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Effects of dispersal rates in a two-stage reaction-diffusion system

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Abstract

It is well known that in reaction-diffusion models for a single unstructured population in a bounded, static, heterogeneous environment, slower diffusion is advantageous. That is not necessarily the case for stage structured populations. In (Cantrell et al. 2020), it was shown that in a stage structured model introduced by Brown and Lin (1980), there can be situations where faster diffusion is advantageous. In this paper we extend and refine the results of (Cantrell et al. 2020) on persistence to more general combinations of diffusion rates and to cases where either adults or juveniles do not move. We also obtain results on the asymptotic behavior of solutions as diffusion rates go to zero, and on competition between species that differ in their diffusion rates but are otherwise ecologically identical. We find that when the spatial distributions of favorable habitats for adults and juveniles are similar, slow diffusion is still generally advantageous, but if those distributions are different that may no longer be the case.

Keywords Evolution of dispersal · Spatial ecology · Stage structure · Reaction-diffusion

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Dedicated to Mark Lewis on the occasion of his 60th birthday

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1 Introduction

The effects and evolution of dispersal in population dynamics have been widely studied from the viewpoint of reaction-advection-diffusion models. See for example (Cantrell and Cosner 2003; Cosner 2014; Lam et al. 2020), and the references cited in those works. In most cases, models have assumed that for any specific population or subpopulation, all individuals have the same dispersal behavior and experience the environment in the same way. In that case, in bounded habitats that are spatially heterogeneous but constant in time, for movement by pure diffusion, there is typically selection for slower movement (Hastings 1983; Dockery et al. 1998; Cantrell and Lam 2020). (In the presence of directed movement by either physical advection or taxis on environmental gradients, this can change; see (Cantrell et al. 2006; Lou and Lutscher 2014; Lam et al. 2020; Fagan et al. 2020). More broadly, many types of models in population dynamics or population genetics where there is movement display a reduction phenomenon, where movement reduces population growth; see (Altenberg 2012). However, it is not always the case that individuals within a population follow movement patterns drawn from the same distribution. Within populations there may be individual variation in dispersal and in responses to environmental conditions. One way this can occur is behaviorally, for example if individuals can switch between different dispersal patterns, such as rapid movement for searching and slower movement for exploiting a resource. Scenarios of this type are discussed in (Skalski and Gilliam 2003; Tyson et al. 2011; Cantrell et al. 2018, 2020). Another way it can occur is if different types of individuals experience the environment differently or have different dispersal abilities or both. A common example of that situation is where adults and juveniles differ in those respects. Papers on both “adult dispersal" and “juvenile" or “natal" dispersal are well represented in the ecological literature. Reaction-diffusion models where the environmental needs of adults and juveniles differ but their diffusion rates are either similar (both large or both small) or completely general were studied in (Cantrell et al. 2020) from the viewpoint of a simple model for a stage structured population introduced by Brown and Zhang (1980). In that setting the results of (Cantrell et al. 2020) showed that either slower or faster diffusion could be more favorable for population persistence, depending on the details of the distributions of favorable regions for adults and juveniles. In the cases considered in (Cantrell et al. 2020), roughly speaking, if the distributions of favorable regions for adults and juveniles are similar, then slower diffusion is advantageous for persistence, but if they are sufficiently different, then faster diffusion may be advantageous. However, in many systems, adults and juveniles may have very different movement rates. Many marine invertebrate species have sessile adults but dispersing larvae. On the other hand, some insect species have adults that can fly but juveniles that cannot, so they move very little relative to adults. In some species of fish, juveniles mostly remain in nursery areas such as mangroves (see (Laegdsgaard and Johnson 2001)) but adults may range more widely. In this paper we will use the same model of Brown and Zhang (1980) as in (Cantrell et al. 2020), but we will refine some of the results of (Cantrell et al. 2020) and consider cases where adults and juveniles may move in very different rates, or where one stage may not move at all. Specifically, we consider cases where one of the diffusion coefficients is zero, obtain results on the asymptotic profiles of solutions as one of the diffusion coefficients approaches zero, and consider cases where one of the diffusion coefficients is fixed or large and the other approaches zero. We also give conditions for the uniqueness of the positive equilibrium, and consider competition between two stage structured populations that are ecologically equivalent but have different diffusion rates. These are all extensions of the ideas and results of (Cantrell et al. 2020). The models for competition between such populations are motivated by the results of (Dockery et al. 1998; Cantrell and Lam 2020) on the evolution of slow diffusion in nonstructured population models. Populations where some individuals move but others do not were studied by Mark Lewis and his coauthors in (Lewis and Schmitz 1996; Hadeler and Lewis 2002; Pachepsky et al. 2005; Hadeler et al. 2009). In this paper we will obtain conditions for the persistence of the system and find the asymptotic profiles of the equilibrium as one or more of the diffusion rates goes to zero or infinity, and consider the stability of populations relative to invasion by other populations using different dispersal rates.

In Section 2, we introduce the single species two stage reaction diffusion system and then investigate the asymptotic profiles of the equilibrium as one or more of the diffusion rates approaches zero or infinity in the Subsection 2.1. This subsection also contains several interesting results on the limits of the principal eigenvalue of a two species cooperative system as one or more of the diffusion rates goes to zero or infinity. Subsection 2.2 is devoted for the study of the uniqueness and global stability of the equilibrium solution of the single species model. The two species competition model is introduced and studied in Section 3. We provide a biological interpretations of our theoretical results and highlight some open problems in Section 4.

2 Single-species two-stage reaction-diffusion system

Consider the single species two-stage reaction diffusion system

$$\begin{cases} \partial_t \tilde{u}_1 = d_1 \Delta \tilde{u}_1 + r(x)\tilde{u}_2 - s(x)\tilde{u}_1 - (a(x) + b(x)\tilde{u}_1 + c(x)\tilde{u}_2)\tilde{u}_1 & x \in \Omega,\ t > 0, \\ \partial_t \tilde{u}_2 = d_2 \Delta \tilde{u}_2 + s(x)\tilde{u}_1 - (e(x) + f(x)\tilde{u}_2 + g(x)\tilde{u}_1)\tilde{u}_2 & x \in \Omega,\ t > 0, \\ 0 = \partial_{\vec{n}} \tilde{u}_1 = \partial_{\vec{n}} \tilde{u}_2 & x \in \partial\Omega,\ t > 0, \end{cases} \tag{2.1}$$

where Ω is a bounded domain in $\mathbb{R}^n$ with smooth boundary $\partial\Omega$. $\vec{n}$ represents the outward unit normal to $\partial\Omega$. $\tilde{\mathbf{u}} = (\tilde{u}_1, \tilde{u}_2)$ represents the density of a species where $\tilde{u}_1$ and $\tilde{u}_2$ are the density functions of juveniles and individuals that have reached reproductive age, respectively. $s(x)$ and $r(x)$ are the local juvenile maturity and adult fecundity rates, respectively. $d_1 > 0$ and $d_2 > 0$ are the diffusion rates. The nonnegative functions $a(x)$, $b(x)$, $c(x)$, $e(x)$, $f(x)$, and $g(x)$ account for per-capita death rates and saturation factors. We shall assume that the parameter functions are Hölder continuous on $\overline{\Omega}$ with $r, s \not\equiv 0$ and $b, f > 0$ on $\overline{\Omega}$. For convenience, given two vectors $\mathbf{u}$ and $\mathbf{v}$ in $\mathbb{R}^2$, we say that $\mathbf{u} \le \mathbf{v}$ if $u_1 \le v_1$ and $u_2 \le v_2$.

In this work, due to biological interpretations of the quantities involved, we are only interested in componentwise nonnegative solutions $\tilde{\mathbf{u}} = (\tilde{u}_1, \tilde{u}_2)$ of (2.1). A steady state solution of (2.1) is a time-independent solution of (2.1), that is a solution of

$$\begin{cases} 0 = d_1\Delta u_1 + r(x)u_2 - s(x)u_1 - (a(x) + b(x)u_1 + c(x)u_2)u_1 & x \in \Omega, \\ 0 = d_2\Delta u_2 + s(x)u_1 - (e(x) + f(x)u_2 + g(x)u_1)u_2 & x \in \Omega, \\ 0 = \partial_{\vec{n}} u_1 = \partial_{\vec{n}} u_2 & x \in \partial\Omega. \end{cases} \tag{2.2}$$

Given $\mathbf{d} := (d_1, d_2)$, with $d_1 > 0$ and $d_2 > 0$, we denote by $\mathbf{u}(\cdot, \mathbf{d}) = (u_1(\cdot, \mathbf{d}), u_2(\cdot, \mathbf{d}))$ positive steady state solutions of (2.1). Clearly the zero function $\mathbf{0} = (0, 0)$ is a steady state solution of (2.1). When (2.1) is linearized at $\mathbf{0}$, its corresponding eigenvalue problem is

$$\begin{cases} \lambda\varphi_1 = d_1\Delta\varphi_1 - (a(x) + s(x))\varphi_1 + r(x)\varphi_2 & x \in \Omega, \\ \lambda\varphi_2 = d_2\Delta\varphi_2 + s(x)\varphi_1 - e(x)\varphi_2 & x \in \Omega, \\ \quad 0 = \partial_{\vec{n}}\varphi_1 = \partial_{\vec{n}}\varphi_2 & x \in \partial\Omega. \end{cases} \tag{2.3}$$

Observe that (2.3) is a cooperative system. Hence, by the Krein-Rutman theorem, (2.3) has a principal eigenvalue, denoted by λ_1, with a corresponding positive eigenfunction. We first recall the following result established in (Cantrell et al. 2020) on the global stability of the zero function $\mathbf{0}$ when $\lambda_1 \leq 0$ and the existence of a positive steady state solution of (2.1) when $\lambda_1 > 0$.

Proposition 2.1 (Lemma 2, (Cantrell et al. 2020)) *If* $\lambda_1 \leq 0$*, then* $\mathbf{0}$ *is globally asymptotically stable for solutions of equation* (2.1)*. If* $\lambda_1 > 0$*, then the system expressed in* (2.1) *is persistent and has at least one positive steady state solution.*

Next, when we take $\mathbf{d} := (d_1, d_2) = \mathbf{0}$ in (2.3), we obtain the ODE-system

$$\begin{cases} \partial_t\tilde{u}_1 = r(x)\tilde{u}_2 - s(x)\tilde{u}_1 - (a(x) + b(x)\tilde{u}_1 + c(x)\tilde{u}21)\tilde{u}_1 & t > 0, \\ \partial_t\tilde{u}_2 = s(x)\tilde{u}_1 - (e(x) + f(x)\tilde{u}_2 + g(x)\tilde{u}_1)\tilde{u}_2 & t > 0. \end{cases} \tag{2.4}$$

For each $x \in \Omega$, the quantity

$$\begin{aligned} \Lambda(x) =& \frac{1}{2}\Big(\sqrt{(s(x) + a(x) - e(x))^2 + 4r(x)s(x)} - (s(x) + a(x) + e(x))\Big) \\ =& \begin{cases} -\min\{e(x), (a(x) + s(x))\} & \text{If } r(x)s(x) = 0, \\ \frac{r(x)s(x) - (a(x)+s(x))e(x)}{\sqrt{(a(x)+s(x)-e(x))^2+4r(x)s(x)}+(a(x)+s(x)+e(x))} & \text{If } r(x)s(x) > 0, \end{cases} \end{aligned} \tag{2.5}$$

is the maximal eigenvalue of the linearization of (2.4) around $\mathbf{0}$. Observe that $\Lambda(x)$ is positive if and only if $r(x)s(x) > (s(x) + a(x))e(x)$. To simplify the notations, given a continuous function h on $\overline{\Omega}$, we set

$$\overline{h} = \int_\Omega h, \qquad h_{\min} = \min_{x\in\overline{\Omega}} h(x) \qquad \text{and} \qquad h_{\max} = \max_{x\in\overline{\Omega}} h(x).$$

(This notation is different from that in (Cantrell et al. 2020), where $\overline{h}$ was used to represent the average of $h(x)$.) The following result is established in (Cantrell et al. 2020).

Proposition 2.2 (Proposition 1 & Lemma 9 (Cantrell et al. 2020)) *The principal eigenvalue λ_1 of* (2.3) *satisfies*

$$\lim_{\mathbf{d}\to\mathbf{0}} \lambda_1 = \Lambda_{\max} \tag{2.6}$$

and

$$\lim_{\mathbf{d}\to\infty} \lambda_1 = \lambda_1^{\infty} := \frac{1}{2|\Omega|}\left(\sqrt{(\overline{s}+\overline{a}-\overline{e})^2 + 4\overline{r}\cdot\overline{s}} - (\overline{s}+\overline{a}+\overline{e})\right). \tag{2.7}$$

2.1 Asymptotic profiles of steady state solutions

The current subsection is devoted to the study of the asymptotic profiles of positive steady state solutions of (2.1) as at least one of the diffusion rates becomes small or large. Since the existence of positive steady state solutions of (2.1) is completely determined by the sign of the principal eigenvalue λ_1 of the cooperative system (2.3) (see Proposition 2.1), we shall first study the limit of the principal eigenvalue of (2.3) as at least one of the diffusion rates becomes small or large, and then state the main results on the asymptotic profiles of the steady state solutions of (2.1).

2.1.1 The case of d_1 small and d_2 small

Recall that (2.1) has a positive steady state solution if and only if $\lambda_1 > 0$. Observe also from (2.5) that $\Lambda_{\max}$ and $(rs-(a+s)e)_{\max}$ have the same signs. Hence, it follows from Proposition 2.2 that if $(rs-(s+a)e)_{\max} < 0$, (2.1) has no positive steady state solution for small diffusion rates, while if $(rs-(a+s)e)_{\max} > 0$ then (2.1) has positive steady state solutions for small diffusion rates. The asymptotic profiles of positive steady states for small diffusion rates are studied in (Cantrell et al. 2020) under the additional assumption that $c = g \equiv 0$. The following result is established in (Cantrell et al. 2020).

Proposition 2.3 (Theorem 1, Cantrell et al. 2020) *If $\big(rs-(s+a)e\big)_{\max} > 0$, then there is $\delta_0 > 0$ such that* (2.1) *has a positive steady state solution $\mathbf{u}(\cdot,\mathbf{d})$ for every $\mathbf{d} = (d_1, d_2) \in (0, \delta_0)^2$. Moreover, if in addition $c = g \equiv 0$, then $\mathbf{u}(\cdot,\mathbf{d}) \to \mathbf{U}^*$ as $\mathbf{d} \to 0$ locally uniformly in Ω, where $\mathbf{U}^*(x) = (U_1^*(x), U_2^*(x))$ is the unique nonnegative steady state solution of the kinetic system* (2.4).

When c and or g are not identically zero, the following result holds.

Theorem 2.4 *Suppose that $\Lambda_{\min} > 0$ such that* (2.4) *has a unique positive steady state solution $\mathbf{U}(x) := (U_1(x), U_2(x))$ for every $x \in \overline{\Omega}$. Suppose also that*

$$\max\left\{\left\|\frac{cU_2}{bU_1}\right\|_\infty, \left\|\frac{gU_1}{fU_2}\right\|_\infty\right\} < 1. \tag{2.8}$$

Then (2.1) *has positive steady state solutions $\mathbf{u}(\cdot,\mathbf{d})$ for small diffusion rates $\mathbf{d} = (d_1, d_2)$ satisfying $\mathbf{u}(\cdot,\mathbf{d}) \to \mathbf{U}(\cdot)$ as $\max\{d_1, d_2\} \to 0$ uniformly in Ω.*

Remark 2.5 Assume that $\Lambda_{\min} > 0$ and let $\mathbf{U}(x)$ denote the unique positive steady state solution of (2.4).

(i) Note that hypothesis (2.8) holds if and only if $c(x)U_2(x) < b(x)U_1(x)$ and $g(x)U_1(x) < f(x)U_2(x)$ for every $x \in \overline{\Omega}$, which will be true if $||c||_\infty$ and $||g||_\infty$ are sufficiently small. Hence hypothesis (2.8) indicates that, at the equilibrium solution of the ODE-system (2.4), each stage's self overcrowding effect is large enough relative to the limitation caused by interstage interactions. This is somewhat analogous to the requirements for the uniqueness of an equilibrium with both components positive in the diffusive Lotka-Volterra competition model. In that model it is well known that there is uniqueness in the case of sufficiently weak competition but uniqueness may fail for strong competition. We do not know if uniqueness holds or not for strong competition in the model we are studying.

(ii) Since the dependence of $\mathbf{U}$ on c and g is non-trivial, it would be helpful to provide a sufficient way to check the validity of (2.8). Observe that U_1 and U_2 satisfy the algebraic equations

$$U_1 = \frac{\sqrt{(a+s+cU_2)^2 + 4rbU_2} - (a+s+cU_2)}{2b}$$
$$\text{and} \quad U_2 = \frac{\sqrt{(e+gU_1)^2 + 4sfU_1} - (e+gU_1)}{2f},$$

which yield

$$bU_1 - cU_2 = \frac{2(rb - (a+s)c - 2U_2c^2))U_2}{\sqrt{(a+s+cU_2)^2 + 4rbU_2} + (a+s+3cU_2)}$$

and

$$fU_2 - gU_1 = \frac{2(sf - eg - 2U_1g^2)U_1}{\sqrt{(e+gU_1)^2 + 4sfU_1} + (e+3gU_1)}.$$

Hence (2.8) holds if and only if

$$c < \frac{2rb}{\sqrt{(a+s)^2 + 8rbU_2} + (a+s)} \quad \text{and} \quad g < \frac{2sf}{\sqrt{e^2 + 8sfU_1} + e}. \tag{2.9}$$

Let $\mathbf{U}^*(x)$ denote the unique positive steady state solution (2.4) when $g = c = 0$. Since $U_i(x) \le U_i^*(x)$ for every $x \in \overline{\Omega}$ and $i = 1, 2$, it follows from (2.9) that (2.8) holds if

$$c < \frac{2rb}{\sqrt{(a+s)^2 + 8rbU_2^*} + (a+s)} \quad \text{and} \quad g < \frac{2sf}{\sqrt{e^2 + 8sfU_1^*} + e}. \tag{2.10}$$

Note that (2.10) gives explicit bounds on c and g.

