}\right)' = 1 - \frac{\bar{u}_1}{\bar{u}_2} + \bar{u}_2'. \end{cases} \tag{3.15}$$

With (3.15), we reexpress (3.14) as

$$g'(d) = \sigma_2 - \sigma_1 + \sigma_2\bar{u}_1' - \sigma_1\bar{u}_2'. \tag{3.16}$$

It follows that

$$g''(d) = \sigma_2\bar{u}_1'' - \sigma_1\bar{u}_2'' < 0,$$

by Proposition 3.1. Thus, the graph of $g(d)$ is concave downward. Therefore, there are two possible situations based on the above analysis: (i) $g(d) < 0$ for all $d > 0$, (ii) there exist $\bar{d}_1, \bar{d}_2 > 0$ such that $g(\bar{d}_1) = g(\bar{d}_2) = 0$, and

$$\begin{cases} g(d) < 0 \text{ if } d < \bar{d}_1 \text{ or } d > \bar{d}_2 \\ g(d) > 0 \text{ if } \bar{d}_1 < d < \bar{d}_2. \end{cases}$$

The graphs of $g(d)$ are illustrated in Figure 3. Accordingly, there are two possibilities for λ_+: (i) $\lambda_+ > 0$ for all $d > 0$, (ii) there exist $\bar{d}_1, \bar{d}_2 > 0$ such that $\lambda_+ = 0$ for $d = \bar{d}_1, \bar{d}_2$ and

$$\begin{cases} \lambda_+ > 0 \text{ if } d < \bar{d}_1 \text{ or } d > \bar{d}_2 \\ \lambda_+ < 0 \text{ if } \bar{d}_1 < d < \bar{d}_2. \end{cases}$$

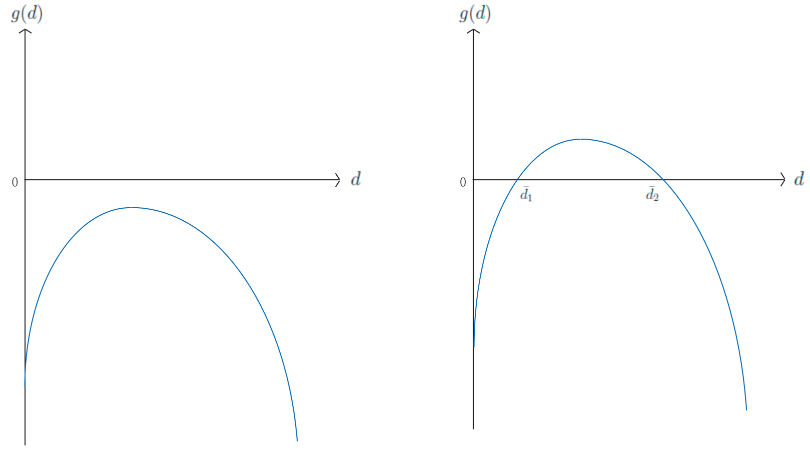

Figure 3. Two situations for $g(d)$, regarding the sign of λ_+ in Theorem 3.3.

Now we investigate the two situations by analyzing $g(d)$ and the stationary equation (3.1). To determine the behavior of g, we seek for its equivalent expression. Let $w := \frac{\bar{u}_2}{\bar{u}_1}$. As $\frac{\bar{u}_2}{\bar{u}_1}(d)$ is strictly decreasing with respect to d, by Proposition 3.2(I), the one-to-one correspondence between d and w can be derived from the stationary equation for $\bar{u}_1$ and $\bar{u}_2$ in (3.1):

$$d = \frac{\alpha_2 - w\alpha_1}{(w-1)(w+\frac{1}{w})}, \tag{3.17}$$

where $1 < w < \frac{\alpha_2}{\alpha_1}$, by Proposition A.5. Then

$$\begin{aligned} g(d) &= d\left(\sigma_2\frac{\bar{u}_2}{\bar{u}_1} - \sigma_1\frac{\bar{u}_1}{\bar{u}_2}\right) - \sigma_1\sigma_2 \\ &= d\left(\frac{\sigma_2 w^2 - \sigma_1}{w}\right) - \sigma_1\sigma_2 \\ &= \left(\frac{\alpha_2 - w\alpha_1}{(w-1)(w+\frac{1}{w})}\right)\left(\frac{\sigma_2 w^2 - \sigma_1}{w}\right) - \sigma_1\sigma_2 \\ &= \frac{(\alpha_2 - w\alpha_1)(\sigma_2 w^2 - \sigma_1) - \sigma_1\sigma_2(w-1)(w^2+1)}{(w-1)(w^2+1)} \\ &=: f(w). \end{aligned}$$

Let us define $q(w) := (\alpha_2 - w\alpha_1)(\sigma_2 w^2 - \sigma_1) - \sigma_1\sigma_2(w-1)(w^2+1)$, which is the numerator of $f(w)$, and thus $f(w) = \frac{q(w)}{(w-1)(w^2+1)}$. Note that

$$\begin{aligned} q(w) &= (\alpha_2 - w\alpha_1)(\sigma_2 w^2 - \sigma_1) - \sigma_1\sigma_2(w-1)(w^2+1) \\ &= (\beta_2 - w\beta_1)(\sigma_2 w^2 - \sigma_1) + w(\sigma_1+\sigma_2)(\sigma_2 w - \sigma_1), \end{aligned} \tag{3.18}$$

by $\beta_1 = \alpha_1 + \sigma_1$ and $\beta_2 = \alpha_2 - \sigma_2$. Thus, we have

$$g(d) < 0 \Leftrightarrow f(w) < 0 \Leftrightarrow q(w) < 0, \tag{3.19}$$

due to $(w-1)(w^2+1) > 0$. In addition,

$$f'(w) = \frac{q'(w)(w-1)(w^2+1) - q(w)(3w^2-2w+1)}{(w-1)^2(w^2+1)^2}, \tag{3.20}$$

where

$$q'(w) = 2\sigma_2 w(\beta_2 - w\beta_1) + (\sigma_1+\sigma_2)(\sigma_2 w - \sigma_1) - \sigma_2\beta_1 w^2 + \sigma_2(\sigma_1+\sigma_2)w + \sigma_1\beta_1. \tag{3.21}$$

Notice that

$$f'(w) < 0 \Leftrightarrow g'(d) > 0,$$

according to Proposition 3.2(I). By a direct computation in (3.18), we obtain

$$q(\frac{\sigma_1}{\sigma_2}) = \frac{\sigma_1}{\sigma_2^2}(\sigma_1-\sigma_2)(\sigma_2\beta_2 - \sigma_1\beta_1)\begin{cases} <0 & \text{if } \sigma_2\beta_2 < \sigma_1\beta_1 \\ =0 & \text{if } \sigma_2\beta_2 = \sigma_1\beta_1 \\ >0 & \text{if } \sigma_2\beta_2 > \sigma_1\beta_1, \end{cases} \tag{3.22}$$

and

$$q(\frac{\beta_2}{\beta_1}) = \frac{\beta_2}{\beta_1^2}(\sigma_1+\sigma_2)(\sigma_2\beta_2 - \sigma_1\beta_1)\begin{cases} <0 & \text{if } \sigma_2\beta_2 < \sigma_1\beta_1 \\ =0 & \text{if } \sigma_2\beta_2 = \sigma_1\beta_1 \\ >0 & \text{if } \sigma_2\beta_2 > \sigma_1\beta_1. \end{cases} \tag{3.23}$$

Case (i) $\sigma_2\beta_2 < \sigma_1\beta_1$, i.e., $\frac{\beta_2}{\beta_1} < \frac{\sigma_1}{\sigma_2}$: We first claim that $q(w) < 0$ for all $\frac{\beta_2}{\beta_1} < w < \frac{\sigma_1}{\sigma_2}$. Consider $w = \frac{\beta_2}{\beta_1} + \delta$, with $\delta > 0$ satisfying $\frac{\beta_2}{\beta_1} < w = \frac{\beta_2+\delta\beta_1}{\beta_1} < \frac{\sigma_1}{\sigma_2}$. Hence, $\sigma_2(\beta_2+\delta\beta_1) < \sigma_1\beta_1$. From (3.18), we obtain

$$\begin{aligned} q(w = \frac{\beta_2+\delta\beta_1}{\beta_1}) &= -\frac{\delta}{\beta_1}[\sigma_2(\beta_2+\delta\beta_1)^2 - \sigma_1\beta_1^2] \\ &- \frac{1}{\beta_1^2}\{(\sigma_1+\sigma_2)(\beta_2+\delta\beta_1)[\sigma_1\beta_1 - \sigma_2(\beta_2+\delta\beta_1)]\} \\ &< 0, \end{aligned}$$

by $\sigma_2\beta_2^2 - \sigma_1\beta_1^2 > 0$ from condition (P), and $\sigma_1\beta_1 > \sigma_2(\beta_2+\delta\beta_1)$.