To prove Theorem 2.4, we first introduce some notations and definitions. First, consider the system

$$\begin{cases} \partial_t \underline{u}_1 = d_1 \Delta \underline{u}_1 + r\underline{u}_2 - (a+s+b\underline{u}_1 + c\overline{u}_2)\underline{u}_1 & x \in \Omega,\ t>0, \\ \partial_t \underline{u}_2 = d_2 \Delta \underline{u}_2 + s\underline{u}_1 - (e+f\underline{u}_2 + g\overline{u}_1)\underline{u}_2 & x \in \Omega,\ t>0, \\ \partial_t \overline{u}_1 = d_1 \Delta \overline{u}_1 + r\overline{u}_2 - (a+s+b\overline{u}_1 + c\underline{u}_2)\overline{u}_1 & x \in \Omega,\ t>0, \\ \partial_t \overline{u}_2 = d_2 \Delta \overline{u}_2 + s\overline{u}_1 - (e+f\overline{u}_2 + g\underline{u}_1)\overline{u}_2 & x \in \Omega,\ t>0, \\ 0 = \partial_{\vec{n}} \underline{u}_1 = \partial_{\vec{n}} \underline{u}_2 = \partial_{\vec{n}} \overline{u}_1 = \partial_{\vec{n}} \overline{u}_2 & x \in \partial\Omega,\ t>0. \end{cases} \tag{2.11}$$

Observe that if $\mathbf{u}(t,x) = (u_1,u_2)(t,x)$ solves (2.1), then $(\mathbf{u}(t,x), \mathbf{u}(t,x))$ solves (2.11). Hence, if (2.1) has a positive steady state solution then (2.11) also has a coexistence steady state solution. Let $C(\overline{\Omega})$ denote the Banach space of uniformly continuous functions on Ω endowed with the usual sup-norm, $C^+(\overline{\Omega}) := \{u \in C(\overline{\Omega})\ :\ u \geq 0\}$ and $C^{++}(\overline{\Omega}) := \{u \in C^+(\overline{\Omega})\ :\ u_{\min} > 0\}$. Note that $C^{++}(\overline{\Omega}) = int(C^+(\overline{\Omega}))$. Next, let

$$\mathbb{X} := C(\overline{\Omega}) \times C(\overline{\Omega}), \quad \mathbb{X}^+ := C^+(\overline{\Omega}) \times C^+(\overline{\Omega}) \quad \text{and} \quad \mathbb{X}^{++} := C^{++}(\overline{\Omega}) \times C^{++}(\overline{\Omega}).$$

For any given $(\underline{\mathbf{u}}(0,\cdot), \overline{\mathbf{u}}(0,\cdot)) := ((\underline{u}_1,\underline{u}_2)(0,\cdot), (\overline{u}_1,\overline{u}_2)(0,\cdot)) \in \mathbb{X}^+ \times \mathbb{X}^+$, it follows from the theory of parabolic systems and the type of nonlinearity (Lotka-Volterra competition type) in (2.11) that there is a corresponding unique global classical solution $(\underline{\mathbf{u}}(t,\cdot), \overline{\mathbf{u}}(t,\cdot))$ defined for all time. Furthermore, $(\underline{\mathbf{u}}(t,\cdot), \overline{\mathbf{u}}(t,\cdot)) \in \mathbb{X}^+ \times \mathbb{X}^+$ for all $t > 0$ and it is uniformly bounded in time. Given $(\underline{\mathbf{u}}(\cdot), \overline{\mathbf{u}}(\cdot)), (\underline{\mathbf{v}}(\cdot), \overline{\mathbf{v}}(\cdot)) \in \mathbb{X} \times \mathbb{X}$ we say that $(\underline{\mathbf{u}}(\cdot), \overline{\mathbf{u}}(\cdot)) \leq_K (\underline{\mathbf{v}}(\cdot), \overline{\mathbf{v}}(\cdot))$ if $(\underline{\mathbf{v}}(\cdot) - \underline{\mathbf{u}}(\cdot), \overline{\mathbf{u}}(\cdot) - \overline{\mathbf{v}}(\cdot)) \in \mathbb{X}^+ \times \mathbb{X}^+$.

Definition 2.6 (Sub/Super-solutions). Let $T > 0$ be given. Given nonnegative vector functions $\underline{\mathbf{u}}, \overline{\mathbf{u}} \in C([0,T) \times \overline{\Omega}) \cap C^{1,2}((0,T) \times \Omega) \cap C^{0,1}((0,T) \times \overline{\Omega})$, we say that $(\underline{\mathbf{u}}, \overline{\mathbf{u}})$ is a subsolution of (2.11) if

$$\begin{cases} \partial_t \underline{u}_1 \leq d_1 \Delta \underline{u}_1 + r\underline{u}_2 - (a+s+b\underline{u}_1 + c\overline{u}_2)\underline{u}_1 & x \in \Omega,\ 0<t<T, \\ \partial_t \underline{u}_2 \leq d_2 \Delta \underline{u}_2 + s\underline{u}_1 - (e+f\underline{u}_2 + g\overline{u}_1)\underline{u}_2 & x \in \Omega,\ 0<t<T, \\ \partial_t \overline{u}_1 \geq d_1 \Delta \overline{u}_1 + r\overline{u}_2 - (a+s+b\overline{u}_1 + c\underline{u}_2)\overline{u}_1 & x \in \Omega,\ 0<t<T, \\ \partial_t \overline{u}_2 \geq d_2 \Delta \overline{u}_2 + s\overline{u}_1 - (e+f\overline{u}_2 + g\underline{u}_1)\overline{u}_2 & x \in \Omega,\ 0<t<T. \end{cases}$$

We say that $(\underline{\mathbf{u}}, \overline{\mathbf{u}})$ is a supersolution of (2.11) when the above inequalities are reversed.

Thanks to the maximum principle for competition systems (Cantrell and Cosner 2003; Cosner 2014; Protter and Weinberger 1967) we can state the following result.

Proposition 2.7 *Let* $(\underline{\mathbf{u}}, \overline{\mathbf{u}}) \in C([0,T) : \mathbb{X}^+ \times \mathbb{X}^+)$ *be a subsolution of* (2.11) *and* $(\underline{\mathbf{v}}, \overline{\mathbf{v}}) \in C([0,T) : \mathbb{X}^+ \times \mathbb{X}^+)$ *be a supersolution of* (2.11). *If* $\partial_{\vec{n}} u = 0$ *on* $\partial\Omega \times (0,T)$ *for each* $u \in \{\underline{u}_i, \underline{v}_i, \overline{u}_i, \overline{v}_i\ :\ i = 1,2\}$ *and* $(\underline{\mathbf{u}}, \overline{\mathbf{u}})(0,\cdot) \leq_K (\underline{\mathbf{v}}, \overline{\mathbf{v}})(0,\cdot)$*, then* $(\underline{\mathbf{u}}, \overline{\mathbf{u}})(t,\cdot) \leq_K (\underline{\mathbf{v}}, \overline{\mathbf{v}})(t,\cdot)$ *for all* $t \in (0,T)$.

It follows from Proposition 2.7 that if $(\underline{\mathbf{u}}, \overline{\mathbf{u}})(t,x)$ and $(\underline{\mathbf{v}}, \overline{\mathbf{v}})(t,x)$ are classical solutions of (2.11) satisfying $(\underline{\mathbf{u}}, \overline{\mathbf{u}})(0,\cdot) \leq_K (\underline{\mathbf{v}}, \overline{\mathbf{v}})(0,\cdot)$, then $(\underline{\mathbf{u}}, \overline{\mathbf{u}})(t,\cdot) \leq_K (\underline{\mathbf{v}}, \overline{\mathbf{v}})(t,\cdot)$

for all $t > 0$. When either $\underline{\mathbf{u}} \equiv \mathbf{0}$ or $\overline{\mathbf{u}} \equiv \mathbf{0}$ in (2.11), it reduces to system (2.1) with $c = g \equiv 0$, which is a cooperative system. This sub-cooperative system has a (unique) positive steady state solution $\mathbf{u}^*(x) := (u_1^*(x), u_2^*(x))$ if and only if $\lambda_1 > 0$. Observe also that if $\lambda_1 \leq 0$, then every solution of (2.11) converges to $(\mathbf{0}, \mathbf{0})$. So, we shall always suppose that $\lambda_1 > 0$. Then $(\mathbf{0}, \mathbf{u}^*)$ and $(\mathbf{u}^*, \mathbf{0})$ are the single species steady state solutions of (2.11). Furthermore, any nontrivial steady state solution $(\underline{\mathbf{u}}, \overline{\mathbf{u}})$ of (2.11) satisfies $(\mathbf{0}, \mathbf{u}^*) \leq_K (\underline{\mathbf{u}}, \overline{\mathbf{u}}) \leq_K (\mathbf{u}^*, \mathbf{0})$. Observe also that if $\mathbf{u}(t, \cdot)$ solves (2.1), and $(\underline{\mathbf{u}}, \overline{\mathbf{u}})(t, \cdot)$ solves (2.11) with $(\underline{\mathbf{u}}, \overline{\mathbf{u}})(0, \cdot) \leq_K (\mathbf{u}, \mathbf{u})(0, \cdot)$ then $(\underline{\mathbf{u}}, \overline{\mathbf{u}})(t, \cdot) \leq_K (\mathbf{u}, \mathbf{u})(t, \cdot)$ for all $t > 0$. Now, we can present a proof of Theorem 2.4.

Proof of Theorem 2.4 Since $\Lambda_{\min} > 0$, then $U_{1,\min} > 0$ and $U_{2,\min} > 0$. Let

$$0 < \varepsilon < \varepsilon_0 := \min \left\{ 1, \frac{b_{\min} U_{1,\min}}{1 + \|c\|_\infty \|U_2\|_\infty}, \frac{f_{\min} U_{2,\min}}{1 + \|g\|_\infty \|U_1\|_\infty} \right\}$$

be fixed. The proof is now divided in three steps.

Step 1. Consider the cooperative elliptic system

$$\begin{cases} 0 = d_1 \Delta \underline{u}_{1,\varepsilon} + r \underline{u}_{2,\varepsilon} - (a + s + b\underline{u}_{1,\varepsilon} + (1+\varepsilon) c U_2) \underline{u}_{1,\varepsilon} & x \in \Omega, \\ 0 = d_2 \Delta \underline{u}_{2,\varepsilon} + s \underline{u}_{1,\varepsilon} - (e + f \underline{u}_{2,\varepsilon} + (1+\varepsilon) g U_1) \underline{u}_{2,\varepsilon} & x \in \Omega, \\ 0 = \partial_{\vec{n}} \underline{u}_{1,\varepsilon} = \partial_{\vec{n}} \underline{u}_{2,\varepsilon} & x \in \partial\Omega \end{cases} \tag{2.12}$$

and the corresponding kinetic problem

$$\begin{cases} 0 = r \underline{U}_{2,\varepsilon} - (a + s + b\underline{U}_{1,\varepsilon} + (1+\varepsilon) c U_2) \underline{U}_{1,\varepsilon} & x \in \Omega, \\ 0 = s \underline{U}_{1,\varepsilon} - (e + f \underline{U}_{2,\varepsilon} + (1+\varepsilon) g U_1) \underline{U}_{2,\varepsilon} & x \in \Omega. \end{cases} \tag{2.13}$$

When (2.13) is linearized at $\mathbf{0}$, the corresponding eigenvalue problem is

$$\begin{cases} \xi Q_1 = r Q_2 - (a + s + (1+\varepsilon) c U_2) Q_1 & x \in \Omega, \\ \xi Q_2 = s Q_1 - (e + (1+\varepsilon) g U_1) Q_2 & x \in \Omega. \end{cases} \tag{2.14}$$

By Perron-Frobenius theorem, (2.14) has a principal eigenvalue $\underline{\xi}_{\varepsilon}(x)$ with a positive eigenvector $(Q_1^\varepsilon(x), Q_2^\varepsilon(x))$ for each $x \in \overline{\Omega}$. Recalling that $(U_1(x), U_2(x))$ solves

$$\begin{cases} (b(x)U_1(x) - \varepsilon c(x) U_2(x)) U_1(x) \\ = r U_1(x) - \Big(a(x) + s(x) + (1+\varepsilon) c(x) U_2(x) \Big) U_1(x) & x \in \Omega, \\ (f(x) U_2(x) - \varepsilon g(x) U_1(x)) U_2(x) = s(x) U_1(x) \\ - \Big(e + (1+\varepsilon) g(x) U_1(x) \Big) U_2(x) & x \in \Omega, \end{cases} \tag{2.15}$$

then

$$0 < \xi_0 := \inf_{0 < \tau < \varepsilon_0, y \in \Omega} \min\{ b(y) U_1(y) - \tau c(y) U_2(y),$$

$$f(y)U_2(y) - \tau g(y)U_1(y)\} \leq \underline{\xi}_\varepsilon(x) \quad \forall\, x \in \Omega.$$

Observe that for every $M > \max\left\{\frac{r_{\max}+(a+s+2cU_2)_{\max}}{b_{\min}}, \frac{s_{\max}+(e+2gU_1)_{\max}}{f_{\min}}\right\}$, the constant vector function (M, M) is a supersolution of (2.12) and (2.13). Hence, (2.13) has at least one positive steady state solution $\underline{\mathbf{U}}_\varepsilon(x)$. Moreover,

$$\begin{aligned} r(\tau\underline{U}_2) - (a+s+b(\tau\underline{U}_1) + (1+\varepsilon)cU_2)(\tau\underline{U}_1) \\ < \tau(r\underline{U}_2 - (a+s+b\underline{U}_1 + (1+\varepsilon)cU_2)\underline{U}_1) \end{aligned}$$

and

$$\begin{aligned} s(\tau\underline{U}_1) - (e+f(\tau\underline{U}_2) + (1+\varepsilon)gU_1)(\tau\underline{U}_2) \\ < \tau(s\underline{U}_1 - (e+f\underline{U}_2 + (1+\varepsilon)gU_1)\underline{U}_2) \end{aligned}$$

for every $0 < \tau < 1$ and $\underline{U}_i > 0$, $i = 1, 2$. Hence (2.13) is subhomogenous, which implies that its positive solution $\underline{\mathbf{U}}_\varepsilon(x)$ is unique. See for example (Hirsch 1994, Theorems 3.1 and 5.5) or results in (López-Gómez and Molina-Meyer 1994). Furthermore, if we linearize (2.13) at $\underline{\mathbf{U}}_\varepsilon(x)$, the corresponding eigenvalue problem is

$$\begin{cases} \tilde{\xi}\tilde{Q}_1 = r\tilde{Q}_2 - (a+s+(1+\varepsilon)cU_2 + 2\underline{U}_{1,\varepsilon})\tilde{Q}_1, \\ \tilde{\xi}\tilde{Q}_2 = s\tilde{Q}_1 - (e+(1+\varepsilon)gU_1 + 2f\underline{U}_{2,\varepsilon})\tilde{Q}_2. \end{cases} \tag{2.16}$$

It then follows from (2.13) that the maximal eigenvalue $\tilde{\xi}_\varepsilon(x)$ of (2.16), whose existence is guaranteed by the Perron-Frobenius theorem, satisfies $\tilde{\xi}_\varepsilon(x) \leq -\min\{(b\underline{U}_{1,\varepsilon})_{\min}, (g\underline{U}_{2,\varepsilon})_{\min}\} < 0$ for all $x \in \overline{\Omega}$. So, $\underline{\mathbf{U}}_\varepsilon(x)$ is linearly and globally stable for every $x \in \overline{\Omega}$. Thus, by Theorem 1.5 of (Lam and Lou 2016), there is $0 < d_0^* \ll 1$ such that (2.12) also has a unique positive stable steady state solution $\underline{\mathbf{u}}_\varepsilon(\cdot, \mathbf{d})$ for every $0 < \varepsilon < \varepsilon_0$, and $0 < d_1, d_2 < d_0^*$. Furthermore,

$$\underline{\mathbf{u}}_\varepsilon(\cdot, \mathbf{d}) \to \underline{\mathbf{U}}_\varepsilon \quad \text{as} \quad \max\{d_1, d_2\} \to 0 \quad \text{uniformly in } \overline{\Omega}. \tag{2.17}$$

Now, observe that

$$\begin{aligned} & r(1-\varepsilon)U_2 - (a+s+b(1-\varepsilon)U_1 + (1+\varepsilon)cU_2)(1-\varepsilon)U_1 \\ & \quad = (1-\varepsilon)\Big(a+s+bU_1+cU_2-a-s-(1-\varepsilon)bU_1-(1+\varepsilon)cU_2\Big)U_1 \\ & \quad = \varepsilon(1-\varepsilon)\Big(1-\frac{cU_2}{bU_1}\Big)bU_1^2 \geq \varepsilon(1-\varepsilon)\Big(1-\Big\|\frac{cU_2}{bU_1}\Big\|_\infty\Big)bU_1^2 > 0 \quad \text{(by (2.8))} \end{aligned}$$

and

$$\begin{aligned} & s(1-\varepsilon)U_1 - \Big(e+(1-\varepsilon)fU_2+(1+\varepsilon)gU_1\Big)(1-\varepsilon)U_2 \\ & \quad \geq \varepsilon(1-\varepsilon)\Big(1-\Big\|\frac{gU_1}{fU_2}\Big\|_\infty\Big)fU_2^2 > 0 \quad \text{(by (2.8))}, \end{aligned}$$

that is $(1-\varepsilon)\mathbf{U}$ is a strict subsolution of (2.13). Hence, by the strong maximum principle for cooperative systems, the uniqueness and global stability of the unique positive steady state $\underline{\mathbf{U}}_{\varepsilon}(x)$ of (2.13), it holds that

$$\min\{(\underline{U}_{1,\varepsilon}-(1-\varepsilon)U_1)_{\min},(\underline{U}_{2,\varepsilon}-(1-\varepsilon)U_2)_{\min}\}>0. \tag{2.18}$$

Thus, by (2.17), we can chose $0<d^*_{1,\varepsilon}\ll d^*_0$ such that

$$\min\left\{(\underline{u}_{1,\varepsilon}-(1-\varepsilon)U_1)_{\min},(\underline{u}_{2,\varepsilon}-(1-\varepsilon)U_2)_{\min}\right\}>0 \quad \text{for} \quad 0<d_1,d_2<d^*_{1,\varepsilon}. \tag{2.19}$$

Step 2. Consider the cooperative elliptic system

$$\begin{cases} 0=d_1\Delta\overline{u}_{1,\varepsilon}+r\overline{u}_{2,\varepsilon}-(a+s+b\overline{u}_{1,\varepsilon}+(1-\varepsilon)cU_2(x))\overline{u}_{1,\varepsilon} & x\in\Omega,\\ 0=d_2\Delta\overline{u}_{2,\varepsilon}+s\overline{u}_{1,\varepsilon}-(e+f\overline{u}_{2,\varepsilon}+(1-\varepsilon)gU_1(x))\overline{u}_{2,\varepsilon} & x\in\Omega,\\ 0=\partial_{\vec{n}}\overline{u}_{1,\varepsilon}=\partial_{\vec{n}}\overline{u}_{2,\varepsilon} & x\in\partial\Omega \end{cases} \tag{2.20}$$

and the corresponding kinetic problem

$$\begin{cases} 0=r\overline{U}_{2,\varepsilon}-(a+s+b\overline{U}_{1,\varepsilon}+(1-\varepsilon)cU_2(x))\overline{u}_{1,\varepsilon} & x\in\Omega,\\ 0=s\overline{U}_{1,\varepsilon}-(e+f\underline{U}_{2,\varepsilon}+(1-\varepsilon)gU_1(x))\overline{u}_{2,\varepsilon} & x\in\Omega. \end{cases} \tag{2.21}$$

When (2.21) is linearized at $\mathbf{0}$, the corresponding eigenvalue problem is

$$\begin{cases} \xi q_1=rq_2-(a+s+(1-\varepsilon)cU_2(x))q_1 & x\in\Omega,\\ \xi q_2=sq_1-(e+(1-\varepsilon)gU_1(x))q_2 & x\in\Omega. \end{cases} \tag{2.22}$$

By Perron-Frobenius theorem, (2.22) has a principal eigenvalue $\overline{\xi}_{\varepsilon}(x)$ with a positive eigenvector $(q_{1,\varepsilon}(x),q_{2,\varepsilon}(x))$ for each $x\in\overline{\Omega}$. It is easy to see that $\underline{\xi}_{\varepsilon}(x)<\overline{\xi}_{\varepsilon}(x)$ for every $x\in\overline{\Omega}$. Observe also that for every $M>\max\left\{\frac{r_{\max}+(a+s+2cU_2)_{\max}}{b_{\min}},\frac{s_{\max}+(e+2gU_1)_{\max}}{f_{\min}}\right\}$, the constant function vector function (M,M) is a supersolution of (2.20) and (2.21). Hence, (2.21) has at least one positive steady state solution $\overline{\mathbf{U}}_{\varepsilon}(x)$, which is unique since (2.21) is subhomogenous. As, in **Step 1**, we have that $\overline{\mathbf{U}}_{\varepsilon}(x)$ is linearly and globally stable for every $x\in\overline{\Omega}$. Therefore, by Theorem 1.5 of (Lam and Lou 2016), there is $0<d^{**}_0\ll 1$ such that (2.20) also has a unique positive stable steady state solution $\overline{\mathbf{u}}_{\varepsilon}(\cdot,\mathbf{d})$ for every $0<\varepsilon<\varepsilon_0$, and $0<d_1,d_2<d^{**}_0$. Furthermore,

$$\overline{\mathbf{u}}_{\varepsilon}(\cdot,\mathbf{d})\to\overline{\mathbf{U}}_{\varepsilon} \quad \text{as} \quad \max\{d_1,d_2\}\to 0 \quad \text{uniformly in } \overline{\Omega}. \tag{2.23}$$