Next, we will show that $f'(\frac{\sigma_1}{\sigma_2}) < 0$ and $f'(\frac{\beta_2}{\beta_1}) > 0$. From (3.20) and (3.21), at $w = \frac{\sigma_1}{\sigma_2}$, a direct calculation yields

$$\begin{aligned} & q'(w)(w-1)(w^2+1) - q(w)(3w^2-2w+1) \\ = & \frac{\sigma_1(\sigma_1-\sigma_2)}{\sigma_2^2}\left\{\frac{\sigma_1^2}{\sigma_2^2}[-\sigma_2\beta_2 + \sigma_2\beta_1 + \sigma_2(\sigma_1+\sigma_2)] + [-\sigma_1\beta_1 + \sigma_2\beta_1 + \sigma_2(\sigma_1+\sigma_2)]\right\} \\ + & \frac{\sigma_1(\sigma_1-\sigma_2)}{\sigma_2^2}\left(2\frac{\sigma_1}{\sigma_2}+1\right)(\sigma_2\beta_2 - \sigma_1\beta_1) \\ < & \frac{\sigma_1(\sigma_1-\sigma_2)}{\sigma_2^2}\left[-\sigma_2\left(\frac{\sigma_1^2}{\sigma_2^2}+1\right)(\beta_2-\beta_1-\sigma_1-\sigma_2) - \left(2\frac{\sigma_1}{\sigma_2}+1\right)(\sigma_1\beta_1 - \sigma_2\beta_2)\right] \end{aligned}$$

$$< \ 0,$$

because of $\beta_2 - \beta_1 \geq \sigma_1 + \sigma_2$. Thus, $f'(\frac{\sigma_1}{\sigma_2}) < 0$ by (3.20) and $(w-1)^2(w^2+1)^2 > 0$. Similarly, from (3.20) and (3.21), at $w = \frac{\beta_2}{\beta_1}$, we have

$$\begin{aligned}
& q'(w)(w-1)(w^2+1) - q(w)(3w^2 - 2w + 1) \\
= \ & \frac{1}{\beta_1^4}[(\sigma_1+\sigma_2)(\sigma_1\beta_1 - \sigma_2\beta_2)(2\beta_2^3 + \beta_1^3 - \beta_1\beta_2^2)] \\
+ \ & \frac{1}{\beta_1^4}\{(\beta_2-\beta_1)(\beta_1^2+\beta_2^2)[-\sigma_2\beta_2^2 + \sigma_1\beta_1^2 + \sigma_2\beta_2(\sigma_1+\sigma_2)]\} \\
> \ & \frac{1}{\beta_1^4}[(\sigma_1+\sigma_2)(\sigma_1\beta_1 - \sigma_2\beta_2)(\beta_2^3 + 2\beta_1^3 - \beta_1^2\beta_2)] \\
> \ & 0,
\end{aligned}$$

due to condition (P), i.e., $\sigma_2\beta_2^2 < \sigma_1\beta_1(\beta_1+\sigma_1+\sigma_2)$ in (2.1). Thus, $f'(\frac{\beta_2}{\beta_1}) > 0$ by (3.20) and $(w-1)^2(w^2+1)^2 > 0$.

Consequently, by (3.19) and concavity of $g(d)$, we conclude $f(w) < 0$ for all $1 < w = \frac{\bar{u}_2}{\bar{u}_1} < \frac{\alpha_2}{\alpha_2}$, i.e., $g(d) < 0$ for all $d > 0$, i.e., $\lambda_+ > 0$ for all $d > 0$.

Case (ii) $\sigma_2\beta_2 > \sigma_1\beta_1$, i.e., $\frac{\beta_2}{\beta_1} > \frac{\sigma_1}{\sigma_2}$: We claim that $q(w) > 0$ for all $\frac{\beta_2}{\beta_1} > w > \frac{\sigma_1}{\sigma_2}$. Consider $w = \frac{\sigma_1}{\sigma_2} + \delta$, with $\delta > 0$ satisfying $\frac{\beta_2}{\beta_1} > w = \frac{\sigma_1+\delta\sigma_2}{\sigma_2} > \frac{\sigma_1}{\sigma_2}$. Hence, $\sigma_2\beta_2 > (\sigma_1+\delta\sigma_2)\beta_1$. From (3.18), we compute

$$\begin{aligned}
q(w = \frac{\sigma_1+\delta\sigma_2}{\sigma_2}) \ &= \ \delta(\sigma_1+\sigma_2)(\sigma_1+\delta\sigma_2) \\
&+ \ \frac{1}{\sigma_2^2}[(\sigma_1+\delta\sigma_2)^2 - \sigma_1\sigma_2][\sigma_2\beta_2 - (\sigma_1+\delta\sigma_2)\beta_1] \\
&> \ 0,
\end{aligned}$$

owing to $\sigma_1 > \sigma_2$ and $\sigma_2\beta_2 > (\sigma_1+\delta\sigma_2)\beta_1$. Combining (3.22) with (3.23), we have $q(w) > 0$ for all $\frac{\beta_2}{\beta_1} \geq w \geq \frac{\sigma_1}{\sigma_2}$. That is, $g(d) > 0$ if $d_3 \leq d \leq d_1$, by Proposition 3.2. Recall the relationship between d and $w(d) = \frac{\bar{u}_2(d)}{\bar{u}_1(d)}$ in Proposition 3.2. We will use the relationship to estimate $\bar{d}_1$ and $\bar{d}_2$. For $\frac{\bar{u}_2}{\bar{u}_1} > \frac{\beta_2}{\beta_1}$, we have $d < d_3$ by Proposition 3.2, and then

$$g(d) > d\left(\frac{\sigma_2\beta_2^2 - \sigma_1\beta_1^2}{\beta_1\beta_2}\right) - \sigma_1\sigma_2 \geq 0 \quad \text{if } d \geq d_4.$$

Thus, $g(d) > 0$ if $d_4 \leq d < d_3$. According to (3.12), (3.13), and Proposition 3.2, we obtain

$$\begin{cases}
g(d) < 0 \text{ if } d \leq \frac{\sigma_1\sigma_2\alpha_1\alpha_2}{\sigma_2\alpha_2^2 - \sigma_1\alpha_1^2} \\
g(d) > 0 \text{ if } d_4 = \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2 - \sigma_1\beta_1^2} \leq d \leq \frac{\sigma_1\sigma_2(\sigma_1^2+\sigma_2^2+\sigma_2\beta_2-\sigma_1\beta_1)}{(\sigma_1-\sigma_2)(\sigma_1^2+\sigma_2^2)} = d_1 \\
g(d) < 0 \text{ if } d \geq \frac{\sqrt{\sigma_1\sigma_2}(\sqrt{\sigma_2}\alpha_2 - \sqrt{\sigma_1}\alpha_1)}{(\sigma_1+\sigma_2)(\sqrt{\sigma_1} - \sqrt{\sigma_2})} = d_5.
\end{cases}$$

In addition, we recall Lemma 2.1(ii): $0 < \frac{\sigma_1\sigma_2\alpha_1\alpha_2}{\sigma_2\alpha_2^2 - \sigma_1\alpha_1^2} < \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2 - \sigma_1\beta_1^2} = d_4$. Accordingly, there exist $\bar{d}_1, \bar{d}_2 > 0$ such that $\lambda_+ = 0$ for $d = \bar{d}_1, \bar{d}_2$ and

$$\begin{cases}
\lambda_+ > 0 \text{ if } d < \bar{d}_1 \text{ or } d > \bar{d}_2 \\
\lambda_+ < 0 \text{ if } \bar{d}_1 < d < \bar{d}_2
\end{cases}$$

where

$$\frac{\sigma_1\sigma_2\alpha_1\alpha_2}{\sigma_2\alpha_2^2-\sigma_1\alpha_1^2} < \bar{d}_1 < \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2} = d_4$$
$$d_1 = \frac{\sigma_1\sigma_2(\sigma_1^2+\sigma_2^2+\sigma_2\beta_2-\sigma_1\beta_1)}{(\sigma_1-\sigma_2)(\sigma_1^2+\sigma_2^2)} < \bar{d}_2 < \frac{\sqrt{\sigma_1\sigma_2}(\sqrt{\sigma_2}\alpha_2-\sqrt{\sigma_1}\alpha_1)}{(\sigma_1+\sigma_2)(\sqrt{\sigma_1}-\sqrt{\sigma_2})} = d_5.$$

By a direct computation, it can be seen that

$$\frac{\sqrt{\sigma_1\sigma_2}(\sqrt{\sigma_2}\alpha_2-\sqrt{\sigma_1}\alpha_1)}{(\sigma_1+\sigma_2)(\sqrt{\sigma_1}-\sqrt{\sigma_2})} < \frac{\sigma_1\sqrt{\sigma_1\sigma_2}+\sigma_1\sigma_2}{\sigma_1^2-\sigma_2^2}(\alpha_2-\alpha_1).$$

Thus, for consistency with the ranges in the assertion of Theorem 2.1, we also write

$$\frac{\sigma_1\sigma_2\alpha_1\alpha_2}{\sigma_2\alpha_2^2-\sigma_1\alpha_1^2} < \bar{d}_1 < \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2}$$
$$\frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2} < \bar{d}_2 < \frac{\sigma_1\sqrt{\sigma_1\sigma_2}+\sigma_1\sigma_2}{\sigma_1^2-\sigma_2^2}(\alpha_2-\alpha_1).$$

This completes the proof. □

Remark 3. *Assume that conditions* (C) *and* (P) *hold. Under* $\sigma_2\beta_2 = \sigma_1\beta_1$ *and* $\beta_2-\beta_1 = \sigma_1+\sigma_1$, *we do have* $g(d_1 = d_2 = d_3 = d_4) = 0$ *and* $g'(d_1 = d_2 = d_3 = d_4) = 0$, *by Proposition 3.2*(V)(iii) *and the proof of Theorem 3.3, and hence* $\bar{d}_1 = \bar{d}_2$.

Next, let us focus on the boundary equilibrium $(0, 0, \bar{v}_1, \bar{v}_2)$. We shall discuss the stability of $(0, 0, \bar{v}_1, \bar{v}_2)$ through analyzing the eigenvalues of the following submatrices in (3.7):

$$\begin{bmatrix} \alpha_1-\bar{v}_1-d & d \\ d & \alpha_2-\bar{v}_2-d \end{bmatrix} \text{ and } \begin{bmatrix} \beta_1-2\bar{v}_1-d & d \\ d & \beta_2-2\bar{v}_2-d \end{bmatrix}. \tag{3.24}$$

Theorem 3.4. *Consider system* (1.3) *under condition* (C). *There exists a* $\bar{d}_3 > 0$ *so that the boundary equilibrium* $(0, 0, \bar{v}_1, \bar{v}_2)$ *is unstable if* $d < \bar{d}_3$ *and asymptotically stable if* $d > \bar{d}_3$. *In addition,*

$$\frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2} < \bar{d}_3 < \frac{\sigma_1}{\sigma_1-\sigma_2}(\alpha_2-\alpha_1).$$

Proof. Under condition (C), it can be shown that the two eigenvalues of the second matrix in (3.24) are negative, by Gerschgorin's Theorem and Proposition A.4 in Appendix II. The stability of $(0, 0, \bar{v}_1, \bar{v}_2)$ is thus determined by the two eigenvalues, denoted by $\lambda_\mp$, of the first matrix in (3.24). By a direct calculation, these two eigenvalues are

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

From Proposition A.4, we have

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

and thus $\lambda_- < 0$ for all $d > 0$. Next, let us identify the sign of $\lambda_+ = \lambda_+(d)$. Note that $\lambda_+(d) \geq 0$ if and only if

$$\begin{aligned} & |\ \alpha_1 - \bar{v}_1 + \alpha_2 - \bar{v}_2 - 2d\ | \leq \sqrt{(\alpha_1 - \bar{v}_1 - \alpha_2 + \bar{v}_2)^2 + 4d^2} \\ \Leftrightarrow\quad & (\alpha_1 - \bar{v}_1)(\alpha_2 - \bar{v}_2) - d(\alpha_1 - \bar{v}_1 + \alpha_2 - \bar{v}_2) \leq 0. \end{aligned} \tag{3.25}$$

By $\alpha_1 = \beta_1 - \sigma_1$, $\alpha_2 = \beta_2 + \sigma_2$, (3.5), and Proposition A.4, (3.25) is equivalent to

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

This inequality can be simplified to

$$d\left(\sigma_1\frac{\bar{v}_1}{\bar{v}_2} - \sigma_2\frac{\bar{v}_2}{\bar{v}_1}\right) - \sigma_1\sigma_2 \leq 0. \tag{3.26}$$

Now, we define

$$h(d) := d\left(\sigma_1\frac{\bar{v}_1}{\bar{v}_2}(d) - \sigma_2\frac{\bar{v}_2}{\bar{v}_1}(d)\right) - \sigma_1\sigma_2. \tag{3.27}$$

Then $\lambda_+(d) \geq 0$ if and only if $h(d) \leq 0$. By Propositions A.4 and A.6, we have $1 < \frac{\bar{v}_2}{\bar{v}_1}(d) < \frac{\beta_2}{\beta_1}$ and $\frac{\bar{v}_2}{\bar{v}_1}(d)$ decreases from $\frac{\beta_2}{\beta_1}$ to 1, as d increases from 0 to ∞. Hence, $h(0) = -\sigma_1\sigma_2 < 0$ and $h(d) \to \infty$ as $d \to \infty$ due to $\sigma_1 > \sigma_2$.

A direct calculation yields

$$h'(d) = \left(\sigma_1\frac{\bar{v}_1}{\bar{v}_2}(d) - \sigma_2\frac{\bar{v}_2}{\bar{v}_1}(d)\right) + d\left[\sigma_1(\frac{\bar{v}_1}{\bar{v}_2})'(d) - \sigma_2(\frac{\bar{v}_2}{\bar{v}_1})'(d)\right]. \tag{3.28}$$

Notably, $\sigma_1(\frac{\bar{v}_1}{\bar{v}_2})' - \sigma_2(\frac{\bar{v}_2}{\bar{v}_1})' > 0$ for all $d > 0$, $\sigma_1\frac{\bar{v}_1}{\bar{v}_2} - \sigma_2\frac{\bar{v}_2}{\bar{v}_1} = -\frac{\sigma_2\beta_2^2 - \sigma_1\beta_1^2}{\beta_1\beta_2}$ if $d = 0$, and $\sigma_1\frac{\bar{v}_1}{\bar{v}_2} - \sigma_2\frac{\bar{v}_2}{\bar{v}_1} \to \sigma_1 - \sigma_2 > 0$ as $d \to \infty$; namely, $\sigma_1\frac{\bar{v}_1}{\bar{v}_2} - \sigma_2\frac{\bar{v}_2}{\bar{v}_1}$ increases from $-\frac{\sigma_2\beta_2^2 - \sigma_1\beta_1^2}{\beta_1\beta_2}$ to $\sigma_1 - \sigma_2$ as d increases from 0 to ∞. Moreover, from (3.5), the equations for $\bar{v}_i$, we have

$$\begin{cases} d\left(\frac{\bar{v}_2}{\bar{v}_1}\right)' = 1 - \frac{\bar{v}_2}{\bar{v}_1} + \bar{v}_1' \\ d\left(\frac{\bar{v}_1}{\bar{v}_2}\right)' = 1 - \frac{\bar{v}_1}{\bar{v}_2} + \bar{v}_2'. \end{cases} \tag{3.29}$$

With (3.28) and (3.29), we obtain

$$h'(d) = (\sigma_1 - \sigma_2) + \sigma_1\bar{v}_2' - \sigma_2\bar{v}_1', \tag{3.30}$$

and then

$$h''(d) = \sigma_1\bar{v}_2'' - \sigma_2\bar{v}_1'' > 0,$$

by Proposition 3.1. Thus, the graph of $h(d)$ is concave upward. Therefore, from the above discussions, there is a unique $\bar{d}_3 > 0$ such that

$$\begin{cases} h(d) < 0 \text{ if } d < \bar{d}_3 \\ h(d) = 0 \text{ if } d = \bar{d}_3 \\ h(d) > 0 \text{ if } d > \bar{d}_3 \end{cases}$$

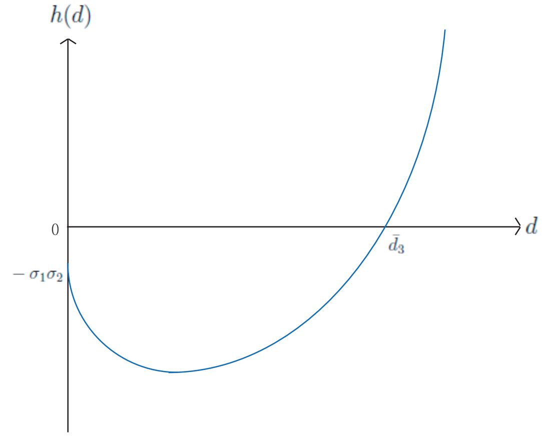

Figure 4. The graph of $h(d)$, regarding the sign of λ_+ in Theorem 3.4.

and accordingly,

$$\begin{cases} \lambda_+(d) > 0 \text{ if } d < \bar{d}_3 \\ \lambda_+(d) = 0 \text{ if } d = \bar{d}_3 \\ \lambda_+(d) < 0 \text{ if } d > \bar{d}_3. \end{cases} \tag{3.31}$$

The graph of $h(d)$ is illustrated in Figure 4.