Now, observe that

$$r(1+\varepsilon)U_2-\Big(a+s+b(1+\varepsilon)U_1+(1-\varepsilon)cU_2\Big)(1+\varepsilon)U_1$$

$$= (1+\varepsilon)\Big(a+s+bU_1+cU_2-a-s-(1+\varepsilon)bU_1-(1-\varepsilon)cU_2\Big)U_1$$
$$= \varepsilon(1+\varepsilon)\Big(\frac{cU_2}{bU_1}-1\Big)bU_1^2 \le \varepsilon(1+\varepsilon)\Big(\Big\|\frac{cU_2}{bU_1}\Big\|_\infty-1\Big)bU_1^2 < 0 \quad \text{(by (2.8))}$$

and

$$s(1+\varepsilon)U_1-(e+(1+\varepsilon)fU_2+(1-\varepsilon)gU_1)$$
$$\le \varepsilon(1+\varepsilon)\Big(\Big\|\frac{gU_1}{fU_2}\Big\|_\infty-1\Big)fU_2^2 < 0 \quad \text{(by (2.8))},$$

so that $(1+\varepsilon)\mathbf{U}$ is a strict supersolution of (2.21). Hence, by the strong maximum principle for cooperative systems, the uniqueness and global stability of the unique positive steady state $\overline{\mathbf{U}}_\varepsilon$ of (2.21), it holds that

$$\min\{((1+\varepsilon)U_1-\overline{U}_{1,\varepsilon})_{\min}, ((1+\varepsilon)U_2-\overline{U}_{2,\varepsilon})_{\min}\} > 0. \tag{2.24}$$

Thus, by (2.23), we can choose $0 < d^*_{2,\varepsilon} \ll \min\{d^*_{1,\varepsilon}, d_0^{**}, d_0^*\}$ such that

$$\min\Big\{((1+\varepsilon)U_1-\overline{u}_{1,\tilde{\varepsilon}})_{\min}, ((1+\varepsilon)U_2-\overline{u}_{2,\tilde{\varepsilon}})_{\min}\Big\} > 0 \quad \text{for} \quad 0 < d_1, d_2 < d^*_{2,\varepsilon}. \tag{2.25}$$

This together with (2.18) implies that for every $0 < d_1, d_2 < d^*_{1,\varepsilon}$, $(\underline{\mathbf{u}}_\varepsilon(\cdot,\mathbf{d}), \overline{\mathbf{u}}_\varepsilon(\cdot,\mathbf{d}))$ satisfies,

$$\begin{cases} 0 \le d_1\Delta\underline{u}_{1,\varepsilon}+r\underline{u}_{2,\varepsilon}-(a+s+b\underline{u}_{1,\varepsilon}+c\overline{u}_{2,\varepsilon})\underline{u}_{1,\varepsilon} & x\in\Omega,\\ 0 \le d_2\Delta\underline{u}_{2,\varepsilon}+s\underline{u}_{1,\varepsilon}-(e+f\underline{u}_{2,\varepsilon}+g\overline{u}_{1,\varepsilon})\underline{u}_{2,\varepsilon} & x\in\Omega,\\ 0 \ge d_1\Delta\overline{u}_{1,\varepsilon}+r\overline{u}_{2,\varepsilon}-(a+s+b\overline{u}_{1,\varepsilon}+c\underline{u}_{2,\varepsilon})\overline{u}_{1,\varepsilon} & x\in\Omega,\\ 0 \ge d_2\Delta\overline{u}_{2,\varepsilon}+s\overline{u}_{1,\varepsilon}-(e+f\overline{u}_{2,\varepsilon}+g\underline{u}_{1,\varepsilon})\overline{u}_{2,\varepsilon} & x\in\Omega,\\ 0 = \partial_{\vec{n}}\overline{u}_{1,\varepsilon}=\partial_{\vec{n}}\overline{u}_{2,\varepsilon}=\partial_{\vec{n}}\underline{u}_{1,\varepsilon}=\partial_{\vec{n}}\underline{u}_{2,\varepsilon} & x\in\partial\Omega. \end{cases} \tag{2.26}$$

Note also from the comparison principle for cooperative systems, uniqueness and stability of $\underline{\mathbf{u}}_\varepsilon(\cdot,\mathbf{d})$ and $\overline{\mathbf{u}}_\varepsilon(\cdot,\mathbf{d})$ that

$$\underline{\mathbf{u}}_\varepsilon(\cdot,\mathbf{d}) < \overline{\mathbf{u}}_\varepsilon(\cdot,\mathbf{d}) \quad \forall\, 0 < d_1, d_2 < d^*_{2,\varepsilon}. \tag{2.27}$$

Step 3. Let $d^*_{2,\varepsilon} > 0$ be as in **Step 2**. Let $0 < d_1, d_2 < d^*_{2,\varepsilon}$ be fixed, and $(\underline{\mathbf{u}}_\varepsilon(\cdot,\mathbf{d}), \overline{\mathbf{u}}_\varepsilon(\cdot,\mathbf{d}))$ be as in **Step 1** and **Step 2**. Consider the set

$$\mathbb{I}^{\mathbf{d},\varepsilon}_{inv} := \{\mathbf{u}\in\mathbb{X}^+ \ : \ \underline{\mathbf{u}}_\varepsilon(\cdot,\mathbf{d}) \le \mathbf{u} \le \overline{\mathbf{u}}_\varepsilon(\cdot,\mathbf{d})\}. \tag{2.28}$$

By Proposition 2.7 and system of inequalities (2.26), it holds that $\mathbb{I}^{\mathbf{d},\varepsilon}_{inv}$ is a connected closed and forward invariant set for the semiflow generated by classical solution of (2.1). So, we can refer to the theory of dynamical systems and the fact that semiflow generated by solutions of (2.1) is precompact, to conclude that (2.1) has a positive steady state $\mathbf{u}(\cdot, \mathbf{d}) \in \mathbb{I}_{inv}^{\mathbf{d},\varepsilon}$, that is

$$\underline{\mathbf{u}}_\varepsilon(\cdot, \mathbf{d}) \le \mathbf{u}(\cdot, \mathbf{d}) \le \overline{\mathbf{u}}_\varepsilon(\cdot, \mathbf{d}),$$

which in view of (2.19) and (2.25) implies that

$$(1-\varepsilon)\mathbf{U}(\cdot) \le \mathbf{u}(\cdot, \mathbf{d}) \le (1+\varepsilon)\mathbf{U}(\cdot) \quad \forall\, 0 < d_1, d_2 < d_{2,\varepsilon}^{**}.$$

Since, $0 < \varepsilon \ll 1$ is arbitrarily chosen, first by letting $\max\{d_1, d_2\} \to 0$ and next $\varepsilon \to 0$ in the last inequality, we obtain that $\mathbf{u}(\cdot, \mathbf{d}) \to \mathbf{U}$ as $\max\{d_1, d_2\} \to 0$ uniformly in Ω. □

2.1.2 The case of d_1 small and d_2 fixed

Next, we study the scenario that one of the diffusion rates is small while the other diffusion rate is fixed. To this end, we first formally set $d_1 = 0$ in (2.1) to obtain

$$\begin{cases} \partial_t u_1 = r(x)u_2 - s(x)u_1 - (a(x) + b(x)u_1 + c(x)u_2)u_1 & x \in \Omega,\ t > 0, \\ \partial_t u_2 = d_2\Delta u_2 + s(x)u_1 - (e(x) + f(x)u_2 + g(x)u_1)u_2 & x \in \Omega,\ t > 0, \\ 0 = \partial_{\vec{n}} u_2 & x \in \partial\Omega,\ t > 0. \end{cases} \tag{2.29}$$

The steady state problem associated with (2.29) is

$$\begin{cases} 0 = r(x)u_2 - s(x)u_1 - (a(x) + bu_1 + cu_2)u_1 & x \in \Omega, \\ 0 = d_2\Delta u_2 + s(x)u_1 - (e(x) + f(x)u_2 + gu_1)u_2 & x \in \Omega, \\ 0 = \partial_{\vec{n}} u_2 & x \in \partial\Omega. \end{cases} \tag{2.30}$$

It turns out that by characterizing precisely the existence/nonexistence of positive steady state solutions of the limiting system (2.30), we are able to completely determine the existence and asymptotic profiles of positive steady state solutions of (2.1) as $d_1 \to 0$ for fixed $d_2 > 0$. So, our first focus is on the study of system (2.30).

Solving for the nonnegative function $u_1(x)$ which solves the first equation of (2.30) gives

$$\begin{aligned} u_1(x) =& \frac{1}{2b(x)}\Big(\sqrt{(a(x)+s(x)+c(x)u_2)^2 + 4b(x)r(x)u_2} - (a(x)+s(x)+c(x)u_2)\Big) \\ =& \frac{2r(x)u_2}{\sqrt{(a(x)+s(x)+c(x)u_2)^2 + 4b(x)r(x)u_2} + (a(x)+s(x)+c(x)u_2)} \\ =& \frac{2r(x)u_2}{G(x,u_2)} \qquad \forall\, x \in \Omega, \end{aligned} \tag{2.31}$$

where

$$G(x,\tau) := \sqrt{(a(x)+s(x)+c(x)\tau)^2 + 4b(x)r(x)\tau} + (a(x)+s(x)+c(x)\tau) \\ \forall\, x \in \Omega,\ \tau \ge 0. \tag{2.32}$$

Note that for $\tau = 0$, we have $G(x, 0) = 0$ whenever $a(x)+s(x) = 0$, in which case the formula for u_1 in terms of G is not appropriate. For that reason, unless otherwise stated, we will assume the following:

Hypothesis: $(a(x) + s(x))_{min} > 0$ on $\overline{\Omega}$.

If we insert (2.31) in the second equation of (2.30), then u_2 solves

$$\begin{cases} 0 = d_2 \Delta u_2 + u_2 F(x, u_2) & x \in \Omega, \\ 0 = \partial_{\vec{n}} u_2 & x \in \partial\Omega, \end{cases} \tag{2.33}$$

where

$$F(x,\tau) = \frac{2r(x)s(x)}{G(x,\tau)} - e(x) - \left(\frac{2g(x)r(x)}{G(x,\tau)} + f(x)\right)\tau \quad \forall\, \tau \geq 0,\ x \in \overline{\Omega}. \tag{2.34}$$

Thanks to (2.31) and (2.33), we say that a nonnegative solution $\mathbf{u} = (u_1, u_2)$ of (2.30) is a positive steady state solution of (2.29) if its second component u_2 is positive on $\overline{\Omega}$. Observe that here $u_1(\cdot)$ is zero on the set $\{x \in \overline{\Omega}\ :\ r(x) = 0\}$. The linearized eigenvalue problem of (2.33) at $u_2 \equiv 0$ is

$$\begin{cases} \lambda\varphi = d_2 \Delta\varphi + \left(\frac{r(x)s(x)}{a(x)+s(x)} - e(x)\right)\varphi & x \in \Omega, \\ 0 = \partial_{\vec{n}}\varphi & x \in \partial\partial\Omega. \end{cases} \tag{2.35}$$

Given $d > 0$ and $h \in L^\infty(\Omega)$, let $\lambda(d, h)$ denote the principal eigenvalue of

$$\begin{cases} \lambda\varphi = d\Delta\varphi + h\varphi & x \in \Omega, \\ 0 = \partial_{\vec{n}}\varphi & x \in \partial\Omega. \end{cases} \tag{2.36}$$

The following result on the dependence of $\lambda(d, h)$ with respect to $d > 0$ and h is well known (see (Cantrell and Cosner 2003)).

Lemma 2.8 *Let $h \in C(\overline{\Omega})$. $\lambda(d, h)$ is constant in d if $h = const.$ and strictly decreasing in d if $h \neq const.$ Furthermore,*

$$\lim_{d\to 0^+} \lambda(d, h) = h_{\max} \quad \text{and} \quad \lim_{d\to\infty} \lambda(d, h) = \frac{\overline{h}}{|\Omega|}. \tag{2.37}$$

Moreover, for every $h_1, h_2 \in C(\overline{\Omega})$ and $d > 0$, $\lambda(d, h_1) < \lambda(d, h_2)$ whenever $h_2 - h_1 \in C^+(\overline{\Omega}) \setminus \{0\}$.

We have the following result on the existence and nonexistence of positive solutions of (2.33).

Lemma 2.9 *Assume $(a+s)_{\min} > 0$ and let $d_2 > 0$ be fixed. The following conclusions hold.*

(i) *If $\lambda(d_2, \frac{rs}{s+a} - e) \leq 0$, then (2.33) has no positive steady state solution.*

(ii) *If* $\lambda(d_2, \frac{rs}{a+s} - e) > 0$*, then* (2.33) *has a unique positive steady state solution.*

Proof

(i) Observe that $G(x,\tau) \ge 2(a(x)+s(x)) \ge 2(a+s)_{\min} > 0$ for all $\tau \ge 0$ and $x \in \Omega$. Hence any nonnegative solution of (2.33) is a subsolution of the logistic elliptic equation

$$\begin{cases} 0 = d_2\Delta w + (\frac{rs}{a+s} - e - fw)w & x \in \Omega, \\ 0 = \partial_{\vec{n}} w & x \in \partial\Omega. \end{cases} \tag{2.38}$$

If $\lambda(d_2, \frac{rs}{a+s} - e) \le 0$, it is well known that (2.38) has no positive solution, which implies that (2.33) also has no positive solution.

(ii) Suppose that $\lambda(d_2, \frac{rs}{a+s} - e) > 0$. It is easy to see that for each $x \in \Omega$, the function $[0,\infty) \ni \tau \mapsto G(x,\tau)$ is increasing, which implies that the function $[0,\infty) \ni \tau \mapsto \frac{2r(x)g(x)}{G(x,\tau)} - \tau f(x)$ is strictly decreasing. Next, set $H(x,\tau) = \frac{\tau}{G(x,\tau)}$ for every $x \in \Omega$ and $\tau \ge 0$. By computations, for each x in Ω, we have

$$\partial_\tau H(x,\tau) = \frac{(a(x)+s(x))}{G(x,\tau)\sqrt{(a(x)+s(x)+c(x)\tau)^2 + 4b(x)r(x)\tau}} > 0 \quad \forall \tau \ge 0.$$

Hence the function $F(x,\tau)$ is decreasing in $\tau \ge 0$ for each $x \in \Omega$. Therefore, by Proposition 3.3 of (Cantrell and Cosner 2003), (2.33) has a unique positive steady state solution. □

Whenever $\lambda(d_2, \frac{rs}{a+s} - e) > 0$, we denote by $w(\cdot, d_2)$ the unique positive solution of (2.33). Thanks to Lemma 2.8 and equation (2.31), we conclude the following result on the existence and nonexistence of steady state solutions of (2.29).

Proposition 2.10 *Assume that* $(a+s)_{\min} > 0$.

(i) *If* $\lambda(d_2, \frac{rs}{s+a} - e) > 0$*, then* $\mathbf{u}(\cdot, d_2) := \left(\frac{2rw(\cdot,d_2)}{G(\cdot,w(\cdot,d_2))}, w(\cdot,d_2)\right)$ *is the unique positive steady state solution of* (2.29)*. Furthermore,* $\mathbf{u}(\cdot,d_2) \to \mathbf{U}$ *as* $d_2 \to 0$ *uniformly in* Ω*, where* $\mathbf{U}(x) = (U_1(x), U_2(x))$ *is the unique nonnegative steady state solution of the kinetic system* (2.4).

(ii) *If* $\lambda(d_2, \frac{rs}{a+s} - e) \le 0$*, the null function* $\mathbf{u} = \mathbf{0}$ *is the only nonnegative steady state solution of* (2.29).

Thanks to Proposition 2.10, we expect that the sign of $\lambda(d_2, \frac{rs}{a+s} - e)$ will completely determine that of the principal eigenvalue λ_1 of (2.3) as d_1 becomes small and d_2 is fixed.

Our next result on the asymptotic limit of the principal eigenvalue λ_1 of (2.3) as $d_1 \to 0$ for each $d_2 > 0$ confirms this expectation.

Lemma 2.11 *Assume that* $(a+s)_{\min} > 0$ *and let* $d_2 > 0$ *be fixed. For every* $d_1 > 0$*, let* λ_1 *denote the principal eigenvalue of* (2.3) *with* $\mathbf{d} = (d_1, d_2)$*. The following conclusions hold.*

(i) *If* $\lambda(d_2, \frac{rs}{a+s} - e) > 0$*, then* $\lim_{d_1\to 0^+}\lambda_1 = \lambda^*$ *where* $\lambda^* > 0$ *and satisfies* $\lambda(d_2, \frac{rs}{a+s+\lambda^*} - (e+\lambda^*)) = 0$.

(ii) *If* $\lambda(d_2, \frac{rs}{a+s} - e) = 0$*, then* $\lim_{d_1\to 0^+}\lambda_1 = 0$.

(iii) *If* $\lambda(d_2, \frac{rs}{a+s} - e) < 0$*, then* $\lim\limits_{d_1\to 0^+}\lambda_1 = \lambda^* := \inf\big\{\eta \in (-(a+s)_{\min}, 0) : \lambda(d_2, \dfrac{rs}{a+s+\eta} - (e+\eta)) < 0\big\}$.