Now, we estimate the range for the values of $\bar{d}_3$. Function h in (3.27) can be expressed by

$$h(d) = \sigma_2(\beta_1 - \bar{v}_1) - \sigma_1(\beta_2 - \bar{v}_2) + d(\sigma_1 - \sigma_2) - \sigma_1\sigma_2, \tag{3.32}$$

via (3.5). Thus, inequality (3.26) is equivalent to

$$\sigma_2(\beta_1 - \bar{v}_1) - \sigma_1(\beta_2 - \bar{v}_2) + d(\sigma_1 - \sigma_2) - \sigma_1\sigma_2 \leq 0. \tag{3.33}$$

According to Proposition A.4(i), we have

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

Then,

$$h\left(\frac{\sigma_1\sigma_2}{\sigma_1 - \sigma_2}\right) < \sigma_1\sigma_2 - \sigma_1\sigma_2 = 0,$$

and

$$\begin{aligned} h\left(\frac{\sigma_1}{\sigma_1 - \sigma_2}(\alpha_2 - \alpha_1)\right) &> -\sigma_1(\beta_2 - \beta_1) + \sigma_1(\alpha_2 - \alpha_1) - \sigma_1\sigma_2 \\ &= -\sigma_1(\beta_2 - \beta_1) + \sigma_1(\beta_2 - \beta_1 + \sigma_1 + \sigma_2) - \sigma_1\sigma_2 \\ &= \sigma_1^2 > 0. \end{aligned}$$

Consequently, (3.31) holds with

$$\frac{\sigma_1\sigma_2}{\sigma_1 - \sigma_2} < \bar{d}_3 < \frac{\sigma_1}{\sigma_1 - \sigma_2}(\alpha_2 - \alpha_1).$$

This completes the proof. □

4. Coexistence of two species and extinction of one species

Let us summarize the main results in Sections 2 and 3:
(i) Under $\sigma_2\beta_2 < \sigma_1\beta_1$ and $\beta_2 - \beta_1 \geq \sigma_1 + \sigma_2$, the positive equilibrium $(u_1^*, u_2^*, v_1^*, v_2^*)$ exists if $d < d_3^*$ (Theorem 2.1); the semitrivial equilibrium $(\bar{u}_1, \bar{u}_2, 0, 0)$ is unstable for all $d > 0$ (Theorem 3.3) and the semitrivial equilibrium $(0, 0, \bar{v}_1, \bar{v}_2)$ is unstable if $d < \bar{d}_3$ and asymptotically stable if $d > \bar{d}_3$ (Theorem 3.4). Besides, the estimated range of d_3^* in Theorem 2.1 coincides with the one of $\bar{d}_3$ in Theorem 3.4.
(ii) Under $\sigma_2\beta_2 > \sigma_1\beta_1$, the positive equilibrium $(u_1^*, u_2^*, v_1^*, v_2^*)$ exists if $d < d_1^*$ or $d_2^* < d < d_3^*$ (Theorem 2.1); the semitrivial equilibrium $(\bar{u}_1, \bar{u}_2, 0, 0)$ is unstable if $d < \bar{d}_1$ or $d > \bar{d}_2$, and asymptotically stable if $\bar{d}_1 < d < \bar{d}_2$ (Theorem 3.3); the semitrivial equilibrium $(0, 0, \bar{v}_1, \bar{v}_2)$ is unstable if $d < \bar{d}_3$ and asymptotically stable if $d > \bar{d}_3$ (Theorem 3.4). In addition, the estimated ranges of d_1^* and d_2^* in Theorem 2.1 respectively coincide with those of $\bar{d}_1$ and $\bar{d}_2$ in Theorem 3.3.

In fact, the following theorem reveals that these critical values of d are consistent in determining the existence of the positive equilibrium and the stability of semitrivial equilibria, namely, $d_1^* = \bar{d}_1$, $d_2^* = \bar{d}_2$ and $d_3^* = \bar{d}_3$. Such interesting consistency makes precise the global dynamics of this competitive species model (1.3), under the framework of monotone dynamics. Let us elaborate.

Theorem 4.1. *$d_1^* = \bar{d}_1$, $d_2^* = \bar{d}_2$ and $d_3^* = \bar{d}_3$.*

Proof. From (3.26), we see that $h(d) = 0$ if and only if

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

That is, $\bar{d}_3$ satisfies

$$\bar{d}_3\left(\sigma_1 \frac{\bar{v}_1}{\bar{v}_2}(\bar{d}_3) - \sigma_2 \frac{\bar{v}_2}{\bar{v}_1}(\bar{d}_3)\right) = \sigma_1\sigma_2.$$

Let $\bar{b} := \frac{\bar{v}_2}{\bar{v}_1}(\bar{d}_3)$, then

$$\bar{d}_3\left(\sigma_1 \frac{1}{\bar{b}} - \sigma_2 \bar{b}\right) = \sigma_1\sigma_2.$$

Thus,

$$\bar{b} = \frac{-\sigma_1 + \sqrt{\sigma_1^2 + 4k\bar{d}_3^2}}{2\bar{d}_3}, \tag{4.1}$$

where $k = \frac{\sigma_1}{\sigma_2}$. Recall the definition of b in (2.7). From Remark 2(I), we see that $(u_1^*, u_2^*, v_1^*, v_2^*) \to (0, 0, \bar{v}_1, \bar{v}_2)$, as $d \to (d_3^*)^-$. Therefore, recalling (2.10), we obtain

$$\frac{-\sigma_1 + \sqrt{\sigma_1^2 + 4k(d_3^*)^2}}{2d_3^*} = \lim_{d \to (d_3^*)^-} b(d) = \lim_{d \to (d_3^*)^-} \frac{v_2^*}{v_1^*}(d) = \frac{\bar{v}_2}{\bar{v}_1}(d_3^*).$$

Noting that $b = b(d)$ in (2.10) is monotone in d (shown in (2.18)), with (4.1), we thus conclude that $d_3^* = \bar{d}_3$.

If $\sigma_2\beta_2 > \sigma_1\beta_1$, from (3.11), we have $g(\bar{d}_1) = 0$ and $g(\bar{d}_2) = 0$. Let $\bar{a}_1 := \frac{\bar{u}_2}{\bar{u}_1}(\bar{d}_1)$, $\bar{a}_2 := \frac{\bar{u}_2}{\bar{u}_1}(\bar{d}_2)$. Then

$$\bar{a}_1 = \frac{\sigma_1 + \sqrt{\sigma_1^2 + 4k\bar{d}_1^2}}{2\bar{d}_1}, \quad \bar{a}_2 = \frac{\sigma_1 + \sqrt{\sigma_1^2 + 4k\bar{d}_2^2}}{2\bar{d}_2}. \tag{4.2}$$

It follows from Remark 2(I) that $(u_1^*, u_2^*, v_1^*, v_2^*) \to (\bar{u}_1, \bar{u}_2, 0, 0)$, as $d \to (d_1^*)^-$. Notice that $a = a(d)$ in (2.10) is monotone in d, shown in (2.25). Therefore, recalling (2.10), we have

$$\frac{\sigma_1 + \sqrt{\sigma_1^2 + 4k(d_1^*)^{\,2}}}{2d_1^*} = \lim_{d\to(d_1^*)^-} a(d) = \lim_{d\to(d_1^*)^-} \frac{u_2^*}{u_1^*}(d) = \frac{\bar{u}_2}{\bar{u}_1}(d_1^*).$$

With (4.2), we thus conclude that $d_1^* = \bar{d}_1$. In addition, by Remark 2(I), we see that $(\bar{u}_1, \bar{u}_2, 0, 0) \to (u_1^*, u_2^*, v_1^*, v_2^*)$ as $d \to (d_2^*)^+$. Consequently,

$$\lim_{d\to(d_2^*)^+} \bar{a}_2(d) = \lim_{d\to(d_2^*)^+} \frac{\bar{u}_2}{\bar{u}_1}(d) = \frac{u_2^*}{u_1^*}(d_2^*) = \frac{\sigma_1 + \sqrt{\sigma_1^2 + 4k(d_2^*)^2}}{2d_2^*}.$$

With (4.2), we conclude that $d_2^* = \bar{d}_2$. This completes the proof. □

Combining the discussions in Sections 2 and 3 with the assertion in Theorem 4.1, we conclude that for system (1.3), either there exists a positive equilibrium representing the coexistence of two species or one species drives the other to extinction, depending on the magnitude of the dispersal rate d.

Theorem 4.2. *Consider system* (1.3) *under conditions* (C)*, and* (P).
(I) *Assume that* $\sigma_2\beta_2 < \sigma_1\beta_1$ *and* $\beta_2 - \beta_1 \geq \sigma_1 + \sigma_2$ *hold.*
(i) *If* $d < d_3^*$*, then the positive equilibrium* $(u_1^*, u_2^*, v_1^*, v_2^*)$ *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* $v_1(0) + v_2(0) > 0$.
(ii) *If* $d \geq d_3^*$*, then* $\lim_{t\to\infty}(u_1(t), u_2(t), v_1(t), v_2(t)) = (0, 0, \bar{v}_1, \bar{v}_2)$*, for all* $(u_1(0), u_2(0), v_1(0), v_2(0)) \in \mathbb{R}_+^4$ *with* $v_1(0) + v_2(0) > 0$.
(II) *Assume that* $\sigma_2\beta_2 > \sigma_1\beta_1$ *holds.*
(i) *If* $d < d_1^*$ *or* $d_2^* < d < d_3^*$*, then the positive equilibrium* $(u_1^*, u_2^*, v_1^*, v_2^*)$ *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* $v_1(0) + v_2(0) > 0$.
(ii) *If* $d_1^* \leq d \leq d_2^*$*, 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* $u_1(0) + u_2(0) > 0$.
(iii) *If* $d \geq d_3^*$*, then* $\lim_{t\to\infty}(u_1(t), u_2(t), v_1(t), v_2(t)) = (0, 0, \bar{v}_1, \bar{v}_2)$*, for all* $(u_1(0), u_2(0), v_1(0), v_2(0)) \in \mathbb{R}_+^4$ *with* $v_1(0) + v_2(0) > 0$.

Proof. The assertions are based on the monotone dynamics theory which is reviewed in Appendix I. (I) Assume that $\sigma_2\beta_2 < \sigma_1\beta_1$ and $\beta_2 - \beta_1 \geq \sigma_1 + \sigma_2$ hold. (i) If $d < d_3^*$, then the positive equilibrium $(u_1^*, u_2^*, v_1^*, v_2^*)$ is unique, by Theorem 2.1, the semitrivial equilibrium $(\bar{u}_1, \bar{u}_2, 0, 0)$ is unstable, by Theorem 3.3, and the semitrivial equilibrium $(0, 0, \bar{v}_1, \bar{v}_2)$ is unstable, by Theorem 3.4. Therefore, the assertion follows from Theorem A.1. (ii) If $d > d_3^*$, then case (a) of the trichotomy in Theorem A.2

does not hold, since the positive steady state does not exist, by Theorem 2.1; case (b) does not hold since $(\bar{u}_1, \bar{u}_2, 0, 0)$ is unstable, by Theorem 3.3, and $(0, 0, \bar{v}_1, \bar{v}_2)$ is asymptotically stable, by Theorem 3.4. Therefore, the assertion follows from case (c) of Theorem A.2.

(II) Assume that $\sigma_2\beta_2 > \sigma_1\beta_1$. (i) If $d < d_1^*$ or $d_2^* < d < d_3^*$, the argument is similar to the one in (I)(i). (ii) If $d_1^* < d < d_2^*$, then case (a) of the trichotomy in Theorem A.2 does not hold, since the positive equilibrium does not exist, by Theorem 2.1; case (c) does not hold since $(0, 0, \bar{v}_1, \bar{v}_2)$ is unstable, by Theorem 3.4, and $(\bar{u}_1, \bar{u}_2, 0, 0)$ is asymptotically stable, by Theorem 3.3. Therefore, the assertion follows from case (b) of Theorem A.2. (iii) If $d > d_3^*$, the argument is similar to the one in (I)(ii). This completes the proof. □

Remark 4. *That the equilibrium* $(0, 0, \bar{v}_1, \bar{v}_2)$ *is globally asymptotically stable for* $d > d_3^*$ *now follows from Theorem 4.2. In fact it also holds true for* $d = d_3^*$. *In this case, the stability for* $(0, 0, \bar{v}_1, \bar{v}_2)$ *can be concluded by some comparison argument. In addition, there is no positive equilibrium and the equilibrium* $(\bar{u}_1, \bar{u}_2, 0, 0)$ *is unstable in both cases (I) and (II), by Theorem 2.1 and Theorem 3.3. Hence the trichotomy in Theorem A.2 implies the global convergence to* $(0, 0, \bar{v}_1, \bar{v}_2)$. *Similarly, we see that the equilibrium* $(\bar{u}_1, \bar{u}_2, 0, 0)$ *is globally asymptotically stable for* $d = d_1^*$ *or* d_2^*.

5. Numerical illustrations

We arrange two examples to illustrate the global dynamics of system (1.3), and the bifurcation with respect to the dispersal rate d, which are concluded in Theorem 4.2. We also present two more examples to demonstrate that the established scenarios still hold without satisfying condition (P).

Example 1. Consider system (1.3) with $\alpha_1 = 1$, $\alpha_2 = 3$, $\beta_1 = 1.5$ and $\beta_2 = 2.8$, i.e., $\sigma_1 = 0.5$ and $\sigma_2 = 0.2$. Let us examine the conditions in Theorem 4.2(I): condition (C): $\alpha_1 = 1 < \beta_1 = 1.5 < \beta_2 = 2.8 < \alpha_2 = 3$ with $\sigma_2 = 0.2 < \sigma_1 = 0.5$; condition (P): $\frac{\sigma_2\beta_2}{\sigma_1+\sigma_2} = 0.8 < \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2} = 0.948$; $\sigma_2\beta_2 = 0.56 < \sigma_1\beta_1 = 0.75$, and $\beta_2 - \beta_1 = 1.3 \geq \sigma_1 + \sigma_2 = 0.7$. We depict in Figure 5 the bifurcation diagram with respect to the dispersal rate d. It appears that $d_3^* \cong 1.22$, which is consistent with Theorems 2.1(i) and 4.2(I): $\frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2} = 0.333 < d_3^* < \frac{\sigma_1}{\sigma_1-\sigma_2}(\alpha_2 - \alpha_1) = 3.33$. The globally stable positive equilibrium $(u_1^*, u_2^*, v_1^*, v_2^*)$ exists for $d < d_3^*$ and collides with the semitrivial equilibrium $(0, 0, \bar{v}_1, \bar{v}_2)$ at $d = d_3^*$. For $d \geq d_3^*$, the semitrivial equilibrium $(0, 0, \bar{v}_1, \bar{v}_2)$ becomes globally attractive.

Example 2. Consider system (1.3) with $\alpha_1 = 1$, $\alpha_2 = 3$, $\beta_1 = 1.7$ and $\beta_2 = 2.5$, i.e., $\sigma_1 = 0.7$ and $\sigma_2 = 0.5$. Let us examine the conditions in Theorem 4.2(II): condition (C): $\alpha_1 = 1 < \beta_1 = 1.7 < \beta_2 = 2.5 < \alpha_2 = 3$ with $\sigma_2 = 0.5 < \sigma_1 = 0.7$; condition (P): $\frac{\sigma_2\beta_2}{\sigma_1+\sigma_2} = 1.042 < \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2} = 1.35$; $\sigma_2\beta_2 = 1.25 > \sigma_1\beta_1 = 1.19$. The bifurcation diagram with respect to the dispersal rate d is depicted in Figure 6. It appears that $d_1^* \cong 0.91$, $d_2^* \cong 1.92$, $d_3^* \cong 4.15$, which are consistent with Theorem 2.1(ii) and 4.2(II): $\frac{\sigma_1\sigma_2\alpha_1\alpha_2}{\sigma_2\alpha_2^2-\sigma_1\alpha_1^2} = 0.276 < d_1^* < \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2} = 1.35$, $\frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2} = 1.75 < d_2^* < \frac{\sigma_1\sqrt{\sigma_1\sigma_2}+\sigma_1\sigma_2}{\sigma_1^2-\sigma_2^2}(\alpha_2 - \alpha_1) = 6.36$, and $\frac{\sigma_1\sigma_2}{\sigma_1-\sigma_2} = 1.75 < d_3^* < \frac{\sigma_1}{\sigma_1-\sigma_2}(\alpha_2 - \alpha_1) = 7$. The globally stable positive equilibrium $(u_1^*, u_2^*, v_1^*, v_2^*)$ exists for $d < d_1^*$ and collides with the semitrivial equilibrium $(\bar{u}_1, \bar{u}_2, 0, 0)$ at $d = d_1^*$. For $d_1^* \leq d \leq d_2^*$, the equilibrium $(\bar{u}_1, \bar{u}_2, 0, 0)$ becomes globally attractive and for $d_2^* < d < d_3^*$, the globally stable positive equilibrium $(u_1^*, u_2^*, v_1^*, v_2^*)$ exists. For $d \geq d_3^*$, the semitrivial equilibrium $(0, 0, \bar{v}_1, \bar{v}_2)$ becomes globally attractive.