Proof (i) Suppose that $\lambda(d_2, \frac{rs}{a+s} - e) > 0$. Note from Lemma 2.8 that the function $[0,\infty) \ni \eta \mapsto \lambda(d_2, \frac{rs}{a+s+\eta} - (e+\eta))$ is strictly decreasing and $\lambda(d_2, \frac{rs}{a+s+\eta} - (e+\eta)) < 0$ for $\eta > \lambda(d_2, \frac{rs}{s+a} - e)$. Hence, there is a unique $\lambda^* > 0$ such that $\lambda(d_2, \frac{rs}{a+s+\lambda^*} - (e+\lambda^*)) = 0$. Let $0 < \eta < \lambda^*$ be fixed. Next, chose $0 < \varepsilon < \lambda^* - \eta$ such that $\lambda(d_2, \frac{rs}{a+s+\eta} - (e+\eta+\varepsilon)) > 0$. Then there is a unique positive solution u_2 of the logistic elliptic equation

$$\begin{cases} 0 = d_2\Delta u_2 + (\frac{rs}{a+s+\eta} - (e+\varepsilon+\eta) - u_2)u_2 & x \in \Omega, \\ 0 = \partial_{\vec{n}} u_2 & x \in \partial\Omega. \end{cases} \tag{2.39}$$

Next, for every $d_1 > 0$, we note that $\lambda(d_1, -(a+s+\eta)) < 0$, hence zero is in the resolvent set of $d_1\Delta - (a+e+\eta)$, subject to the homogeneous Neumann boundary conditions. Thus for every $d_1 > 0$, there is a unique solution u_1 of the elliptic equation

$$\begin{cases} 0 = d_1\Delta u_1 + ru_2 - (a+s+\eta)u_1 & x \in \Omega, \\ 0 = \partial_{\vec{n}} u_1 & x \in \partial\Omega. \end{cases} \tag{2.40}$$

Moreover, since $ru_2 \geq 0$ and $ru_2 \not\equiv 0$, it follows from the maximum principle that $u_1 > 0$. By the singular perturbation theory (Cantrell and Cosner 2003), we have that $u_1 \to \frac{ru_2}{s+a+\eta}$ as $d_1 \to 0^+$ uniformly in Ω. Hence, since $\min_{x\in\overline{\Omega}} u_2(x) > 0$, there is $d_{\varepsilon,\eta} > 0$ such that

$$\left\| \frac{ru_2}{a+s+\eta} - u_1 \right\|_\infty < \frac{\varepsilon}{\varepsilon + \|s\|_\infty} \min_{x\in\overline{\Omega}} u_2(x) \quad \forall\, 0 < d_1 < d_{\varepsilon,\eta},$$

which implies that

$$\frac{ru_2}{s+a+\eta} \leq u_1 + \frac{\varepsilon}{\varepsilon + \|s\|_\infty} u_2 \quad \forall\, 0 < d_1 < d_{\varepsilon,\eta}. \tag{2.41}$$

It then follows from (2.39) and (2.41) that

$$\begin{cases} 0 \leq d_2\Delta u_2 + su_1 - eu_2 - \eta u_2 - u_2^2 & x \in \Omega, \\ 0 = \partial_{\vec{n}} u_2 & x \in \partial\Omega \end{cases}$$

for every $0 < d_1 < d_{\varepsilon,\eta}$. As a result,

$$\begin{cases} \eta u_2 \leq d_2\Delta u_2 + su_1 - eu_2 & x \in \Omega, \\ 0 = \partial_{\vec{n}} u_2 & x \in \partial\Omega, \end{cases} \tag{2.42}$$

for every $0 < d_1 < d_{\varepsilon,\eta}$. In view of (2.40) and (2.42), we have

$$\begin{cases} \eta u_1 \le d_1 \Delta u_1 + r u_2 - (a+s) u_1 & x \in \Omega, \\ \eta u_2 \le d_2 \Delta u_2 + s u_1 - e u_2 & x \in \Omega, \\ 0 = \partial_{\vec{n}} u_1 = \partial_{\vec{n}} u_2 & x \in \partial\Omega, \end{cases} \tag{2.43}$$

for every $0 < d_1 < d_{\varepsilon,\eta}$. Since $u_1 > 0$ and $u_2 > 0$, we conclude from (2.43) that

$$0 < \eta \le \lambda_1 \quad \forall\, 0 < d_1 < d_{\varepsilon,\eta}. \tag{2.44}$$

Since $0 < \eta < \lambda^*$ is arbitrarily chosen, we conclude from (2.44) that

$$\liminf_{d_1 \to 0^+} \lambda_1 \ge \lambda^*. \tag{2.45}$$

Next, let $\eta > \lambda^*$. Then $\lambda(d_2, \frac{rs}{a+s+\eta} - (e+\eta)) < 0$. Taking $\varepsilon = -\lambda(d_2, \frac{rs}{a+s+\eta} - (e+\eta))$, then $\varepsilon > 0$ and $\lambda(d_2, \frac{rs}{a+s+\eta} - (e+\eta-\varepsilon)) = 0$. For such η and ε, let φ_2 denote the positive eigenfunction with $\max \varphi_2 = 1$ of

$$\begin{cases} 0 = d_2 \Delta \varphi_2 + (\frac{rs}{a+s+\eta} - (e+\eta-\varepsilon))\varphi_2 & x \in \Omega, \\ 0 = \partial_{\vec{n}} \varphi_2 & x \in \partial\Omega. \end{cases} \tag{2.46}$$

For every $d_1 > 0$, let φ_1 denote the unique positive solution of

$$\begin{cases} 0 = d_1 \Delta \varphi_1 + r\varphi_2 - (a+s+\eta)\varphi_1 & x \in \Omega, \\ 0 = \partial_{\vec{n}} \varphi_1 & x \in \partial\Omega. \end{cases} \tag{2.47}$$

The existence and positivity of φ_1 follows as in the case of existence of positive solution of (2.40). Similarly, as in (2.41), since $\varphi_1 \to \frac{r\varphi_2}{a+s+\eta}$ as $d_1 \to 0^+$ uniformly in Ω, there is $d_{\eta,\varepsilon} > 0$ such that

$$\frac{rs\varphi_2}{s+a+\eta} \ge s\varphi_1 - \varepsilon\varphi_2 \quad \forall\, x \in \Omega,\ 0 < d_1 < d_{\eta,\varepsilon}.$$

Hence, (φ_1, φ_2) satisfies

$$\begin{cases} \eta\varphi_1 \ge d_1 \Delta \varphi_1 + r\varphi_2 - (a+s)\varphi_1 & x \in \Omega, \\ \eta\varphi_2 \ge d_2 \Delta \varphi_2 + s\varphi_1 - e\varphi_2 & x \in \Omega, \\ 0 = \partial_{\vec{n}} \varphi_1 = \partial_{\vec{n}} \varphi_2 & x \in \partial\Omega, \end{cases}$$

for every $0 < d_1 < d_{\eta,\varepsilon}$ and $\varphi_1 > 0$ and $\varphi_2 > 0$ on $\overline{\Omega}$. As a result, we have that $\lambda_1 \le \eta$ whenever $0 < d_1 < d_{\eta,\varepsilon}$. Since $\eta > \lambda^*$ is arbitrarily chosen, then

$$\limsup_{d_1 \to 0^+} \lambda_1 \le \lambda^*. \tag{2.48}$$

The conclusion of (i) readily follows from (2.45) and (2.48).

(ii) Suppose that $\lambda(d_2, \frac{rs}{a+s} - e) = 0$. Then for every $0 < \nu < (a+s)_{\min}$, it holds that $\lambda(d_2, \frac{rs}{a+s-\nu} - (e-\nu)) > 0$. Now by (i), we have

$$\lim_{d_1 \to 0} \lambda_{1,\nu} = \lambda_\nu^*, \quad 0 < \nu < (a+s)_{\min}, \tag{2.49}$$

where $\lambda_\nu^* > 0$ satisfies

$$\lambda(d_2, \frac{rs}{a+s-\nu+\lambda_\nu^*} - (e - \nu + \lambda_\nu^*)) = 0 \tag{2.50}$$

and $\lambda_{1,\nu}$ is the principal eigenvalue of the cooperative system

$$\begin{cases} \lambda\varphi_1 = d_1\Delta\varphi_1 - (a(x) + s(x) - \nu)\varphi_1 + r(x)\varphi_2 & x \in \Omega, \\ \lambda\varphi_2 = d_2\Delta\varphi_2 + s(x)\varphi_1 - (e(x) - \nu)\varphi_2 & x \in \Omega, \\ \quad 0 = \partial_{\vec{n}}\varphi_1 = \partial_{\vec{n}}\varphi_2 & x \in \partial\Omega. \end{cases} \tag{2.51}$$

Clearly, by the uniqueness of the principal eigenvalue, $\lambda_{1,\nu} = \nu + \lambda_1$. Moreover, from (2.50), we have $\lambda_\nu^* = \nu$ since $\lambda(d_2, \frac{rs}{a+s} - e) = 0$. We then deduce from (2.49) that $\lim_{d_1 \to 0} \lambda_1 = 0$.

(iii) Suppose that $\lambda(d_2, \frac{rs}{a+s} - e) < 0$. Observe that in the proof of (2.48), the only information used was the fact that $\lambda(d_2, \frac{rs}{a+s+\eta} - (e+\eta)) < 0$. Hence, for every $\eta > -(a+s)_{\min}$ satisfying $\lambda(d_2, \frac{rs}{a+s+\eta} - (e+\eta)) < 0$, we have that $\limsup_{d_1 \to 0^+} \lambda_1 \le \eta$, which yields

$$\limsup_{d_1 \to 0^+} \lambda_1 \le \lambda^* := \inf \left\{ \eta \in (-(a+s)_{\min}, 0) \ : \ \lambda(d_2, \frac{rs}{a+s+\eta} - (e+\eta)) < 0 \right\}. \tag{2.52}$$

From this point, we distinguish two cases.

Case 1. $\lambda^* > -(a+s)_{\min}$. Then $(a+s+\lambda^*)_{\min} = (a+s)_{\min} + \lambda^* > 0$. It then follows from the definition of λ^* that $\lambda(d_2, \frac{rs}{r+s+\lambda^*} - (e+\lambda^*)) = 0$. Now, taking $\nu = -\lambda^*$ in (2.51) and denoting the corresponding eigenvalue by λ_{1,λ^*}, we can employ (ii) to conclude that $\lim_{d_1 \to 0^+} \lambda_{1,\lambda^*} = 0$. But $\lambda_{1,\lambda^*} = \lambda_1 - \lambda^*$, thus we conclude that $\lim_{d_1 \to 0^+} \lambda_1 = \lambda^*$.

Case 2. $\lambda^* = -(a+s)_{\min}$. First observe from the first equation of (2.3) that

$$\begin{cases} \lambda_1\varphi_1 \ge d_1\Delta\varphi_1 - (a+s)\varphi_1 & x \in \Omega, \\ \partial_{\vec{n}}\varphi_1 = 0 & x \in \partial\Omega. \end{cases}$$

Hence, since $\varphi_1 > 0$, we have $\lambda_1 \ge \lambda(d_1, -(a+s))$ for all $d_1 > 0$. As a result, in view of Lemma 2.8, we obtain

$$\liminf_{d_1 \to 0^+} \lambda_1 \ge \lim_{d_1 \to 0^+} \lambda(d_1, -(a+s)) = (-a-s)_{\max} = -(a+s)_{\min} = \lambda^*.$$

This together with (2.52) implies that $\lim_{d_1\to 0^+}\lambda_1=\lambda^*$, which completes the proof of the result. □

Remark 2.12 Assume that $(a+s)_{\min}>0$, $\lambda\Big(d_2,\frac{rs}{a+s}-e\Big)<0$, and set

$$\lambda^*=\inf\Big\{\eta\in(-(a+s)_{\min},0)\text{ such that }\lambda(d_2,\frac{rs}{a+s+\eta}-(e+\eta))<0\Big\}. \quad (2.53)$$

It is easy to see that $\lambda^*=\max\{\lambda(d_2,-e),-(a+s)_{\min}\}$ when $rs\equiv 0$. Hence, when $rs\equiv 0$ it holds that

$$\lambda^*=\begin{cases}-(a+s)_{\min} & \text{If }\ \lambda(d_2,-e)\le -(a+s)_{\min}\\ \lambda(d_2,-e) & \text{If }\ \lambda(d_2,-e)\ge -(a+s)_{\min}.\end{cases} \quad (2.54)$$

So, when $rs\equiv 0$, the infimum in (2.53) is achieved at an interior point in $(-(a+s)_{\min},0)$ if and and only if $\lambda(d_2,-e)>-(a+s)_{\min}$. In fact, whenever $\lambda(d_2,-e)>-(a+s)_{\min}$, it always holds that $\lambda^*>-(a+s)_{\min}$, and hence the infimum in (2.53) is achieved at an interior point in $(-(a+s)_{\min},0)$. Also, when $\lambda(d_2,-e)=-(a+s)_{\min}$ and $\|rs\|_\infty>0$, observing that

$$\begin{aligned}&\lim_{\eta\searrow\lambda(d_2,-e)}\lambda\Big(d_2,\frac{rs}{a+s+\eta}-(e+\eta)\Big)\\ &=\lim_{\eta\searrow\lambda(d_2,-e)}\lambda\Big(d_2,\frac{rs}{a+s+\eta}-(e+\lambda(d_2,-e))\Big)\\ &=\sup_{\eta\in(\lambda(d_2,-e),0)}\lambda\Big(d_2,\frac{rs}{a+s+\eta}-(e+\lambda(d_2,-e))\Big)\\ &>\lambda\Big(d_2,\frac{rs}{a+s+\eta}-(e+\lambda(d_2,-e))\Big)\quad\forall\,\eta\in(-(a+s)_{\min},0)\\ &>\lambda(d_2,-(e+\lambda(d_2,-e)))=0,\end{aligned}$$

then $\lambda^*>\lambda(d_2,-e)=-(a+s)_{\min}$ and $\lambda(d_2,\frac{rs}{a+s+\lambda^*}-(e+\lambda^*))=0$.

The case of $rs\not\equiv 0$ and $\lambda(d_2,-e)<-(a+s)_{\min}$ is subtle. Indeed, observe that

$$\begin{aligned}&\lim_{\eta\searrow-(a+s)_{\min}}\lambda\Big(d_2,\frac{rs}{a+s+\eta}-(e+\eta)\Big)\\ &\ge\lim_{\eta\searrow-(a+s)_{\min}}\frac{1}{|\Omega|}\int\Big(\frac{rs}{a+s+\eta}-(e+\eta)\Big)\\ &=\lim_{\eta\searrow-(a+s)_{\min}}\frac{1}{|\Omega|}\int\Big(\frac{rs}{a+s+\eta}-(e-(a+s)_{\min})\Big).\end{aligned}$$

Hence if

$$\lim_{\eta\searrow-(a+s)_{\min}}\overline{\Big(\frac{rs}{a+s+\eta}\Big)}>\overline{(e-(a+s)_{\min})}, \quad (2.55)$$

then $\lambda^* > -(a+s)_{\min}$ and $\lambda(d_2, \frac{rs}{a+s+\lambda^*} - (e+\lambda^*)) = 0$. In particular, if

$$rs > 0 \ \text{ on } \{x \in \overline{\Omega} \ : \ (a+s)(x) = (a+s)_{\min}\} \ \text{ and } a+s \text{ is Lipschitz continuous,} \tag{2.56}$$

then $\lambda^* > -(a+s)_{\min}$ and $\lambda(d_2, \frac{rs}{a+s+\lambda^*} - (e+\lambda^*)) = 0$. However, when the inequality (2.55) is reversed, there is $d^* \gg 1$ such that for every $d_2 > d^*$, $\lambda^* = -(a+s)_{\min}$.

Thanks to Lemma 2.11, we can state our result on the asymptotic profile of positive steady state solutions of (2.1) when d_1 is small and d_2 is fixed.

Theorem 2.13 *Assume that* $(a+s)_{\min} > 0$. *Let* $d_2 > 0$ *be given. The following conclusions hold.*

(i) *If* $\lambda(d_2, \frac{rs}{s+a} - e) > 0$, *then there is* $d_1^* > 0$ *such that* $\lambda_1 > 0$ *for every* $0 < d_1 < d_1^*$, *so that* (2.1) *has a positive steady state solution* $\mathbf{u}(\cdot, \mathbf{d})$ *for every* $\mathbf{d} = (d_1, d_2)$ *with* $0 < d_1 < d_1^*$. *Furthermore, any positive steady state solution* $\mathbf{u}(\cdot, \mathbf{d})$ *of* (2.1) *for* $0 < d_1 \ll 1$, *satisfies* $\mathbf{u} \to \left(\frac{2rw(\cdot,d_2)}{G(\cdot, w(\cdot,d_2))}, w(\cdot, d_2)\right)$ *as* $d_1 \to 0$, *uniformly in* Ω *where* $w(\cdot, d_2)$ *is the unique positive solution of* (2.33).

(ii) *If* $\lambda(d_2, \frac{rs}{s+a} - e) < 0$, *then there is* $d_1^* > 0$ *such that* $\lambda_1 < 0$ *for every* $0 < d_1 < d_1^*$, *so that* (2.1) *has no positive steady state solution* $\mathbf{u}(\cdot, \mathbf{d})$ *for every* $\mathbf{d} = (d_1, d_2)$ *with* $0 < d_1 < d_1^*$.

Proof (i) Suppose that $\lambda(d_2, \frac{rs}{a+s} - e) > 0$. By Lemma 2.11 (i), there exists $d_1^* > 0$ such that $\lambda_1 > 0$ for every $0 < d_1 < d_1^*$. Whence there is a positive steady state solution of (2.1) for every $\mathbf{d} = (d_1, d_2)$ when $0 < d_1 < d_1^*$. Next, let $\mathbf{u}(\cdot, \mathbf{d})$ be a positive steady state of (2.1) for every $\mathbf{d} = (d_1, d_2)$ with $0 < d_1 < d_1^*$.

Step 1. We claim that

$$\frac{\lambda_1}{\max\left\{\|c+b\|_\infty, \|f+g\|_\infty\right\}(1 + \|\frac{r}{a+s}\|_\infty)} \le \|u_2\|_\infty \tag{2.57}$$

whenever $\mathbf{u}(\cdot, \mathbf{d})$ is a positive steady state solution of (2.1) for $\mathbf{d} = (d_1, d_2)$ with $d_1, d_2 > 0$. To this end, let $\mathbf{u}(\cdot, \mathbf{d})$, with $\mathbf{d} = (d_1, d_2)$, be a positive steady state solution of (2.1). From the first equation of (2.2), we have

$$\begin{cases} 0 \le d_1 \Delta u_1 + r u_2 - (a+s) u_1 & x \in \Omega, \\ 0 = \partial_{\vec{n}} u_1 & x \in \partial\Omega. \end{cases}$$

Hence, it follows from the comparison principle for elliptic equations that

$$\|u_1\|_\infty \le \left\|\frac{r u_2}{a+s}\right\|_\infty \le \left\|\frac{r}{a+s}\right\|_\infty \|u_2\|_\infty.$$

This implies that

$$\begin{cases} \|c+b\|_\infty(1+\|\frac{r}{a+s}\|_\infty)\|u_2\|_\infty u_1 \geq d_1\Delta u_1 + ru_2 - (a+s)u_1 & x\in\Omega, \\ \|f+g\|_\infty(1+\|\frac{r}{a+s}\|_\infty)\|u_2\|_\infty u_2 \geq d_2\Delta u_2 + su_1 - eu_2 & x\in\Omega, \\ 0=\partial_{\vec{n}}u_1 = \partial_{\vec{n}}u_2 & x\in\partial\Omega. \end{cases} \tag{2.58}$$

Since $u_1 > 0$ and $u_2 > 0$, we conclude from (2.58) that

$$\lambda_1 \leq \max\left\{\|c+b\|_\infty, \|f+g\|_\infty\right\}(1+\|\frac{r}{a+s}\|_\infty)\|u_2\|_\infty,$$

from which we deduce that (2.57) holds.

Step 2. In this step, we complete the proof of (i). First, observe that any positive steady state solution $\mathbf{u}(\cdot,\mathbf{d})$ of (2.1) satisfies

$$\begin{cases} 0 \leq d_1\Delta u_1 + ru_2 - (a+bu_1)u_1 & x\in\Omega, \\ 0 \leq d_2\Delta u_2 + su_1 - (e+fu_2)u_2 & x\in\Omega, \\ 0=\partial_{\vec{n}}u_1 = \partial_{\vec{n}}u_2 & x\in\partial\Omega, \end{cases}$$

that is, $\mathbf{u}(\cdot,\mathbf{d})$ is a subsolution of (2.1) with $c=g\equiv 0$, which is a subhomogeneous cooperative system. Observe also that

$$\begin{cases} rm_1 - (a+bm_1)m_1 \leq \|r+a\|_\infty(m_1+m_2) - b_{\min}m_1^2 \\ \quad\text{and} \\ sm_2 - (e+fm_2)m_2 \leq \|s+e\|_\infty(m_1+m_2) - f_{\min}m_2^2 \end{cases} \quad \forall\, m_1, m_2 \geq 0.$$

Thus, taking $m^* := \max\{\frac{2\|a+r\|_\infty}{b_{\min}}, \frac{2\|s+e\|_\infty}{f_{\min}}\}$, we have that the constant function (m^*, m^*) is a super-solution of (2.1) with $c=g\equiv 0$. As a result, we conclude that

$$\mathbf{u}(\cdot,\mathbf{d}) \leq \mathbf{m}^* = (m^*, m^*). \tag{2.59}$$

Note that (2.59) provides a priori upper bound estimates on positive steady state solutions of (2.1). Now, let $\mathbf{u}^n = (u_1^n, u_2^n)$ be a sequence of positive steady state solutions of (2.1) with $\mathbf{d}^n = (d_{1,n}, d_2)$ with $d_{1,n}\to 0$ as $n\to\infty$. By (2.59), we have that

$$\|\Delta u_2^n\|_\infty \leq \frac{1}{d_2}\Big(\|s\|_\infty + \|e\|_\infty + (\|f\|_\infty + \|g\|_\infty)m^*\Big)m^* \quad \forall\, n\geq 1.$$

Hence, by regularity theory for elliptic equations, without loss of generality, possibly after passing to a subsequence, we may suppose that there is $u_2^* \in C^{1,\mu}(\Omega)$ such that $u_2^n \to u_2^*$ in $C^{1,\mu}(\Omega)$ as $n\to\infty$. Thus, by the singular perturbation theory (Cantrell and Cosner 2003, Proposition 3.16), letting $n\to\infty$ in the first equation of (2.1), we have that $u_1^n \to u_1^*$ uniformly in Ω where $u_1^*(x)$ is the unique nonnegative solution of the first equation of (2.30) with (u_1, u_2) replaced by (u_1^*, u_2^*). Thus, similar arguments leading to (2.31) yield that

$$u_1^*(x) = \frac{2r(x)u_2^*(x)}{G(x, u_2^*(x))} \quad \forall\, x \in \Omega.$$

This in turn, together with regularity property for elliptic equations, implies that u_2^* is a nonnegative weak solution of (2.33). Using regularity theory for elliptic equations again, we derive that u_2^* is a nonnegative classical solution of (2.33). But by (2.57) and (2.44),

$$\|u_2^*\|_\infty \geq \frac{\eta}{\max\Big\{\|c+b\|_\infty, \|f+g\|_\infty\Big\}(1+\|\frac{r}{a+s}\|_\infty)} > 0 \quad \forall\, 0 < \eta < \lambda^*,$$

where λ^* is given by Lemma 2.11 (i). This shows that $u_2^* > 0$ by the strong maximum principle. By the uniqueness of solution of (2.33) (see Lemma 2.8), we deduce that $u_2^* = w(\cdot, d_2)$. Since $u_2^* = w(\cdot, d_2)$ is independent of the sequence we choose, we derive the desired result.