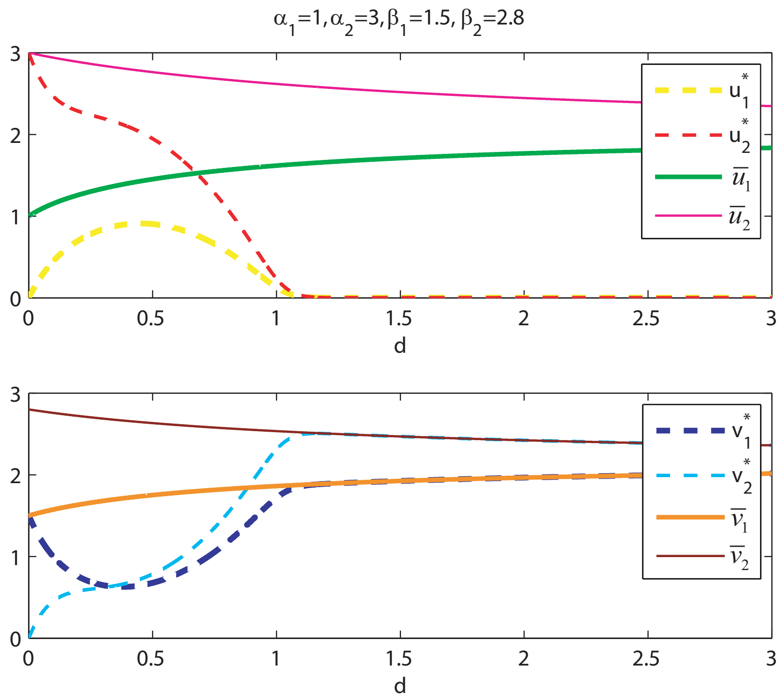

Figure 5. Bifurcation diagram, with respect to d, for the equilibria of system (1.3) with $\alpha_1 = 1, \alpha_2 = 3, \beta_1 = 1.5, \beta_2 = 2.8, \sigma_1 = 0.5$ and $\sigma_2 = 0.2$, where $\sigma_2\beta_2 < \sigma_1\beta_1$.

Example 3. Consider system (1.3) with $\alpha_1 = 1$, $\alpha_2 = 3$, $\beta_1 = 1.4$ and $\beta_2 = 2.85$, i.e., $\sigma_1 = 0.4$ and $\sigma_2 = 0.15$. For such parameter values, condition (C) holds: $\alpha_1 = 1 < \beta_1 = 1.4 < \beta_2 = 2.85 < \alpha_2 = 3$ with $\sigma_2 = 0.15 < \sigma_1 = 0.4$. In addition, $\sigma_2\beta_2 = 0.4275 < \sigma_1\beta_1 = 0.56$. Such parameter values violate condition (P), as $\frac{\sigma_2\beta_2}{\sigma_1+\sigma_2} = 0.777 > \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2} = 0.551$. Nevertheless, the same dynamical scenario as Example 1 takes place, as seen in Figure 7.

Example 4. Consider system (1.3) with $\alpha_1 = 1$, $\alpha_2 = 3$, $\beta_1 = 1.35$ and $\beta_2 = 2.8$, i.e., $\sigma_1 = 0.35$ and $\sigma_2 = 0.2$. With such parameter values, condition (C) holds: $\alpha_1 = 1 < \beta_1 = 1.35 < \beta_2 = 2.8 < \alpha_2 = 3$ with $\sigma_2 = 0.2 < \sigma_1 = 0.35$; $\sigma_2\beta_2 = 0.56 > \sigma_1\beta_1 = 0.4725$. These parameter values violate condition (P), as $\frac{\sigma_2\beta_2}{\sigma_1+\sigma_2} = 1.0182 > \frac{\sigma_1\sigma_2\beta_1\beta_2}{\sigma_2\beta_2^2-\sigma_1\beta_1^2} = 0.2845$. Nevertheless, the dynamical scenario shown in Figure 8 remains identical to Example 2.

6. Discussions and conclusions

We have exhibited the global dynamics for a model on two-species competition in a two-patch environment, under certain conditions. The main condition (C): $\alpha_1 < \beta_1 < \beta_2 < \alpha_2$, $(\beta_1 + \beta_2) - (\alpha_1 + \alpha_2) = \sigma_1 - \sigma_2 > 0$, indicates that the birth rate of u-species in the second patch is the largest among all birth rates of two species on two patches, yet the average birth rate of v-species is larger than u-species. This means that the birth rate for v-species is larger than u-species in the first patch. The present investigation exploited analytically two dynamical scenarios for such competition, as demonstrated in Examples 1 and 2, respectively. The first scenario takes place under $\sigma_2\beta_2 < \sigma_1\beta_1$. As expressed by

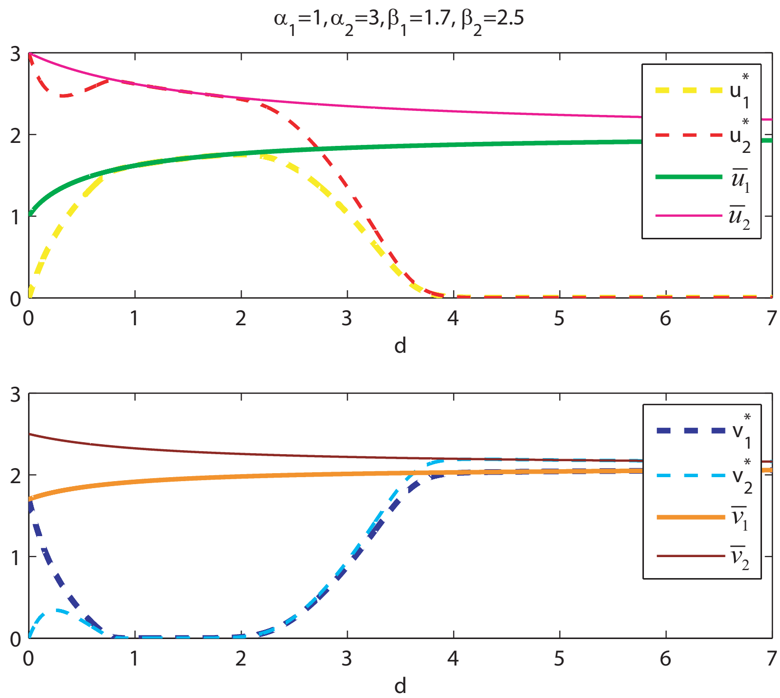

Figure 6. Bifurcation diagram, with respect to d, for the equilibria of system (1.3) with $\alpha_1 = 1, \alpha_2 = 3, \beta_1 = 1.7, \beta_2 = 2.5, \sigma_1 = 0.7$ and $\sigma_2 = 0.5$, where $\sigma_2\beta_2 > \sigma_1\beta_1$.

$\frac{\sigma_1}{\sigma_2} > \frac{\beta_2}{\beta_1} > 1$, it indicates that the value of σ_1 is larger than the value of σ_2 in a way that its ratio exceeds the ratio of β_2 over β_1. This includes the situation that σ_1 is much bigger than σ_2, which is denoted by $(\beta_1 + \beta_2) \gg (\alpha_1 + \alpha_2)$. The second scenario comes about under $\sigma_2\beta_2 > \sigma_1\beta_1$. On the contrary, as expressed by $1 < \frac{\sigma_1}{\sigma_2} < \frac{\beta_2}{\beta_1}$, it indicates that the value of σ_1 may be merely a little over the value of σ_2, depending on the ratio of β_2 over β_1. In this case, the average birth rate of v-species may be merely a little more than and close to the average birth rate of u-species; we denote this situation by $(\beta_1 + \beta_2) \approx (\alpha_1 + \alpha_2)$.

In the first case, including the sense $(\beta_1 + \beta_2) \gg (\alpha_1 + \alpha_2)$, coexistence of two species occurs for dispersal rate $d < d_3^*$, and $(0, 0, \bar{v}_1, \bar{v}_2)$ is globally attractive for $d \geq d_3^*$, where d_3^* has been estimated by system parameters. In this situation, $(\bar{u}_1, \bar{u}_2, 0, 0)$ is unstable for any $d > 0$ and an eigenvalue of the linearized system at $(0, 0, \bar{v}_1, \bar{v}_2)$ changes from positive to negative as d, being increasing from 0, exceeds d_3^*, and $(0, 0, \bar{v}_1, \bar{v}_2)$ becomes stable for $d \geq d_3^*$.

In the second case, including the sense $(\beta_1 + \beta_2) \approx (\alpha_1 + \alpha_2)$, the coexistence of two species takes place for $d < d_1^*$ or $d_2^* < d < d_3^*$, $(\bar{u}_1, \bar{u}_2, 0, 0)$ is globally attractive for $d_1^* \leq d \leq d_2^*$, and $(0, 0, \bar{v}_1, \bar{v}_2)$ becomes globally attractive for $d \geq d_3^*$, where d_1^*, d_2^*, d_3^* have been estimated. An eigenvalue of the linearized system at $(\bar{u}_1, \bar{u}_2, 0, 0)$ changes from positive to negative at d_1^*, and then back to positive at d_2^*. In addition, an eigenvalue of the linearized system at $(0, 0, \bar{v}_1, \bar{v}_2)$ changes from positive to negative at d_3^*, and $d_2^* < d_3^*$.