(ii) The result follows from Lemma 2.11 (iii) and Proposition 2.1. □

If we suppose that $e_{\min} > 0$ and introduce the function

$$\tilde{F}(x,\tau) = \frac{2s(x)r(x)}{\tilde{G}(x,\tau)} - (a(x)+s(x)) - \Big(b(x) + \frac{2c(x)s(x)}{\tilde{G}(x,\tau)}\Big)\tau \quad \tau \geq 0,\ x \in \overline{\Omega}, \tag{2.60}$$

where $\tilde{G}(x,\tau) = \sqrt{(e(x)+\tau g(x)^2 + 4\tau s(x) f(x)} - (e(x)+\tau g(x))^2$ for all $x \in \overline{\Omega}$ and $\tau \geq 0$, similar arguments as in the proof of Lemma 2.11 and Theorem 2.13 give :

Lemma 2.14 *Assume that $e_{\min} > 0$ and let $d_1 > 0$ be fixed. For every $d_2 > 0$, let λ_1 denote the principal eigenvalue of (2.3) with $\mathbf{d} = (d_1, d_2)$. The following conclusions hold.*

(i) *If $\lambda(d_1, \frac{rs}{e} - (a+s)) > 0$, then $\lim_{d_2\to 0^+} \lambda_1 = \lambda^*$ where $\lambda^* > 0$ and satisfies $\lambda(d_1, \frac{rs}{e+\lambda^*} - (a+s+\lambda^*)) = 0$.*

(ii) *If $\lambda(d_1, \frac{rs}{e} - (a+s)) = 0$, then $\lim_{d_2\to 0^+} \lambda_1 = 0$.*

(iii) *If $\lambda(d_1, \frac{rs}{e} - (a+s)) < 0$, then $\lim\limits_{d_2\to 0^+} \lambda_1 = \lambda^* := \inf\Big\{\eta \in (-(a+s)_{\min}, 0) :$*
$$\lambda(d_1, \frac{rs}{e+\eta} - (a+s+\eta)) < 0\Big\}.$$

Theorem 2.15 *Assume that $e_{\min} > 0$ and let $d_1 > 0$ be given. The following conclusions hold.*

(i) *If $\lambda(d_1, \frac{rs}{e} - (a+s)) > 0$, then there is $d_2^* > 0$ such that $\lambda_1 > 0$ for every $0 < d_2 < d_2^*$, so that (2.1) has a positive steady state solution $\mathbf{u}(\cdot, \mathbf{d})$ for every $\mathbf{d} = (d_1, d_2)$ with $0 < d_2 < d_2^*$. Furthermore, any positive steady state solution $\mathbf{u}(\cdot, \mathbf{d})$ of (2.1) for $0 < d_2 \ll 1$, satisfies $\mathbf{u} \to (\tilde{w}(\cdot, d_1), \frac{2s\tilde{w}(\cdot,d_1)}{\tilde{G}(\cdot,\tilde{w}(\cdot,d_1))})$ as $d_2 \to 0$,* *uniformly in* Ω, *where* $\tilde{w}(\cdot, d_1)$ *is the unique positive solution of*

$$\begin{cases} 0 = d_1 \Delta w + w \tilde{F}(x, w) & x \in \Omega, \\ 0 = \partial_{\vec{n}} w & x \in \partial\Omega. \end{cases} \tag{2.61}$$

(ii) *If* $\lambda(d_1, \frac{rs}{e} - (a+s)) < 0$, *then there is* $d_2^* > 0$ *such that* $\lambda_1 < 0$ *for every* $0 < d_2 < d_2^*$, *so that* (2.1) *has no positive steady state solution for every diffusion* $\mathbf{d} = (d_1, d_2)$ *with* $0 < d_2 < d_2^*$.

2.1.3 The case of d_1 large and d_2 fixed

We first study the limit of the principal eigenvalue of (2.3) as $d_1 \to \infty$ for each fixed $d_2 > 0$.

Lemma 2.16 *Assume that* $e \geq 0$. *Let* $d_2 > 0$ *be fixed. Then* $\lim_{d_1 \to \infty} \lambda_1 = \lambda^*$ *where* λ^* *is the unique number* $\lambda^* > \lambda(d_2, -e)$ *for which there is a positive solution* ψ *of the system*

$$\begin{cases} \lambda^* \psi = d_2 \Delta \psi - e\psi + s & x \in \Omega, \\ 0 = \partial_{\vec{n}} \psi & x \in \partial\Omega, \\ \lambda^* |\Omega| + (\overline{a} + \overline{s}) - \overline{r\psi} = 0. \end{cases} \tag{2.62}$$

Moreover, if $e \not\equiv 0$, *then* $\lambda^* > -\frac{(\overline{a}+\overline{s})}{|\Omega|}$ *and*

$$\lambda^* \begin{cases} < 0 & \text{if } \overline{rs_{d_2,e}} < (\overline{a} + \overline{s}), \\ = 0 & \text{if } \overline{rs_{d_2,e}} = (\overline{a} + \overline{s}), \\ > 0 & \text{if } \overline{rs_{d_2,e}} > (\overline{a} + \overline{s}), \end{cases} \tag{2.63}$$

where $s_{d_2,e}$ *is the unique positive solution of the elliptic equation*

$$\begin{cases} 0 = d_2 \Delta s_{d_2,e} - e s_{d_2,e} + s & x \in \Omega, \\ 0 = \partial_{\vec{n}} s_{d_2,e} & x \in \partial\Omega. \end{cases} \tag{2.64}$$

Proof **Step 1.** We first show uniqueness. To this end, for every $\lambda > \lambda(d_2, -e)$, let Ψ_λ denote the unique positive solution of

$$\begin{cases} \lambda \Psi = d_2 \Delta \Psi - e(x)\Psi + s(x) & x \in \Omega, \\ 0 = \partial_{\vec{n}} \Psi & x \in \partial\Omega, \end{cases} \tag{2.65}$$

and define

$$Q(\lambda) = \lambda |\Omega| + (\overline{a} + \overline{s}) - \int_\Omega r \Psi_\lambda. \tag{2.66}$$

Since the resolvent operator is smooth, the function $(\lambda(d_2, -e), \infty) \ni \lambda \mapsto \Psi_\lambda \in C^2(\Omega)$ is continuously differentiable. Moreover, setting $\Psi'_\lambda = \partial_\lambda \Psi_\lambda$, it follows from (2.65) that

$$\begin{cases} \lambda\Psi'_\lambda = d_2\Delta\Psi'_\lambda - e(x)\Psi'_\lambda - \Psi_\lambda & x \in \Omega, \\ 0 = \partial_{\vec{n}}\Psi'_\lambda & x \in \partial\Omega. \end{cases} \tag{2.67}$$

Hence, since $\lambda > \lambda(d_2, -e)$ and $\Psi_\lambda > 0$, we deduce that $\Psi'_\lambda < 0$ on $\overline{\Omega}$ by the maximum principle for elliptic equations. Observe that the function $\lambda \mapsto Q(\lambda)$ is also continuously differentiable with

$$\frac{d}{d\lambda}Q(\lambda) = |\Omega| - \int_\Omega r\Psi'_\lambda > 0 \quad \text{since } r \not\equiv 0, r \geq 0 \text{ and } \Psi'_\lambda < 0.$$

Therefore the function $Q(\lambda)$ is strictly increasing. As a result, there is at most one number $\lambda > \lambda(d_2, -e)$ for which $Q(\lambda) = 0$, that is the system (2.62) has a positive solution.

Step 2. Existence. We show that for any limit point λ^* of λ_1, the system (2.62) has a positive solution. Let $(\lambda_{1,n}, \varphi_{1,n}, \varphi_{2,n})$ be a sequence of eigenpairs of (2.3) for $\mathbf{d} = (d_{1,n}, d_2)$ with, $\varphi_{i,n} > 0$, $i = 1, 2$, $\|\varphi_{1,n} + \varphi_{2,n}\|_\infty = 1$ and $d_{1,n} \to \infty$ as $n \to \infty$. We divide the first equation of (2.3) by $\varphi_{1,n}$ and then integrate the resulting expression to get

$$\lambda_{1,n}|\Omega| = d_{1,n}\int_\Omega |\nabla \ln \varphi_{1,n}|^2 - (\overline{a} + \overline{s}) + \int_\Omega \frac{r\varphi_{2,n}}{\varphi_{1,n}} \geq -(\overline{a} + \overline{s}) \quad \forall\, n \geq 1.$$

Hence

$$\lambda_{1,n} > -\frac{(\overline{a} + \overline{s})}{|\Omega|} \quad \forall\, n \geq 1. \tag{2.68}$$

Next, let $\tilde{\psi}$ denote the positive eigenfunction associated with $\lambda(d_2, -e)$ satisfying $\tilde{\psi}_{\max} = 1$. We multiply the second equation of (2.3) by $\tilde{\psi}$ and integrate the resulting equation to get

$$\lambda_{1,n}\int_\Omega \varphi_{2,n}\tilde{\psi} = -d_2\int_\Omega \nabla\tilde{\psi}\cdot\nabla\varphi_2 + \int_\Omega s\varphi_{1,n}\tilde{\psi} - \int_\Omega e\varphi_{2,n}\tilde{\psi} \quad \forall\, n \geq 1. \tag{2.69}$$

If we multiply the equation of $\tilde{\psi}$ by $\varphi_{2,n}$ and then integrate the resulting equation, we obtain

$$\lambda(d_2, -e)\int_\Omega \varphi_{2,n}\tilde{\psi} = -d_2\int_\Omega \nabla\tilde{\psi}\cdot\nabla\varphi_2 - \int_\Omega e\varphi_{2,n}\tilde{\psi} \quad \forall\, n \geq 1. \tag{2.70}$$

From (2.69) and (2.70),

$$(\lambda_{1,n} - \lambda(d_2, -e))\int_\Omega \varphi_{2,n}\tilde{\psi} = \int_\Omega s\varphi_{1,n}\tilde{\psi} > 0 \quad \forall n \geq 1. \tag{2.71}$$

Hence

$$\lambda_{1,n} > \lambda(d_2, -e) \quad \forall n \geq 1. \tag{2.72}$$

Observe from (2.57) that

$$\lambda_{1,n} \leq M^* := m^* \max\left\{\|c+b\|_\infty, \|f+g\|_\infty\right\}(1+\|\frac{r}{a+s}\|_\infty) \quad \forall\, n \geq 1, \quad (2.73)$$

where m^* is the positive constant in (2.59). In view of (2.68), (2.72) and (2.73), without loss of generality, possibly after passing to a subsequence, we may suppose that there is $\lambda^* \geq \max\{\lambda(d_2, -e), \frac{-(\overline{a}+\overline{s})}{|\Omega|}\}$ such that $\lambda_{1,n} \to \lambda^*$ as $n \to \infty$. Next, observe that

$$\begin{aligned}\|\Delta\varphi_{2,n}\|_\infty &= \frac{1}{d_2}\left\|s\varphi_{1,n} - e\varphi_{2,n} - \lambda_{1,n}\varphi_{2,n}\right\|_\infty \\ &\leq \frac{1}{d_2}(\|s\|_\infty + \|e\|_\infty + |\lambda(d_2,-e)| + M^*) \quad \forall\, n \geq 1,\end{aligned}$$

where we have used the fact that $\|\varphi_{1,n}+\varphi_{2,n}\|_\infty = 1$. Hence, by the regularity theory for elliptic equations, after passing to a further subsequence, there is a nonnegative function $\varphi_2 \in C^1(\overline{\Omega})$ such that $\varphi_{2,n} \to \varphi_2$ as $n \to \infty$ in $C^1(\overline{\Omega})$. Observe also that

$$\begin{aligned}\|\Delta\varphi_{1,n}\|_\infty &= \frac{1}{d_{1,n}}\left\|(s+a)\varphi_{1,n} - r\varphi_{2,n} + \lambda_{1,n}\varphi_{2,n}\right\|_\infty \\ &\leq \frac{1}{d_{1,n}}(\|s+a\|_\infty + \|r\|_\infty + |\lambda(d_2,-e)| + M^*) \to 0\end{aligned}$$

as $n \to \infty$. Hence, since $\partial_{\vec{n}}\varphi_{1,n} = 0$ on $\partial\Omega$, then after passing to another subsequence and then relabelling, we may suppose that there is a nonnegative constant c_1 such that $\varphi_{1,n} \to c_1$ as $n \to \infty$ in $C^1(\overline{\Omega})$. Now, integrating the first equation of (2.3) and then letting $n \to \infty$, we get

$$\lambda^* c_1|\Omega| = \int_\Omega r\varphi_2 - (\overline{a}+\overline{s})c_1.$$

Equivalently,

$$(\lambda^*|\Omega| + (\overline{a}+\overline{s}))c_1 = \int_\Omega r\varphi_2. \quad (2.74)$$

Letting $n \to \infty$ in the second equation of (2.3), it follows from the closedness of the Laplace operator, subject to the homogeneous Neumann boundary condition on $\partial\Omega$, on $W^{1,p}(\Omega)$, $p > 1$, and the regularity theory for elliptic equations (Gilbarg and Trudinger 2001) that φ_2 is a classical solution of

$$\lambda^*\varphi_2 = d_2\Delta\varphi_2 - e\varphi_2 + c_1 s \quad x \in \Omega, \qquad \partial_{\vec{n}}\varphi_2 = 0 \quad x \in \partial\Omega. \quad (2.75)$$

Finally, letting $n \to \infty$ in the equation $1 = \|\varphi_{1,n}+\varphi_{2,n}\|_\infty$, yields

$$1 = c_1 + \|\varphi_2\|_\infty. \quad (2.76)$$

Now, if $c_1 = 0$, it would follow from (2.74) that $\int_\Omega r\varphi_2 = 0$, contradicting (2.75) and (2.76) . Thus $c_1 > 0$. Next, letting $n \to \infty$ in (2.71) yields

$$(\lambda^* - \lambda(d_2, -e)) \int_\Omega \tilde{\psi}\varphi_2 = c_1 \int_\Omega s\tilde{\psi} > 0. \tag{2.77}$$

Hence, since $\lambda^* \geq \lambda(d_2, -e)$ (which follows from (2.72) by letting $n \to \infty$), $c_1 > 0$ and $\int_\Omega s\tilde{\psi} > 0$, we conclude from (2.77) that $\lambda^* > \lambda(d_2, -e)$ and $\int_\Omega \varphi_2\tilde{\psi} > 0$. Since $\lambda^* > \lambda(d_2, -e)$, $c_1 s \geq 0$ and $c_1 s \not\equiv 0$, we can employ the strong maximum principle to derive from (2.75) that $\varphi_2 = (\lambda^* + e - \Delta)^{-1}(c_1 s) > 0$ on $\overline{\Omega}$. Clearly, taking $\psi = \frac{\varphi_2}{c_1}$, (λ^*, ψ) satisfies system (2.62).

Step 3. In this step, we complete the proof of the lemma. By **Step 1** and **Step 2**, $\lambda_1 \to \lambda^*$ where λ^* is the unique number $\lambda^* > \lambda(d_2, -e)$ for which (2.62) has a positive solution. Next, observe from (2.74) that $\lambda^* > -\frac{\overline{a}+\overline{s}}{|\Omega|}$. Now, we distinguish two cases.

Case 1. $e \equiv 0$. From **Step 1** and **Step 2**, we know that $\lambda_1 \to \lambda^* > \lambda(d_2, 0) = 0$ where λ^* is the unique positive number for which system (2.62) has a positive solution ψ.

Case 2. $e \not\equiv 0$. Observe also that $0 > \lambda(d_2, -e)$ since $e \geq 0$ and $e \not\equiv 0$. By recalling the functions Ψ_λ and $Q(\lambda)$ introduced in **Step 1**, we have that $\Psi_0 = s_{d_2,e}$ and

$$Q(0) = (\overline{a} + \overline{s}) - \overline{rs_{d_2,e}}.$$

Since $Q(\lambda^*) = 0$ and the function $Q(\lambda)$ is strictly increasing, then if $\overline{rs_{d_2,e}} < (\overline{a} + \overline{s})$ then $Q(0) > 0$, and hence $\lambda^* < 0$. Similarly, if $\overline{rs_{d_2,e}} > (\overline{a} + \overline{s})$ then $Q(0) < 0$, and hence $\lambda^* > 0$. Finally, if $\overline{rs_{d_2,e}} = (\overline{a} + \overline{s})$ then $Q(0) = 0$, and hence $\lambda^* = 0$. □

Now, we state our result on the asymptotic profiles of positive steady state solutions of (2.1) when d_2 is fixed but d_1 is sufficiently large.

Theorem 2.17 *Let $d_2 > 0$ be given and suppose that $e \geq 0$. When $e \not\equiv 0$, let $s_{d_2,e}$ denote the unique positive solution of (2.64). The following conclusions hold.*

(i) *If either $e \equiv 0$ or $e \not\equiv 0$ and $\overline{rs_{d_2,e}} > \overline{a + s}$, then there is $d^* > 0$ such that (2.1) has a positive steady state solution for every diffusion rate $\mathbf{d} = (d_1, d_2)$ with $d_1 > d^*$. Furthermore, any positive steady state solution $\mathbf{u}(\cdot, \mathbf{d})$ of (2.1) for $\mathbf{d} = (d_1, d_2)$ with $d_1 > d^*$ satisfies, up to a subsequence, $\mathbf{u}(\cdot, \mathbf{d}) \to \mathbf{u}^\infty(\cdot, d_2) := (u_1^\infty, u_2^\infty)$ as $d_1 \to \infty$ uniformly in Ω where u_1^∞ is a positive number, $u_2^\infty > 0$ on $\overline{\Omega}$, and (u_1^∞, u_2^∞) is a positive solution of*

$$\begin{cases} 0 = d_2\Delta u_2^\infty + u_1^\infty s - (e + fu_2^\infty + gu_1^\infty)u_2^\infty & x \in \Omega, \\ 0 = \partial_{\vec{n}} u_2^\infty & x \in \partial\Omega, \\ u_1^\infty = \frac{1}{2\overline{b}}\left(\sqrt{(\overline{a} + \overline{s} + \overline{cu_2^\infty})^2 + 4(\overline{b})(\overline{ru_2^\infty})} - (\overline{a} + \overline{s} + \overline{cu_2^\infty})\right). \end{cases} \tag{2.78}$$

(ii) *If $e \not\equiv 0$ and $\overline{rs_{d_2,e}} < (\overline{a} + \overline{s})$, then there is $d^* \gg 1$ such that (2.1) has no positive steady state solution for every diffusion rates $\mathbf{d} = (d_1, d_2)$ with $d_1 > d^*$.*

Proof (i) Suppose that either $e \equiv 0$ or $e \not\equiv 0$ and $\overline{rs_{d_2,e}} > (\overline{a} + \overline{s})$. Thanks to Proposition 2.1 and Lemma 2.16, there is $d^* > 0$ such that such that (2.1) has a positive steady state solution for every diffusion rate $\mathbf{d} = (d_1, d_2)$ with $d_1 > d^*$. Next, consider a sequence of positive steady state solutions $\mathbf{u}^n(\cdot) = (u_1^n, u_2^n)$ with $\mathbf{d}^n = (d_{1,n}, d_2)$ such that $d_{1,n} \to \infty$ as $n \to \infty$. For each $n \geq 1$, let $\lambda_{1,n} > 0$ denote the principal eigenvalue of (2.3) corresponding to $\mathbf{d}^n$. From (2.57), we have

$$l_n := \frac{\lambda_{1,n}}{\max\left\{\|c+b\|_\infty, \|f+g\|_\infty\right\}(1+\|\frac{r}{a+s}\|_\infty)} \leq \|u_2^n\|_\infty \quad \forall\, n \geq 1. \tag{2.79}$$

And by Lemma 2.16 (i), we have

$$\lim_{n\to\infty} l_n = \frac{\lambda^*}{\max\left\{\|c+b\|_\infty, \|f+g\|_\infty\right\}(1+\|\frac{r}{a+s}\|_\infty)} > 0,$$

where $\lambda^* = \lim_{n\to\infty} \lambda_{1,n}$ is a positive number. Thus, we obtain that

$$l_{\inf} := \inf_{n\geq 1} l_n > 0.$$

But

$$\begin{cases} 0 \leq d_2 \Delta u_2^n + s u_1^n - f_{\min}[u_2^n]^2 & x \in \Omega, \\ 0 = \partial_{\vec{n}} u_2^n & x \in \partial\Omega, \end{cases}$$

which in turn by the comparison principle for elliptic equations implies that $\|u_2^n\|_\infty^2 \leq \frac{\|su_1^n\|_\infty}{f_{\min}}$. As a result, it follows from (2.79) that

$$\|u_2^n\|_\infty \leq \frac{\|s\|_\infty}{l_{\inf} f_{\min}} \|u_1^n\|_\infty. \tag{2.80}$$

From (2.79) and (2.80), we get

$$0 < \min\left\{l_{\inf}, \frac{l_{\inf}^2 f_{\min}}{\|s\|_\infty}\right\} \leq \min\{\|u_1^n\|_\infty, \|u_2^n\|_\infty\} \quad \forall\, n \geq 1. \tag{2.81}$$

Next, thanks to the a priori upper bound for positive steady solutions of (2.1) obtained in (2.59), we can proceed as in the proof of Lemma 2.16 (the arguments used to show that $(\varphi_{1,n}, \varphi_{2,n}) \to (c_1, \varphi_2)$ as $n \to \infty$ in $C^{1,\mu}(\Omega)$ where c_1 is a constant) to obtain that there exist a nonnegative number u_1^∞ and a nonnegative function $u_2^\infty \in C^{1,\mu}(\overline{\Omega})$ such that, possibly after passing to a subsequence, $\mathbf{u}^n \to (u_1^\infty, u_2^\infty)$ as $n \to \infty$ in $C^{1,\mu}(\overline{\Omega})$. Moreover, letting $n \to \infty$ in the second equation of system (2.2), it follows from the closedness of the Laplace operator, subject to the homogeneous Neumann boundary condition on $\partial\Omega$, on $W^{1,p}(\Omega)$, $p > 1$, and the regularity theory for elliptic equations (Gilbarg and Trudinger 2001) that u_2^{∞} is a classical solution of

$$0 = d_2\Delta u_2^{\infty} + su_1^{\infty} - (e + fu_2^{\infty} + gu_1^{\infty})u_2^{\infty} \quad x \in \Omega, \quad \partial_{\vec{n}} u_2^{\infty} = 0 \;\; x \in \partial\Omega. \tag{2.82}$$

Integrating the first equation of system (2.2) on Ω and then letting $n \to \infty$ gives

$$0 = \overline{ru_2^{\infty}} - u_1^{\infty}(\overline{a} + \overline{s} + \overline{cu_2^{\infty}}) - \overline{b}(u_1^{\infty})^2, \tag{2.83}$$

where we have used the fact that u_1^{∞} is a constant number. But by (2.81), we must have that u_1^{∞} is a positive constant and $\|u_2^{\infty}\|_{\infty} > 0$. Since, $u_2^{\infty} \geq 0$ and $u_2^{\infty} \not\equiv 0$, we conclude from (2.82) and the maximum principle for elliptic equations that $u_2^{\infty} > 0$ on $\overline{\Omega}$. Solving for u_1^{∞} in the last equation gives

$$u_1^{\infty} = \frac{1}{2\overline{b}}\left(\sqrt{(\overline{a} + \overline{s} + \overline{cu_2^{\infty}})^2 + 4(\overline{b})(\overline{ru_2^{\infty}})} - (\overline{a} + \overline{s} + \overline{cu_2^{\infty}})\right).$$

Hence, $(u_1^{\infty}, u_2^{\infty})$ solves system (2.78).

(ii) The result follows from Lemma 2.16 (iii) and Proposition 2.1. □

Remark 2.18 Let $d_2 > 0$, $e \not\equiv 0$ and $s_{d_2,e}$ denote the unique positive solution of (2.64).

(i) Observe that if $(u_1^{\infty}, u_2^{\infty})$ is a positive classical solution of (2.78), then $p_{d_2} := \frac{u_2^{\infty}}{u_1^{\infty}}$ is a strict subsolution of (2.64), which implies that $p_{d_2} < s_{d_2,e}$. It then follows from (2.83) that

$$\overline{a+s} < \overline{a+s} + (\overline{cp_{d_2}} + \overline{b})u_1^{\infty} = \overline{rp_{d_2}} < \overline{rs_{d_2,e}}.$$

On the other hand, Theorem 2.17 (i) shows that system (2.78) has a positive classical solution whenever $\overline{rs_{d_2,e}} > \overline{a+s}$. Therefore, we conclude that system (2.78) has a positive classical solution if and only if $\overline{rs_{d_2,e}} > \overline{a+s}$.

(ii) Observe that for any positive solution $(u_1^{\infty}, u_2^{\infty})$ of (2.78), u_2^{∞} is also a positive solution of the nonlocal elliptic equation

$$\begin{cases} 0 = d_2\Delta u + \frac{2\overline{ru}s(x)}{(\overline{a}+\overline{s}+\overline{cu})+\sqrt{(\overline{a}+\overline{s}+\overline{cu})^2+4\overline{b}\cdot\overline{ru}}} \\ -\left(e + fu + \frac{2\overline{ru}g(x)}{(\overline{a}+\overline{s}+\overline{cu})+\sqrt{(\overline{a}+\overline{s}+\overline{cu})^2+4\overline{b}\cdot\overline{ru}}}\right)u & x \in \Omega, \\ 0 = \partial_{\vec{n}} u & x \in \partial\Omega. \end{cases} \tag{2.84}$$

Conversely if the nonlocal elliptic equation (2.84) has a positive classical solution u_2, by setting

$$u_1 = \frac{1}{2\overline{b}}\left(\sqrt{(\overline{a} + \overline{s} + \overline{cu_2})^2 + 4(\overline{b})(\overline{ru_2})} - (\overline{a} + \overline{s} + \overline{cu_2})\right),$$

we have that (u_1, u_2) is a positive classical solution of (2.78). Hence, the nonlocal elliptic equation (2.84) has a positive solution if and only if system (2.78) has a positive classical solution. As a result, we conclude that the nonlocal elliptic equation (2.84) has a positive classical solution if and only if $\overline{rs_{d_2,e}} > \overline{a+s}$.

2.1.4 The case of d_1 small and d_2 large

Our next result is concerned with the existence and asymptotic profiles of positive steady state solutions of (2.1) when d_1 is small and d_2 is large.

Lemma 2.19 *Assume that $(a+s)_{\min} > 0$. For every $d_1 > 0$ and $d_2 > 0$, let λ_1 denote the principal eigenvalue of (2.3) with $\mathbf{d} = (d_1, d_2)$. The following conclusions hold.*

(i) *If $\overline{\left(\frac{rs}{a+s}\right)} - \overline{e} > 0$, then $\lim_{d_1\to 0, d_2\to\infty} \lambda_1 = \lambda^*$ where $\lambda^* > 0$ and satisfies $\overline{\left(\frac{rs}{a+s+\lambda^*}\right)} - \overline{(e+\lambda^*)} = 0$.*

(ii) *If $\overline{\left(\frac{rs}{a+s}\right)} - \overline{e} = 0$, then $\lim_{d_1\to 0, d_2\to\infty} \lambda_1 = 0$.*

(iii) *If $\overline{\left(\frac{rs}{a+s}\right)} - \overline{e} < 0$, then $\lim_{d_1\to 0, d_2\to\infty} \lambda_1 = \lambda^* := \inf\Big\{\eta \in (-(a+s)_{\min}, 0) : \overline{\left(\frac{rs}{a+s+\eta}\right)} - \overline{(e+\eta)} < 0\Big\}$.*

Proof (i) Suppose that $\overline{\left(\frac{rs}{a+s}\right)} - \overline{e} > 0$. Since the mapping $(-(a+s)_{\min}, \infty) \ni \eta \mapsto L_\eta := \overline{\left(\frac{rs}{a+s+\eta}\right)} - \overline{(e+\eta)}$ is strictly decreasing and goes to $-\infty$ as $\eta \to \infty$ and $L_0 > 0$, then there is a unique $\lambda^* > 0$ such that $L_{\lambda^*} = 0$. From this point, the proof is divided into two steps.

Step 1. In this step, we shall show that

$$\limsup_{d_1\to 0, d_2\to\infty} \lambda_1 \leq \lambda^*. \tag{2.85}$$

Let $\eta > \lambda^*$ be fixed. So, we have $\overline{\left(\frac{rs}{a+s+\eta}\right)} - \overline{(e+\eta)} < 0$, which implies that there is $d_2^{1,\eta} \gg 1$ such that $\varepsilon_{\eta,d_2} := -\lambda(d_2, \frac{rs}{a+s+\eta} - (e+\eta)) < 0$ for every $d_2 > d_2^{1,\eta}$. Moreover,

$$\varepsilon_{\eta,\infty} := \lim_{d_2\to\infty} \varepsilon_{\eta,d_2} = -\frac{1}{|\Omega|}\left(\overline{\left(\frac{rs}{a+s+\eta}\right)} - \overline{e+\eta}\right) > 0.$$

Hence, there is $d_2^{2,\eta} > 1$ such that

$$\varepsilon_{\eta,d_2} > \frac{\varepsilon_{\eta,\infty}}{2} > 0 \quad \forall\, d_2 > d_2^{2,\eta}. \tag{2.86}$$

Note that $\lambda\Big(d_2, \frac{rs}{a+s+\eta} - (e+\eta-\varepsilon_{\eta,d_2})\Big) = 0$ for every $d_2 > 0$. For every $d_2 > 0$, let φ_2 denote the eignfunction of $\lambda\Big(d_2, \frac{rs}{a+s+\eta} - (e+\eta-\varepsilon_{\eta,d_2})\Big)$ with $\varphi_{2,\max} = 1$.

Hence

$$\begin{cases} 0 = d_2\Delta\varphi_2 + \left(\frac{rs}{a+s+\eta} - (e+\eta-\varepsilon_{\eta,d_2})\right)\varphi_2 & x \in \Omega, \\ 0 = \partial_{\vec{n}}\varphi_2 & x \in \partial\Omega. \end{cases} \tag{2.87}$$

Observe that

$$\|\Delta\varphi_2\|_\infty \le \frac{1}{d_2}\left\|\frac{rs}{a+s+\eta} - (e+\eta-\varepsilon_{\eta,d_2})\right\|_\infty \to 0 \quad \text{as} \quad d_2 \to \infty.$$

Thus, since $\varphi_{2,\max} = 1$ for every d_2, we can invoke the regularity theory for elliptic equations (Gilbarg and Trudinger 2001) to conclude that $\varphi_2 \to 1$ as $d_2 \to \infty$ uniformly in Ω. Hence for all $\tau > 0$, there is $D_2^{\tau,\eta} \gg 1$ such that

$$1-\tau \le \varphi_2 \le 1 \quad \forall\, d_2 > D_2^{\tau,\eta}. \tag{2.88}$$

Next, for each $d_1 > 0$, let φ_1 denote the unique positive solution of the elliptic equation

$$\begin{cases} 0 = d_1\Delta\varphi_1 + r - (a+s+\eta)\varphi_1 & x \in \Omega, \\ 0 = \partial_{\vec{n}}\varphi_1 & x \in \partial\Omega. \end{cases} \tag{2.89}$$

It follows from the singular perturbation theory for elliptic equations (Cantrell and Cosner 2003, Proposition 3.16) that $\varphi_1 \to \frac{r}{a+s+\eta}$ as $d_1 \to 0$ uniformly in Ω. Hence, for every $\tau > 0$, there exists $D_1^{\tau,\eta} > 0$ such that

$$\frac{r}{a+s+\eta} - \tau < \varphi_1 < \frac{r}{a+s+\eta} + \tau \quad \forall\, 0 < d_1 < D_1^{\tau,\eta}. \tag{2.90}$$

It is clear from (2.88) and (2.89) that

$$\begin{cases} \eta\varphi_1 \ge d_1\Delta\varphi_1 + r\varphi_2 - (a+s)\varphi_1 & x \in \Omega, \\ 0 = \partial_{\vec{n}}\varphi_1 & x \in \partial\Omega, \end{cases} \tag{2.91}$$

for all $0 < d_1 < D_1^{\tau,\eta}$ and $d_2 > D_2^{\tau,\eta}$. Next, using (2.86), (2.87) and (2.90), we get

$$\begin{aligned} \eta\varphi_2 \ge& d_2\Delta\varphi_2 + s(\varphi_1 - \tau) - e\varphi_2 + \varepsilon_{\eta,d_2}\varphi_2 \\ \ge& d_2\Delta\varphi_2 + s\varphi_1 - e\varphi + \frac{1}{2}\varepsilon_{\eta,\infty}(1-\tau) - \tau\|s\|_\infty \\ >& d_2\Delta\varphi_2 + s\varphi_1 - e\varphi_2 \end{aligned} \tag{2.92}$$

whenever $0 < \tau < \min\{1, \frac{\varepsilon_{\eta,\infty}}{2\|s\|_\infty + \varepsilon_{\eta,\infty}}\}$, $0 < d_1 < D_1^{\tau,\eta}$ and $d_2 > \max\{d_2^{1,\eta}, d_2^{2,\eta}, D_2^{\tau,\eta}\}$. Since $\varphi_1 > 0$ and $\varphi_2 > 0$, we conclude from (2.91) and (2.92) that

$$\eta > \lambda_1 \quad \forall\, 0 < d_1 < D_1^{\tau,\eta},\ d_2 > \max\left\{d_2^{1,\eta}, d_2^{2,\tau}, D_2^{\tau.\eta}\right\},$$

$$0 < \tau < \min\left\{1, \frac{\varepsilon_{\eta,\infty}}{2\|s\|_\infty + \varepsilon_{\eta,\infty}}\right\},$$

which implies that $\eta \geq \limsup_{d_1\to 0, d_2\to\infty} \lambda_1$. This proves (2.85) since $\eta > \lambda^*$ is arbitrarily chosen.

Step 2. In the current step, we show that

$$\liminf_{d_1\to 0, d_2\to\infty} \lambda_1 \geq \lambda^*. \tag{2.93}$$

Let $0 < \eta < \lambda^*$ be fixed. For every $d_1 > 0$, let φ_1 denote the unique positive solution of (2.89). Since $\varphi_1 \to \frac{r}{a+s+\eta}$ uniformly in Ω as $d_1 \to 0$, then

$$\overline{s\varphi_1} \to \overline{\left(\frac{rs}{a+s+\eta}\right)} \quad \text{as } d_1 \to 0. \tag{2.94}$$

Next, for every $d_2 > 0$ and $d_1 > 0$, let φ_2 denote the unique positive solution of the elliptic equation

$$\begin{cases} 0 = d_2\Delta\varphi_2 - (e+\eta)\varphi_2 + s\varphi_1 & x \in \Omega, \\ 0 = \partial_{\vec{n}}\varphi_2 & x \in \partial\Omega. \end{cases} \tag{2.95}$$

Observe from the comparison principle for elliptic equations that $\|\varphi_1\|_\infty \leq \left\|\frac{r}{a+s+\eta}\right\|_\infty$ for every $d_1 > 0$. Hence, again by the comparison principle for elliptic equations, $\|\varphi_2\|_\infty \leq \left\|\frac{s\varphi_1}{e+\eta}\right\|_\infty \leq \frac{\|s\|_\infty}{\|e+\eta|_\infty}\left\|\frac{r}{a+s+\eta}\right\|_\infty$ for every $d_2 > 0$ and $d_1 > 0$. It then follows from (2.95) that

$$\|\Delta\varphi_2\|_\infty \leq \frac{1}{d_2}\|s\varphi_1 - (e+\eta)\varphi_2\|_\infty \to 0 \quad \text{as } d_2 \to \infty \quad \text{and} \quad d_1 \to 0.$$

As a result, by the regularity theory for elliptic equations, up to a subsequence, there is a nonnegative constant c^* such that $\varphi_2 \to c^*$ in $C^1(\overline{\Omega})$ as $d_2 \to \infty$ and $d_1 \to 0$. Integrating (2.95) on Ω and using (2.94), we get

$$c^* = \frac{\overline{\left(\frac{rs}{a+s+\eta}\right)}}{\overline{(e+\eta)}} = 1 + \frac{L_\eta}{\overline{(e+\eta)}}.$$

Since the expression of c^* is independent of the subsequence we choose, we conclude that $\varphi_2 \to c^*$ in $C^1(\overline{\Omega})$ as $d_2 \to \infty$ and $d_1 \to 0$. Recalling that $0 < \eta < \lambda^*$, the function $(-(a+s)_{\min}, \infty) \ni \tau \mapsto L_\tau$ is strictly decreasing, and $L_{\lambda^*} = 0$, we obtain that $L_\eta > 0$. This shows that $c^* > 1$. Thus there is $d_{2,*} \gg 1$ and $0 < d_{1,*} \ll 1$ such that $\varphi_2 > 1$ for every $0 < d_1 < d_{1,*}$ and $d_2 > d_{2,*}$, which together with (2.89) and (2.95) yield

$$\begin{cases} \eta\varphi_1 \le d_1\Delta\varphi_1 + r\varphi_2 - (a+s)\varphi_1 & x \in \Omega, \\ \eta\varphi_2 \le d_2\Delta\varphi_2 + s\varphi_1 - e\varphi_2 & x \in \Omega, \\ 0 = \partial_{\vec{n}}\varphi_i & x \in \partial\Omega,\ i = 1, 2, \end{cases}$$

for every $d_2 > d_{2,*}$ and $0 < d_1 < d_{1.*}$. We then conclude that $\eta \le \liminf_{d_2\to\infty, d_1\to 0} \lambda_1$, which yields the desired result since $0 < \eta < \lambda^*$ is arbitrarily chosen.