Our analytical investigation on this model strongly suggests that, in high-dispersal situations, one species will prevail if its average birth rate is larger than the other competing species, whereas in low-dispersal situations, the two species can coexist or one species that has the greatest birth rate in one

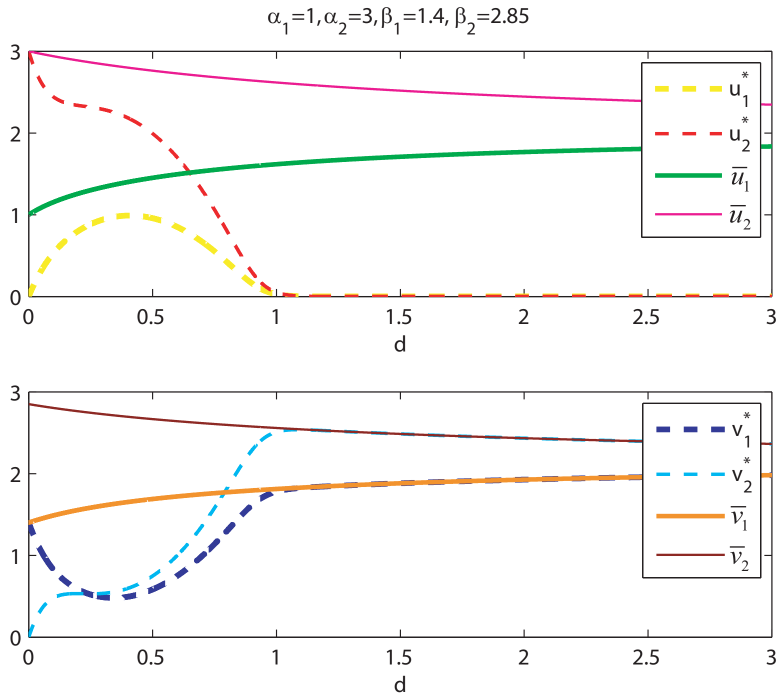

Figure 7. Bifurcation diagram, with respect to d, for the equilibria of system (1.3) with $\alpha_1 = 1, \alpha_2 = 3, \beta_1 = 1.4, \beta_2 = 2.85, \sigma_1 = 0.4$ and $\sigma_2 = 0.15$, where $\sigma_2\beta_2 < \sigma_1\beta_1$.

patch among all species and patches will be able to persist and drive the other species to extinction, even though its average birth rate is lower. Such findings may illuminate some insights into how species learn to compete and point out the evolution directions.

Condition (C) is a basic assumption for the present results. Although there are additional conditions (P) and $\beta_2 - \beta_1 \geq \sigma_1 + \sigma_2$, due to mathematical technicality, it is believed that such scenarios remain true under condition (C) only. However, it is very difficult to remove these additional conditions, as the algebraic operations involving five parameters are rather involved. In Examples 3, 4, we have demonstrated exactly the same dynamical scenarios for parameter values which do not satisfy condition (P).

To compare our results with those in [19], we set $\sigma_1 = \xi\sigma_2$, $\xi > 1$, according to condition (C). The resource difference between two species can be depicted as $(\sigma_1, -\sigma_2)$ among two patches, where $\beta_1 - \alpha_1 = \sigma_1 > 0$ means that v-species has an advantage over v-species in competing the resource in patch-1, while $\beta_2 - \alpha_2 = -\sigma_2 < 0$ means that it is disadvantageous for v-species to compete with u-species for the resource in patch-2. We rewrite it as $\sigma_2(\xi, -1)$ with fixed $\xi > 1$, and now the value of σ_2 measures the difference between two species and resembles the value of τ in [19]. We accordingly rewrite the conditions in Theorem 4.2 to explore how the magnitude of resource difference affects the invasion of mutant species:

$$(\mathrm{P}) \Leftrightarrow \sigma_2 > \sigma_2^* := \frac{\beta_2^2 - \xi\beta_1^2}{\xi(\xi + 1)\beta_1},$$

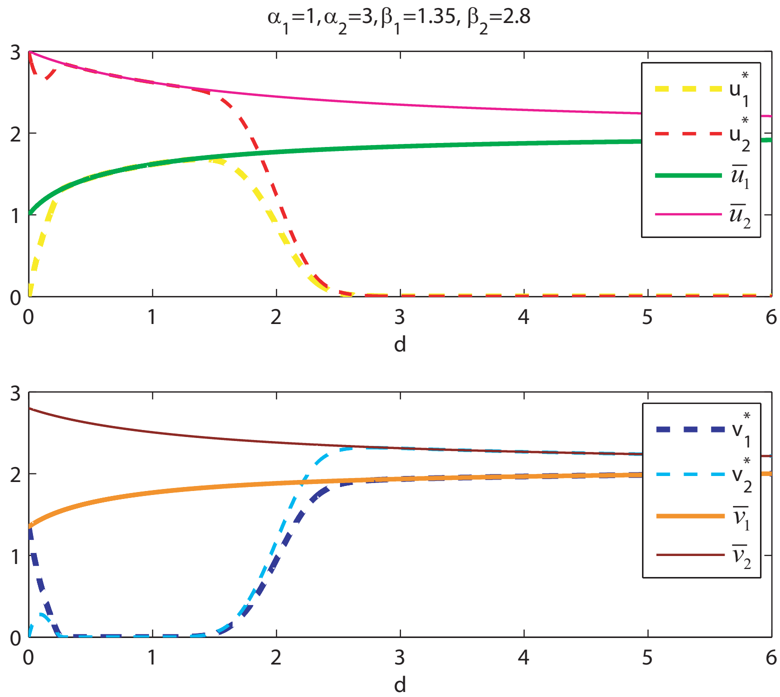

Figure 8. Bifurcation diagram, with respect to d, for the equilibria of system (1.3) with $\alpha_1 = 1, \alpha_2 = 3, \beta_1 = 1.35, \beta_2 = 2.8, \sigma_1 = 0.35$ and $\sigma_2 = 0.2$, where $\sigma_2\beta_2 > \sigma_1\beta_1$.

$$\beta_2 - \beta_1 \geq \ (<)\ \sigma_1 + \sigma_2 \Leftrightarrow \sigma_2 \leq \ (>)\ \sigma_2^{**} := \frac{\beta_2 - \beta_1}{\xi + 1},$$
$$\sigma_2\beta_2 < \ (>)\ \sigma_1\beta_1 \Leftrightarrow \xi > \ (<)\ \frac{\beta_2}{\beta_1}.$$

Note that the criteria in Theorem 4.2(II) imply $\beta_2-\beta_1 < \sigma_1+\sigma_2$. Therefore, by increasing the dispersal rate d, the global convergence of system (1.1) switches in case (I) of Theorem 4.2 from the coexistence to extinction of u-species when $\sigma_2^* < \sigma_2 \leq \sigma_2^{**}$ and $\xi > \frac{\beta_2}{\beta_1}$; on the other hand, in case (II), the dynamics switches three times from global convergence to the coexistence to extinction of (mutant) v-species, again to the coexistence and then the persistence of v-species, when $\sigma_2 > \sigma_2^{**}$ and $\xi < \frac{\beta_2}{\beta_1}$. This result enhances the understanding on the dynamics of competitive species from the viewpoint of patchy habitat in the following aspects: Compared to concluding global convergence under small magnitude of spatial heterogeneity (τ) in [19, Theorem 1.2], our result in Theorem 4.2 admits a large range of magnitudes (σ_2) depicting spatial heterogeneity. The multiple stability switches in Theorem 4.2 are global dynamics, as compared to local dynamics in [19, Theorem 1.1].

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Conflict of interest

All authors declare no conflicts of interest in this paper.