(ii) Suppose that $\overline{\left(\frac{rs}{a+s}\right)} - \overline{e} = 0$. Hence $\overline{\left(\frac{rs}{a+s-\nu}\right)} - \overline{(e-\nu)} > 0$ for every $0 < \nu < (a+s)_{\min}$. It then follows from (i) that

$$\lim_{d_1\to 0, d_2\to\infty} \lambda_{1,\nu} = \lambda^*_\nu, \quad 0 < \nu < (a+s)_{\min}, \tag{2.96}$$

where $\lambda^*_\nu > 0$ satisfies

$$\overline{\left(\frac{rs}{a+s-\nu+\lambda^*_\nu}\right)} - \overline{(e-\nu+\lambda^*_\nu))} = 0 \tag{2.97}$$

and $\lambda_{1,\nu}$ is the principal eigenvalue of the cooperative system

$$\begin{cases} \lambda\varphi_1 = d_1\Delta\varphi_1 - (a(x)+s(x)-\nu)\varphi_1 + r(x)\varphi_2 & x \in \Omega, \\ \lambda\varphi_2 = d_2\Delta\varphi_2 + s(x)\varphi_1 - (e(x)-\nu)\varphi_2 & x \in \Omega, \\ \quad 0 = \partial_{\vec{n}}\varphi_1 = \partial_{\vec{n}}\varphi_2 & x \in \partial\Omega. \end{cases} \tag{2.98}$$

Clearly, by the uniqueness of the principal eigenvalue, $\lambda_{1,\nu} = \nu + \lambda_1$. Moreover, from (2.97), we have that $\lambda^*_\nu = \nu$ since $\overline{\left(\frac{rs}{a+s}\right)} - \overline{e} = 0$. We deduce from (2.96) that $\lim_{d_1\to 0, d_2\to\infty} \lambda_1 = 0$.

(iii) Suppose that $\overline{\left(\frac{rs}{a+s}\right)} - \overline{e} < 0$ and let $\lambda^* := \inf\Big\{\eta \in (-(a+s)_{\min}, 0) : \overline{\left(\frac{rs}{a+s+\eta}\right)} - \overline{(e+\eta)} < 0\Big\}$. We distinguish two cases.

Case 1. $\lambda^* > -(s+a)_{\min}$. Hence $\overline{\left(\frac{rs}{a+s+\lambda^*}\right)} - \overline{(e+\lambda^*)} = 0$. By (ii), we conclude that

$$\lim_{d_1\to 0, d_2\to\infty} \lambda_{1,\lambda^*} = 0 \tag{2.99}$$

where λ_{1,λ^*} is the principal eigenvalue of (2.98) with $\nu = -\lambda^*$. But $\lambda_{1,\lambda^*} = \lambda_1 - \lambda^*$, whence the result follows from (2.99).

Case 2. $\lambda^* = -(a+s)_{\min}$. Recalling that $\lambda_1 \ge \lambda(d_1, -(a+s))$ for all $d_1 > 0$ and $d_2 > 0$, we obtain

$$\liminf_{d_1\to 0, d_2\to\infty} \lambda_1 \ge \lim_{d_1\to 0^+} \lambda(d_1, -(a+s)) = -(a+s)_{\min}.$$

On the other hand, since $\overline{\left(\frac{rs}{a+s+\eta}\right)} - \overline{(e+\eta)} < 0$ for all $\eta > \lambda^* = -(a+s)_{\min}$, it follows from (2.85) that

$$\limsup_{d_1 \to 0, d_2 \to \infty} \lambda_1 \leq -(a+s)_{\min},$$

which completes the proof of the result. □

Next, we state our result on the asymptotic profiles of positive steady state solutions of (2.1) as $d_1 \to 0^+$ and $d_2 \to \infty$.

Theorem 2.20 *Suppose that* $(a+s)_{\min} > 0$.

(i) *If* $\overline{\left(\frac{rs}{a+s}\right)} > \bar{e}$, *then there is* $d^* \gg 1$ *such that for every* $0 < d_1 < \frac{1}{d^*}$ *and* $d_2 > d^*$, $\lambda_1 > 0$. *Hence,* (2.1) *has a positive steady state solution* $\mathbf{u}(\cdot, \mathbf{d})$ *for every* $\mathbf{d} \in (0, \frac{1}{d^*}) \times (d^*, \infty)$. *Furthermore, any positive steady state solution* $\mathbf{u}(\cdot, \mathbf{d})$ *of* (2.1) *for* $0 < d_1 < \frac{1}{d^*}$ *and* $d_2 > d^*$ *satisfies* $\mathbf{u}(\cdot, \mathbf{d}) \to (\frac{2r\mu^*}{G(\cdot,\mu^*)}, \mu^*)$ *as* $\min\{\frac{1}{d_1}, d_2\} \to \infty$ *uniformly in* Ω, *where* μ^* *is the positive constant uniquely determined by the algebraic equation*

$$\int_\Omega F(x, \mu^*) = 0, \tag{2.100}$$

where the functions G and F are introduced in (2.32) *and* (2.34)*, respectively.*

(ii) *If* $\overline{\left(\frac{rs}{a+s}\right)} < \bar{e}$, *then there is* $d^* \gg 1$ *such that for every* $0 < d_1 < \frac{1}{d^*}$ *and* $d_2 > d^*$, $\lambda_1 < 0$. *Hence* (2.1) *has no positive steady state solution for every diffusion rate* $\mathbf{d} \in (0, \frac{1}{d^*}) \times (d^*, \infty)$.

Proof (i) Suppose that $\overline{\left(\frac{rs}{a+s}\right)} > \bar{e}$. By Lemma 2.19 (i), there is $d^* \gg 1$ such that $\lambda_1 > 0$ for all $0 < d_1 < \frac{1}{d^*}$ and $d_2 > d^*$. It then follows from Proposition 2.1 that system (2.1) has a positive steady state solution of every $0 < d_1 < \frac{1}{d^*}$ and $d_2 > d^*$. Next, let $\mathbf{u}^n = (u_1^n, u_2^n)$ be a positive steady state solution of (2.1) for $\mathbf{d} = (d_{1,n}, d_{2,n}) \in (0, \frac{1}{d^*}) \times (d^*, \infty)$ for every $n \geq 1$ where $d_{1,n} \to 0$ and $d_{2,n} \to \infty$ as $n \to \infty$. Since by Lemma 2.19 (i), $\lambda^* := \lim_{d_1 \to 0, d_2 \to \infty} \lambda_1 > 0$, we can proceed as in (2.81) to show that

$$\inf_{n \geq 1} \min\{\|u_1^n\|_\infty, \|u_2^n\|_\infty\} > 0. \tag{2.101}$$

Furthermore, by the a priori upper bound (2.59) for positive steady state solutions, we have that

$$\sup_{n \geq 1} \|d_{2,n} \Delta u_2^n\|_\infty < \infty,$$

which implies that $\|\Delta u_2^n\|_\infty \to 0$ as $n \to \infty$. Hence, by the regularity theory for elliptic equations, there is a positive constant u_2^* such that, after passing to a subsequence, $u_2^n \to u_2^*$ as $n \to \infty$ in $C^{1,\mu}(\overline{\Omega})$. Next, by the singular perturbation theory, letting $n \to \infty$ in first equation of (2.2), we deduce that $u_1^n \to \frac{2r(x)u_2^*}{G(x,u_2^*)}$ as $n \to \infty$ uniformly in Ω, where G is defined in (2.32). Now, integrating the second equation in (2.2) and then letting $n \to \infty$ yield

$$0 = \int_\Omega \left(\frac{2r(x)s(x)}{G(x,u_2^*)} - e + \left(f(x) + \frac{2g(x)r(x)}{G(x,u_2^*)} \right) u_2^* \right) u_2^* = \int_\Omega u_2^* F(x,u_2^*).$$

where F is introduced in (2.34). Since u_2^* is a positive constant, we deduce that $\int_\Omega F(x,u_2^*) = 0$, which implies that $u_2^* = \mu^*$, since the function $F(x,\tau)$ is strictly decreasing in $\tau \geq 0$ for each $x \in \Omega$. This shows that $\mathbf{u}^n \to \left(\frac{2r(x)\mu^*}{G(x,\mu^*)}, \mu^* \right)$ as $n \to \infty$ uniformly in $x \in \Omega$, up to a subsequence. Since the limit point $\left(\frac{2r(x)\mu^*}{G(x,\mu^*)}, \mu^* \right)$ is independent of the subsequence we chose, then the result holds.

(ii) The result follows from Lemma 2.19 (iii) and Proposition 2.1. □

2.1.5 The case of d_1 large and d_2 large.

Next, we discuss the asymptotic profiles of positive steady state solutions of (2.1) for large diffusion rates. First, note that the quantity λ_1^∞ introduced in (2.7) and the quantity $\overline{r}\cdot\overline{s} - (\overline{a}+\overline{s})\overline{e}$ have the same signs. It then follows from Proposition 2.2 that if $\overline{r}\cdot\overline{s} < (\overline{a}+\overline{s})\overline{e}$, then (2.1) has no positive steady state solution for large diffusion rates. However, if $\overline{r}\cdot\overline{s} > (\overline{a}+\overline{s})\overline{e}$, then (2.1) has positive steady state solutions for large diffusion rates. Concerning the asymptotic profiles of positive steady state solutions for large diffusion rates, we have the following result.

Theorem 2.21 *If $\overline{r}\cdot\overline{s} > (\overline{a}+\overline{s})\overline{e}$ then there is $d^* \gg 1$ such that (2.1) has a positive steady state solution for any diffusion rate $\mathbf{d} \in (d^*,\infty)^2$. Furthermore, any positive steady state solution $\mathbf{u}(\cdot,\mathbf{d})$ for $\mathbf{d} \in (d^*,\infty)^2$ satisfies $\mathbf{u}(\cdot,d) \to (\frac{2\overline{r}\mu^*}{\hat{G}(\mu^*)}, \mu^*)$ as $\mathbf{d} \to \infty$ uniformly in Ω, where*

$$\hat{G}(\mu) = \sqrt{(\overline{a}+\overline{s}+\mu\overline{c})^2 + 4\overline{b}\overline{r}\mu} + (\overline{a}+\overline{s}+\overline{c}\mu) \quad \forall\, \mu \geq 0 \tag{2.102}$$

and μ^* is the unique positive solution of the algebraic equation

$$2\frac{\overline{s}\cdot\overline{r}}{\hat{G}(\mu)} - \overline{e} - \left(\overline{f} + 2\frac{\overline{g}\cdot\overline{r}}{\hat{G}(\mu)} \right)\mu = 0. \tag{2.103}$$

Proof First, by Proposition (2.1) and (2.2), since $\overline{r}\cdot\overline{s} > (\overline{a}+\overline{s})\overline{e}$, there is $d^* \gg 1$ such that (2.1) has a positive steady state solution for every $\mathbf{d} \in (d^*,\infty)\times(d^*,\infty)$. Next, let $\{\mathbf{u}^n\}_{n\geq 1}$ be a sequence of positive steady state solutions of (2.1) for $\mathbf{d}^n =$

$(d_{1,n}, d_{2,n}) \in (d^*, \infty) \times (d^*, \infty)$, $n \geq 1$, where $\min\{d_{1,n}, d_{2,n}\} \to \infty$ as $n \to \infty$. Since, by Proposition 2.2,

$$\lim_{\mathbf{d}\to\infty} \lambda_1 = \lambda_1^\infty > 0$$

it follows as in the case of (2.81) that

$$\inf_{n\geq 1} \min\{\|u_1^n\|_\infty, \|u_2^n\|_\infty\} > 0.$$

Furthermore, by the a priori bound (2.59) for positive steady state solutions of (2.1), we have

$$\sup_{n\geq 1} \max\{\|d_{1,n}\Delta u_1^n\|_\infty, \|d_{2,n}\Delta u_2^n\|_\infty\} < \infty,$$

which implies

$$\|\Delta u_1^n\|_\infty + \|\Delta u_2^n\|_\infty \to 0 \quad \text{as } n \to \infty.$$

Hence, by the regularity theory of elliptic equations, there exist positive constants u_1^∞ and u_2^∞ such that $\mathbf{u}^n \to (u_1^\infty, u_2^\infty)$ as $n \to \infty$ in $C^{1,\mu}(\overline{\Omega})$. Finally, integrating the first two equations of (2.2), next letting $n \to \infty$, and solving for the positive constants u_1^∞ and u_2^∞ of the resulting system of two algebraic equations, we obtain that $u_2^\infty = \mu^*$ and $u_1^\infty = \frac{2\overline{r}}{\hat{G}(\mu^*)}\mu^*$ where μ^* is the unique positive solution of (2.103) and $\hat{G}(\mu)$ is defined by (2.102). Since, this limit point is independent of the sequence we chose, we conclude that $\mathbf{u}(\cdot, \mathbf{d}) \to \left(\frac{2\overline{r}\mu^*}{\hat{G}(\mu^*)}, \mu^*\right)$ as $\mathbf{d} \to \infty$ uniformly in Ω. □

2.2 Uniqueness and stability of steady state solutions

We derive some sufficient conditions on the parameters of the PDE model (2.1) to ensure the uniqueness and stability of steady state solutions when $\lambda_1 > 0$. Recall that when $c = g \equiv 0$, the PDE system (2.2) becomes the cooperative system

$$\begin{cases} \partial_t u_1 = d_1\Delta u_1 + r(x)u_2 - (s(x) + a(x) + b(x)u_1)u_1 & x \in \Omega,\ t > 0, \\ \partial_t u_2 = d_2\Delta u_2 + s(x)u_1 - (e(x) + f(x)u_2)u_2 & x \in \Omega,\ t > 0, \\ 0 = \partial_{\vec{n}} u_1 = \partial_{\vec{n}} u_2 & x \in \partial\Omega,\ t > 0, \end{cases} \tag{2.104}$$

which always has a unique globally stable nonnegative steady state solution $\tilde{\mathbf{u}}(\cdot, \mathbf{d})$. Moreover, $\tilde{\mathbf{u}}(\cdot, \mathbf{d})$ is positive if and only if $\lambda_1 > 0$. The following result provides some sufficient smallness hypothesis on c and g which guarantee the uniqueness and global stability of positive steady state solution of (2.2).

Theorem 2.22 *Let $\mathbf{d} > 0$ be given and suppose that $\lambda_1 > 0$. Let $\tilde{\mathbf{u}}(\cdot, \mathbf{d})$ be the unique positive steady state solution of* (2.104) *and suppose that the following hypothesis holds.*

(H0) $\min_{x\in\overline{\Omega}}(r(x)-c(x)\tilde{u}_1(x,\mathbf{d}))>0$ *and* $\min_{x\in\overline{\Omega}}(s(x)-g(x)\tilde{u}_2(x,\mathbf{d}))>0$.

Then (2.1) *has a unique positive steady state solution* $\mathbf{u}(\cdot,\mathbf{d})$. *Furthermore, any classical solution of* (2.1) *with a non null initial data converges to* $\mathbf{u}(\cdot,\mathbf{d})$ *as* t *goes to infinity uniformly for* $x\in\overline{\Omega}$.

Proof **Uniqueness of positive steady state solution.** Since $\tilde{\mathbf{u}}(\cdot,\mathbf{d})$ is the global attractor for solutions of the initial value problem (2.104) with non null initial data and every nonnegative classical solution of (2.1) is a subsolution of (2.104), then any positive steady state solution $\mathbf{u}(\cdot,\mathbf{d})$ must satisfy $\mathbf{u}(\cdot,\mathbf{d})\leq\tilde{\mathbf{u}}(\cdot,\mathbf{d})$. Thus, by introducing the set

$$\mathcal{I}_{inv}^{[\mathbf{0},\tilde{u}(\cdot,\mathbf{d})]}:=\{\mathbf{u}\in\mathbb{X}\ :\ \mathbf{0}\leq\mathbf{u}\leq\tilde{\mathbf{u}}(\cdot,\mathbf{d})\},$$

we have that every positive steady state solution of (2.1) lies in $\mathcal{I}_{inv}^{[\mathbf{0},\tilde{u}(\cdot,\mathbf{d})]}$. It is clear that $\mathcal{I}_{[\mathbf{0},\tilde{u}(\cdot,\mathbf{d})]}$ is an invariant set for the flow generated by the solution of the initial value problem (2.1). Observe that by hypothesis **(H0)**, the system (2.1) is cooperative and subhomogeneous in $\mathcal{I}_{inv}^{[\mathbf{0},\tilde{u}(\cdot,\mathbf{d})]}$. Hence, since (2.1) is subhomogenous in $\mathcal{I}_{inv}^{[\mathbf{0},\tilde{u}(\cdot,\mathbf{d})]}$ and $\lambda_1>0$, it has a unique positive steady state $\mathbf{u}(\cdot,\mathbf{d})$ in $\mathcal{I}_{inv}^{[\mathbf{0},\tilde{u}(\cdot,\mathbf{d})]}$. This proves the uniqueness of positive steady state solution of (2.1).

Global Stability of $\mathbf{u}(\cdot,\mathbf{d})$. Recalling that (2.104) is cooperative, $\tilde{\mathbf{u}}(\cdot,\mathbf{d})$ is the global attractor for positive solution of (2.104), and nonnegative classical solutions of (2.1) are subsolutions of (2.104), then $\mathcal{I}_{inv}^{[\mathbf{0},\tilde{u}(\cdot,\mathbf{d})]}$ attracts all nonnegative classical solutions of (2.1) as t tends to infinity uniformly for $x\in\overline{\Omega}$. Furthermore, since (2.1) is cooperative on $\mathcal{I}_{inv}^{[\mathbf{0},\tilde{u}(\cdot,\mathbf{d})]}$, $\mathbf{u}(\cdot,\mathbf{d})\in\mathcal{I}_{inv}^{[\mathbf{0},\tilde{u}(\cdot,\mathbf{d})]}$ is the only positive steady solution of (2.1), $\mathbf{0}$ and $\tilde{\mathbf{u}}(\cdot,\mathbf{d})$ give a subsolution and supersolution of (2.1), respectively, we can refer to the theory of monotone dynamical system to conclude that $\mathbf{u}(\cdot,\mathbf{d})$ is globally stable for classical solution of (2.1) with non null initial data in $\mathcal{I}_{inv}^{[\mathbf{0},\tilde{u}(\cdot,\mathbf{d})]}$. As a result, since system (2.1) is uniformly persistent because $\lambda_1>0$, we deduce that $\mathbf{u}(\cdot,\mathbf{d})$ attracts all classical solutions of the initial value problem (2.1) with non null initial data. □

Observe that hypothesis **(H0)** involves also the diffusion rate $\mathbf{d}$, unless $\tilde{\mathbf{u}}(\cdot,\mathbf{d})$ is spatially homogeneous. By obtaining some upper bound on $\tilde{\mathbf{u}}(\cdot,\mathbf{d})$ independent of $\mathbf{d}$, we can employ Theorem 2.22 to derive a sufficient condition on the parameters not involving the diffusion rate that ensures the uniqueness of positive steady state solution of (2.1) whenever it exists. Now, observe that any nonnegative steady state solution of (2.104) is a sub-solution of the cooperative ODE system

$$\begin{cases}\frac{du_1}{dt}=r_{\max}u_2-((a+s)_{\min}+b_{\min}u_1)u_1\\ \frac{du_2}{dt}=s_{\max}u_1-(e_{\min}+f_{\min}u_2)u_2.\end{cases}\tag{2.105}$$

Hence, if (2.105) has a positive equilibrium solution $\tilde{\mathbf{u}}^*$, then $\tilde{\mathbf{u}}(\cdot,\mathbf{d})\leq\tilde{\mathbf{u}}^*$ for all diffusion rate $\mathbf{d}$. But, thanks to the computations leading to the expressions (2.31) and (2.34), (2.105) has a positive steady state solution if and only if $r_{\max}s_{\max}>$

$(a+s)_{\min}e_{\min}$. We can now state the following result which follows from the above discussions and Theorem 2.22.

Corollary 2.23 *Suppose that $r_{\max}s_{\max} > (a+s)_{\min}e_{\min}$ and let $\tilde{\mathbf{u}}^*$ denote the unique positive equilibrium solution of (2.105). Suppose also that*

(H1) $\min_{x\in\overline{\Omega}}(r(x) - c(x)\tilde{u}_1^*) > 0$ *and* $\min_{x\in\overline{\Omega}}(s(x) - g(x)\tilde{u}_2^*) > 0.$

Then for every diffusion rate $\mathbf{d}$ such that $\lambda_1 > 0$, (2.1) has a unique positive steady state solution which is globally stable with respect to positive perturbations.