References

1. E. Braveman and Md. Kamrujjamam, Lotka systems with directed dispersal dynamics: Competition and influence of diffusion strategies, *Math. Biosci.*, **279** (2016), 1–12.
2. R. S. Cantrell and C. Cosner, *Spatial ecology via reaction-diffusion equations*, Series in Mathematical and Computational Biology, John Wiley and Sons, Chichester, UK, 2003.
3. R. S. Cantrell, C. Cosner and Y. Lou, Multiple reversals of competitive dominance in ecological reserves via external habitat degradation, *J. Dyn. Diff. Eqs.*, **16** (2004), 973–1010.
4. R. S. Cantrell, C. Cosner, D. L. DeAngelis and V. Padron, The ideal free distribution as an evolutionarily stable strategy, *J. Biol. Dyn.*, **1** (2007), 249–271.
5. R. S. Cantrell, C. Cosner and Y. Lou, Evolutionary stability of ideal free dispersal strategies in patchy environments, *J. Math. Biol.*, **65** (2012), 943–965.
6. X. Chen, K. Y. Lam and Y. Lou, Dynamics of a reaction-diffusion-advection model for two competing species, *Discret. Contin. Dyn. Syst.*, **32** (2012), 3841–3859.
7. J. Clobert, E. Danchin, A. A. Dhondt and J. D. Nichols, *Dispersal*, Oxford University Press, 2001.
8. R. Cressman and V. Krivan, Two-patch population models with adaptive dispersal the effects of varying dispersal speeds, *J. Math. Biol.*, **67** (2013), 329–358.
9. J. Dockery, V. Hutson, K. Mischaikow and M. Pernarowski, The evolution of slow dispersal rates: a reaction diffusion model, *J. Math. Biol.*, **37** (1998), 61–83.
10. G. F. Gause, *The Struggle for Existence*, Williams Wilkins, Baltimore, MD, 1934.
11. S. A. Gourley and Y. Kuang, Two-species competition with high dispersal: the winning strategy, *Math. Biosci. Eng.*, **2** (2005), 345–362.
12. A. Hastings, Can spatial variation alone lead to selection for dispersal?, *Theor. Popul. Biol.*, **24** (1983), 244–251.
13. X. Q. He and W. M. Ni, The effects of diffusion and spatial variation in LotkaVolterra competitiondiffusion system I: Heterogeneity vs. homogeneity, *J. Differ. Eqs.*, **254** (2013), 528–546.
14. X. Q. He and W. M. Ni, The effects of diffusion and spatial variation in LotkaVolterra competitiondiffusion system II: The general case, *J. Differ. Eqs.*, **254** (2013), 4088–4108.
15. X. Q. He and W. M. Ni, Global dynamics of the Lotka-Volterra competition-diffusion system: diffusion and spatial heterogeneity I, *Commun. Pure Appl. Math.*, **LXIX** (2016), 981–1014.
16. R. D. Holt, Population dynamics in two-patch environments some anomalous consequences of an optimal habitat distribution, *Theor. Popul. Biol.*, **28** (1985), 181–208.
17. S. B. Hsu, H. Smith and P. Waltman, Competitive exclusion and coexistence for competitive systems on ordered Banach spaces, *Trans. Amer. Math. Soc.*, **348** (1996), 4083–4094.

18. V. Hutson, J. Lopez-Gomez, K. Mischaikow and G. Vickers, Limit behaviour for a competing species problem with diffusion, in Dynamical Systems and Applications, in *World Sci. Ser. Appl. Anal. 4*, World Scientific, River Edge, NJ, (1995), 343–358.
19. V. Hutson, Y. Lou, K. Mischaikow and P. Poláčik, Competing species near a degenerate limit, *SIAM. J. Math. Anal.*, **35** (2003), 453–491.
20. V. Hutson, S. Martinez, K. Mischaikow and G. T. Vickers, The evolution of dispersal, *J. Math. Biol.*, **47** (2003), 483–517.
21. J. Jiang and X. Liang, Competitive systems with migration and the Poincaré-Bendixson theorem for a 4-dimensional case, *Quar. Appl. Math.*, **LXIV** (2006), 483–498.
22. Y. Kuang and Y. Takeuchi, Predator-prey dynamics in models of prey dispersal in two-patch environments, *Math. Biosci.*, **120** (1994), 77–98.
23. K. Y. Lam and W. M. Ni, Uniqueness and complete dynamics in heterogeneous competition-diffusion systems, *SIAM J. Appl. Math.*, **72** (2012), 1695–1712.
24. K. H. Lin, Y. Lou, C. W. Shih and T. H. Tsai, Global dynamics for two-species competition in patchy environment, *Math. Biosci. Eng.*, **11** (2014), 947–970.
25. Y. Lou, S. Martinez and P. Polacik, Loops and branches of coexistence states in a Lotka-Volterra competition model, *J. Differ. Eqs.*, **230** (2006), 720–742.
26. A. Okubo and S. A. Levin, *Diffusion and ecological problems: modern perspectives*, second ed., Interdisciplinary Applied Mathematics, 14, Springer, New York, 2001.
27. H. L. Smith, Competing subcommunities of mutualists and a generalized Kamke theorem, *SIAM J. Appl. Math.*, **46** (1986), 856–874.
28. H. L. Smith, *Monotone Dynamical Systems: an introduction to the theory of competitive and cooperative systems*, Math. Surveys and Monographs, Amer. Math. Soc., 41, 1995.
29. Y. Takeuchi, Diffusion-mediated persistence in two-species competition Lotka-Volterra model, *Math. Biosci.*, **95** (1989), 65–83.
30. Y. Takeuchi and Z. Lu, Permanence and global stability for competitive Lotka-Volterra diffusion systems, *Nonlinear Anal. TMA*, **24** (1995), 91–104.
31. Y. Takeuchi, *Global dynamical properties of Lotka-Volterra systems*, River Edge, NJ 07661, World Scientic, 1996.

Appendix I. Monotone dynamics theory

For reader's convenience, we review some theory on monotone dynamical systems from [17] and [28]. Denote by $\mathbb{R}^n_+ = \{\mathbf{x} = (x_1, \ldots, x_n) \in \mathbb{R}^n : x_i \geq 0, 1 \leq i \leq n\}$ the first octant of $\mathbb{R}^n$. For $\mathbf{x}, \mathbf{y} \in \mathbb{R}^n_+$, define the following order: $\mathbf{x} \leq_m \mathbf{y}$ if $\mathbf{y} - \mathbf{x} \in K_m$, and $\mathbf{x} \ll_m \mathbf{y}$ whenever $\mathbf{y} - \mathbf{x} \in \text{Int}K_m$, where

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

If $\mathbf{x} \leq_m \mathbf{y}$, we define $[\mathbf{x}, \mathbf{y}]_m = \{\mathbf{z} \in \mathbb{R}^n_+ : \mathbf{x} \leq_m \mathbf{z} \leq_m \mathbf{y}\}$ 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

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

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 $\mathbf{f}$ takes the form

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

where A_1 is an $k \times k$ matrix, A_4 an $(n-k) \times (n-k)$ matrix, A_2 an $k \times (n-k)$ matrix, A_3 an $(n-k) \times k$ matrix, every off-diagonal entry of A_1 and A_4 is nonnegative, and A_2 and A_3 are nonnegative matrices, for some k with $1 \le k \le n$. It was shown in [27] 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 $k+1 \le j \le n$.

System (1.3) 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 its Jacobian matrix is

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

For system (1.3), 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 semitrivial equilibria. If $(u_1, u_2, v_1, v_2) \in \mathbb{R}^4_+$, then $(0, 0, v_1, v_2) \le_m (u_1, u_2, v_1, v_2) \le_m (u_1, u_2, 0, 0)$, and therefore,

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

for all $t \ge 0$. 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 $(u_1, u_2, v_1, v_2) \in \mathbb{R}^4_+$, and $u_1 + u_2 > 0$, $v_1 + v_2 > 0$, it follows that all points in $\mathbb{R}^4_+$ are attracted to the set

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

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 [28] for system (1.3), see also [27, 31].

Theorem A.1. If $e_{\bar{\mathbf{u}}}$ and $e_{\bar{\mathbf{v}}}$ are both linearly unstable, then system (1.3) is permanent. More precisely, there exist positive equilibria e_* and e_{**}, not necessarily distinct, satisfying

$$e_{\bar{\mathbf{v}}} \ll_m e_{**} \le_m e_* \ll_m e_{\bar{\mathbf{u}}}.$$

The order interval

$$[e_{**}, e_*]_m := \{\mathbf{w} : e_{**} \le_m \mathbf{w} \le_m e_*\}$$

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.

It was shown in [17] that, for models of two competing species, either there is a positive equilibrium representing coexistence of two species, or one species drives the other to extinction. Note that system (1.3) satisfies conditions (H1)-(H4) in [17], and thus Theorem B in [17] can be restated as follows.

Theorem A.2. Consider system (1.3). The ω-limit set of every orbit evolved from a point in $\mathbb{R}^4_+$ is contained in Γ and exactly one of the following holds:
(a) There exists a positive equilibrium e_* of 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, then either $\phi_t(\mathbf{w}) \to e_{\bar{\mathbf{u}}}$ or $\phi_t(\mathbf{w}) \to e_{\bar{\mathbf{v}}}$, as $t \to \infty$, for $\mathbf{w} = (u_1, u_2, v_1, v_2) \in \mathbb{R}^4_+ \setminus \Gamma$.

Appendix II.

We recall some qualitative properties of the semitrivial equilibria for system (1.3) in [24]. The following results are independent of the order between σ_1 and σ_2.

Proposition A.3 (Proposition 3.7 [24]). 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) $\alpha_1 < \bar{u}_1 < \frac{\alpha_1+\alpha_2}{2} < \bar{u}_2 < \alpha_2$.

Proposition A.4 (Proposition 3.8 [24]). 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) $\beta_1 < \bar{v}_1 < \frac{\beta_1+\beta_2}{2} < \bar{v}_2 < \beta_2$.

Proposition A.5 (Proposition 3.9 [24]). 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 $(\alpha_1, \frac{\alpha_1+\alpha_2}{2})$.

Proposition A.6 (Proposition 3.10 [24]). 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 $(\beta_1, \frac{\beta_1+\beta_2}{2})$.