Remark 2.24 While hypothesis **(H1)** provides a sufficient condition which guarantee the uniqueness and stability of positive steady solution solution (2.1), whenever it exists, it seems difficult to check its validity because of the lack of explicit formula for the positive equilibrium $\tilde{\mathbf{u}}^*$. But note that with

$$\tilde{m}^* = \max\left\{\frac{(r_{\max} - (a+s)_{\min})_+}{b_{\min}}, \frac{(s_{\max} - e_{\min})_+}{f_{\min}}\right\},$$

$(\tilde{m}^*, \tilde{m}^*)$ is always a nonnegative supersolution of (2.105). Moreover, $r_{\max}s_{\max} > (a+s)_{\min}e_{\min}$ if and only if $\tilde{m}^* > 0$. Then it always holds that $\tilde{\mathbf{u}}^* \leq (\tilde{m}^*, \tilde{m}^*)$. Therefore, if

$$\min_{x\in\overline{\Omega}}(r(x) - c(x)\tilde{m}^*) > 0 \quad \text{and} \quad \min_{x\in\overline{\Omega}}(s(x) - g(x)\tilde{m}^*) > 0, \tag{2.106}$$

then for every diffusion rate $\mathbf{d}$ such that $\lambda_1 > 0$, (2.1) has a unique positive steady state solution which attracts all classical solutions of the initial value problem with non null initial in the long run uniformly on $\overline{\Omega}$. We note that when $\tilde{m}^* = 0$, $\lambda_1 \leq 0$ for every diffusion rate $\mathbf{d}$. However, if

$$\int_\Omega \sqrt{rs} > \frac{1}{2}\int_\Omega (a+s+e), \tag{2.107}$$

it follows from (Cantrell et al. 2020, Proposition 2) that $\lambda_1 > 0$ for every diffusion rate $\mathbf{d}$, in which case $\tilde{m}^* > 0$. So, if (2.106) and (2.107) hold, then (2.1) has a unique globally stable positive steady state solution for every diffusion rate $\mathbf{d}$. When (2.106) holds, it is enough to require either for c and g to be sufficiently small, or for $b_{\min}$ and $f_{\min}$ to be sufficiently large to guarantee that (2.106) is also satisfied. By using the definition of $\tilde{m}^*$ it is possible to explicitly determine how small c and g must and/or how large $b_{\min}$ and $f_{\min}$ must be in specific cases, although the algebraic conditions for that may be complicated.

3 Two-species competition two-stage reaction-diffusion system

In the current section, we let $\tilde{\mathbf{u}} = (\tilde{u}_1, \tilde{u}_2)$ and $\tilde{\mathbf{v}} = (\tilde{v}_1, \tilde{v}_2)$ denote the population densities of two competing species, where $\tilde{u}_1$ and $\tilde{v}_1$ denote the density functions of the juveniles, while $\tilde{u}_2$ and $\tilde{v}_2$ are the density functions of the adults, respectively.

We suppose that the adults of each species can give birth to only their corresponding juveniles. Likewise, we suppose that the juveniles of each species grow into the corresponding adult species at maturation age. The following system of partial differential equations can be used to study the dynamics of the two species,

$$\begin{cases} \partial_t \tilde{u}_1 = d_1^{\mathbf{u}} \Delta \tilde{u}_1 + r(x)\tilde{u}_2 - s(x)\tilde{u}_1 - (a(x) \\ \qquad +b(x)(\tilde{u}_1 + \tilde{v}_1) + c(x)(\tilde{u}_2 + \tilde{v}_2))\tilde{u}_1 & x \in \Omega,\ t > 0, \\ \partial_t \tilde{u}_2 = d_2^{\mathbf{u}} \Delta \tilde{u}_2 + s(x)\tilde{u}_1 - (e(x) \\ \qquad + f(x)(\tilde{u}_2 + \tilde{v}_2) + g(x)(\tilde{u}_1 + \tilde{v}_1))\tilde{u}_2 & x \in \Omega,\ t > 0, \\ \partial_t \tilde{v}_1 = d_1^{\mathbf{v}} \Delta \tilde{v}_1 + r(x)\tilde{v}_2 - s(x)\tilde{v}_1 \\ \qquad -(a(x) + b(x)(\tilde{u}_1 + \tilde{v}_1) + c(x)(\tilde{u}_2 + \tilde{v}_2))\tilde{v}_1 & x \in \Omega,\ t > 0, \\ \partial_t \tilde{v}_2 = d_2^{\mathbf{v}} \Delta \tilde{v}_2 + s(x)\tilde{v}_1 - (e(x) \\ \qquad + f(x)(\tilde{u}_2 + \tilde{v}_2) + g(x)(u_1 + v_1))\tilde{v}_2 & x \in \Omega,\ t > 0. \end{cases} \tag{3.1}$$

To avoid confusion, we denote by $\lambda_1^{\mathbf{d}}$ the principal eigenvalue of (2.3) to indicate its dependence with respect to the diffusion coefficient $\mathbf{d} = (d_1, d_2)$. As in the previous section, we are only interested in nonnegative solutions of (3.1). It is easy to see that if $(\tilde{\mathbf{u}}, \tilde{\mathbf{v}})$ is a nonnegative solution of (3.1), then $\tilde{\mathbf{u}}$ and $\tilde{\mathbf{v}}$ are both subsolutions of the single-species system (2.1), which implies that they are both subsolutions of the linearized single-species system at $\mathbf{0} = (0, 0)$. As a result, the following result holds.

Proposition 3.1 *Let* $\mathbf{d}^{\mathbf{u}} = (d_1^{\mathbf{u}}, d_2^{\mathbf{u}})$ *and* $\mathbf{d}^{\mathbf{v}} = (d_1^{\mathbf{v}}, d_2^{\mathbf{v}})$ *denote the diffusion vectors of the species* $\tilde{\mathbf{u}}$ *and* $\tilde{\mathbf{v}}$*, respectively. Let* $(\tilde{\mathbf{u}}(t,\cdot), \tilde{\mathbf{v}}(t,\cdot))$ *be a classical solution of* (3.1) *with positive initial data. The following conclusions hold.*

(i) *If* $\max\{\lambda_1^{\mathbf{d^u}}, \lambda_1^{\mathbf{d^v}}\} \le 0$ *then* $(\tilde{\mathbf{u}}(t,\cdot), \tilde{\mathbf{v}}(t,\cdot)) \to (\mathbf{0}, \mathbf{0})$ *as* $t \to \infty$.
(ii) *If* $\lambda_1^{\mathbf{d^u}} \le 0 < \lambda_1^{\mathbf{d^v}}$ *then* $\tilde{\mathbf{u}}(t,\cdot) \to \mathbf{0}$ *as* $t \to \infty$ *and* $\tilde{\mathbf{v}}(t,\cdot)$ *is persistent.*
(iii) *If* $\lambda_1^{\mathbf{d^v}} \le 0 < \lambda_1^{\mathbf{d^u}}$ *then* $\tilde{\mathbf{v}}(t,\cdot) \to \mathbf{0}$ *as* $t \to \infty$ *and* $\tilde{\mathbf{u}}(t,\cdot)$ *is persistent.*

Thanks to Proposition 3.1, throughout the rest of this section, we will always suppose that $\min\{\lambda_1^{\mathbf{d^u}}, \lambda_1^{\mathbf{d^v}}\} > 0$, so that each species persists in absence of competition. Next, for each $x \in \Omega$, let $\mathbf{E}(x)$ be defined

$$\mathbf{E}(x) = \begin{cases} \mathbf{0} & \text{if } \Lambda(x) \le 0 \\ \text{The unique positive equilibrium of (2.4)} & \text{if } \Lambda(x) > 0, \end{cases}$$

where $\Lambda(x)$ is given by (2.5). From the definition of $\mathbf{E}(x)$, it is easily seen that if the function $x \mapsto \mathbf{E}(x)$ is not constant, then $\mathbf{u} = \mathbf{0}$ is the unique constant equilibrium solution of systems (2.1) and (2.29). For our interests, we shall also suppose that

(H2) There exist $x \neq y \in \Omega$ such that $\mathbf{E}(x) \neq \mathbf{E}(y)$.

Note that hypothesis **(H2)** implies that $\Lambda_{\max} > 0$.

3.1 Stability of single species steady states solutions of system (3.1)

Let $(\mathbf{u}(\cdot, \mathbf{d^u}), \mathbf{0})$ and $(\mathbf{0}, \mathbf{v}(\cdot, \mathbf{d^v}))$ be single species steady states solutions of (3.1). We linearize (3.1) at $(\mathbf{u}(\cdot, \mathbf{d^u}), \mathbf{0})$ and obtain the eigenvalue problem

$$\begin{cases} \lambda\varphi_1 = d_1^{\mathbf{u}}\Delta\varphi_1 - (s + a + 2bu_1 + cu_2)\varphi_1 + (r - cu_1)\varphi_2 - bu_1\psi_1 - cu_1\psi_2 & x \in \Omega, \\ \lambda\varphi_2 = d_2^{\mathbf{u}}\Delta\varphi_2 + (s - gu_2)\varphi_1 - (e + 2fu_2 + gu_1)\varphi_2 - fu_2\psi_1 - gu_2\psi_2 & x \in \Omega, \\ \lambda\psi_1 = d_1^{\mathbf{v}}\Delta\psi_1 - (s + a + bu_1 + cu_2)\psi_1 + r\psi_2 & x \in \Omega, \\ \lambda\psi_2 = d_2^{\mathbf{v}}\Delta\psi_2 + s\psi_1 - (e + fu_2 + gu_1)\psi_2 & x \in \Omega, \\ 0 = \partial_{\vec{n}}\varphi_i = \partial_{\vec{n}}\psi_i & x \in \partial\Omega,\ i = 1, 2. \end{cases} \tag{3.2}$$

Observe that the subsystem

$$\begin{cases} \lambda\psi_1 = d_1^{\mathbf{v}}\Delta\psi_1 - (s + a + bu_1 + cu_2)\psi_1 + r\psi_2 & x \in \Omega, \\ \lambda\psi_2 = d_2^{\mathbf{v}}\Delta\psi_2 + s\psi_1 - (e + fu_2 + gu_1)\psi_2 & x \in \Omega \\ 0 = \partial_{\vec{n}}\psi_i & x \in \partial\Omega,\ i = 1, 2. \end{cases} \tag{3.3}$$

formed by the last two equations of (3.2) decouples from its first two equations. Observe also that (3.3) is a cooperative system. Hence by the Krein-Rutman theorem, it has a principal eigenvalue $\lambda_1^{\mathbf{d^v}}(\mathbf{u}(\cdot, \mathbf{d^u}))$, with a corresponding positive eigenfunction $\psi = (\psi_1, \psi_2)$. Note that when $\mathbf{u} = 0$ in (3.2), $\lambda_1^{\mathbf{d^v}} := \lambda_1^{\mathbf{d^v}}(\mathbf{0})$ is the principal eigenvalue of (2.3). To be consistent with the notations of the previous sections, we introduce the function

$$\begin{aligned} &\Lambda(x, \mathbf{u}) \\ &= \frac{1}{2}\Big(\sqrt{((s(x) + a(x) + b(x)u_1(x) + c(x)u_2(x)) - (e(x) + f(x)u_2(x) + g(x)u_1(x)))^2 + 4r(x)s(x)} \\ &\quad - ((s(x) + a(x) + b(x)u_1(x) + c(x)u_2(x)) + (e(x) + f(x)u_2(x) + g(x)u_1(x)))\Big) \quad x \in \overline{\Omega}, \end{aligned} \tag{3.4}$$

which is positive if and only if

$$r(x)s(x) > (s(x) + a(x) + b(x)u_1(x) + c(x)u_2(x))(e(x) + f(x)u_2(x) + g(x)u_1(x)). \tag{3.5}$$

Note that $\Lambda(\cdot, \mathbf{0}) = \Lambda(\cdot)$, where $\Lambda(\cdot)$ is defined by (2.5).

3.1.1 Case of $\mathbf{d^v}$ small or large

By Theorem 1.4 of (Lam and Lou 2016) and Lemma 9 of (Cantrell et al. 2020), the following hold.

Proposition 3.2 *Suppose that* $\lambda_1^{\mathbf{d^u}} > 0$ *and let* $\mathbf{u}(\cdot, \mathbf{d^u})$ *be a positive steady state solution of* (2.1). *Let* $\lambda_1^{\mathbf{d^v}}(\mathbf{u}(\cdot, \mathbf{d^u}))$ *denote the principal eigenvalue of* (3.3). *Then*

$$\lim_{\mathbf{d^v} \to \mathbf{0}} \lambda_1^{\mathbf{d^v}}(\mathbf{u}(\cdot, \mathbf{d^u})) = \Lambda_{\max}(\cdot, \mathbf{u}(\cdot, \mathbf{d^u})) \tag{3.6}$$

and

$$\lim_{\mathbf{d^v}\to\infty} \lambda_1^{\mathbf{d^v}}(\mathbf{u}(\cdot,\mathbf{d^u})) = \frac{\sqrt{((\overline{s}+\overline{a}+\overline{bu_1}+\overline{cu_2})-(\overline{e}+\overline{fu_2}+\overline{gu_1}))^2+4\overline{r}\cdot\overline{s}}-((\overline{s}+\overline{a}+\overline{bu_1}+\overline{cu_2})+(\overline{e}+\overline{fu_2}+\overline{gu_1}))}{2|\Omega|}. \quad (3.7)$$

Remark 3.3 Observe from (3.6) that when $\mathbf{d^v}$ is sufficiently small, the sign of $\Lambda_{\max}(\cdot,\mathbf{u}(\cdot,\mathbf{d^u}))$ determines the linear stability of the single species steady state solution $\mathbf{u}(\cdot,\mathbf{d^u})$. To be precise, when $\Lambda_{\max}(\cdot,\mathbf{u}(\cdot,\mathbf{d^u}))<0$, (3.6) indicates that the slower competitor $\mathbf{v}(\cdot,\mathbf{d^v})$ cannot invade when rare while the faster competitor $\mathbf{u}(\cdot,\mathbf{d^u})$ is favored by competition. However, when $\Lambda_{\max}(\cdot,\mathbf{u}(\cdot,\mathbf{d^u}))>0$, (3.6) indicates that the slower competitor $\mathbf{v}(\cdot,\mathbf{d^v})$ has a competitive advantage and, when rare, can invade the faster competitor. Hence it is important to determine the sign of the quantity $\Lambda_{\max}(\cdot,\mathbf{u}(\cdot,\mathbf{d^u}))$. It turns out that the quantity $\Lambda_{\max}(\cdot,\mathbf{u}(\cdot,\mathbf{d^u}))$ may be negative or positive, depending on how the diffusion $\mathbf{d^u}$ is selected :

(i) When either $d_1^{\mathbf{u}}$ approaches zero and $d_2^{\mathbf{u}}>0$ is fixed or $d_1^{\mathbf{u}}$ approaches zero and $d_2^{\mathbf{u}}$ is very large, it follows from the asymptotic profiles of $\mathbf{u}(\cdot,\mathbf{d^u})$ described in Theorem 2.13 (i) and Theorem 2.20 (i) that $\Lambda_{\max}(\cdot,\mathbf{u}(\cdot,\mathbf{d^u}))>0$. Recall that to use these theorems we need to have $\lambda(d_2^{\mathbf{v}},(\frac{rs}{a+s+bu_1+cu_2}-(e+fu_2+gu_1))>0$. In these two scenarios, we see that the slower competitor $\mathbf{v}(\cdot,\mathbf{d^v})$ has a competitive advantage and the steady state solution $\mathbf{u}(\cdot,\mathbf{d^u})$ is linearly unstable.

(ii) When the competitor $\mathbf{u}(\cdot,\mathbf{d^u})$ moves very fast, in the sense that $\min\{d_1^{\mathbf{u}},d_2^{\mathbf{u}}\}$ is sufficiently large, it is possible to have $\Lambda_{\max}(\cdot,\mathbf{u}(\cdot,\mathbf{d^u}))<0$. We illustrate this with an example. To this end, let a,b,c,f, and g be positive and Hölder continuous functions on $\overline{\Omega}$. For simplicity, we take $e\equiv 0$. Next, let $r\not\equiv 0$ and $s\not\equiv 0$ be Hölder continuous functions such that $rs\equiv 0$ and set $r^\varepsilon:=r+\varepsilon$ and $s^\varepsilon:=s+\varepsilon$ for $0\le\varepsilon<1$. For every $0<\varepsilon<1$, considering system (2.1) with r^ε and s^ε and observing that $(r^\varepsilon s^\varepsilon-(a+s^\varepsilon)e)_{\min}>0$, by Proposition 2.1, there is $\mathbf{d}_\varepsilon^{\mathbf{v}}$ such that (2.1) has a positive steady state solution $\mathbf{v}_\varepsilon(\cdot,\mathbf{d^v})$ for $0<\mathbf{d^v}<\mathbf{d}_\varepsilon^{\mathbf{v}}$. Observing also that $\lim_{\varepsilon\to 0}(\overline{r^\varepsilon}\cdot\overline{s^\varepsilon}-(\overline{a}+\overline{s^\varepsilon})\overline{e})=\overline{r}\cdot\overline{s}>0$, then there is $0<\varepsilon^*\ll 1$ and $\mathbf{d}_{\varepsilon^*}^{\mathbf{u}}$ such that (2.1) has a positive steady state solution $\mathbf{u}_\varepsilon(\cdot,\mathbf{d^u})$ for every $\mathbf{d^u}>\mathbf{d}_{\varepsilon^*}^{u}$ and $0\le\varepsilon<\varepsilon^*$. By Theorem 2.21, for every $0\le\varepsilon<\varepsilon_*$, $\mathbf{u}_\varepsilon(\cdot,d^{\mathbf{u}})\ \to(\frac{2\overline{r}\mu_\varepsilon^*}{\hat{G}_\varepsilon(\mu_\varepsilon^*)},\mu_\varepsilon^*)$ as $\mathbf{d}\to\infty$ uniformly in Ω, where

$$\hat{G}_\varepsilon(\mu)=\sqrt{(\overline{a}+\overline{s^\varepsilon}+\mu\overline{c})^2+4\overline{br^\varepsilon}\mu}+(\overline{a}+\overline{s^\varepsilon}+\overline{c}\mu)\quad\forall\,\mu\ge 0 \quad (3.8)$$

and μ_ε^* is the unique positive solution of the algebraic equation

$$2\frac{\overline{s^\varepsilon}\cdot\overline{r^\varepsilon}}{\hat{G}_\varepsilon(\mu)}-\overline{e}-\Big(\overline{f}+2\frac{\overline{g}\cdot\overline{r^\varepsilon}}{\hat{G}_\varepsilon(\mu)}\Big)\mu=0. \quad (3.9)$$

It is clear from (3.8) and (3.9) that $\lim_{\varepsilon\to 0^+}\mu_\varepsilon^* = \mu_0^*$. Hence, since

$$\max_{x\in\overline{\Omega}}\Big(r^0(x)s^0(x) - (s^0(x)+a(x)+b(x)\frac{2\overline{r^0}\mu_0^*}{\hat{G}_0(\mu_0^*)} \\ +c(x)\mu_0^*)(e(x)+f(x)\mu_0^*+g(x)\frac{2\overline{r^0}}{\hat{G}_0(\mu_0^*)})\Big) < 0,$$

there is $0 < \tilde{\varepsilon}_* \ll \varepsilon_*$ such that

$$\max_{x\in\overline{\Omega}}\Big(r^\varepsilon(x)s^\varepsilon(x) - (s^\varepsilon(x)+a(x)+b(x)\frac{2\overline{r^\varepsilon}\mu_\varepsilon^*}{\hat{G}_\varepsilon(\mu_\varepsilon^*)} \\ +c(x)\mu_\varepsilon^*)(e(x)+f(x)\mu_\varepsilon^*+g(x)\frac{2\overline{r^\varepsilon}}{\hat{G}_\varepsilon(\mu_\varepsilon^*)})\Big) < 0 \quad \forall\, 0<\varepsilon<\tilde{\varepsilon}_*.$$

Whence, for every $0 < \varepsilon < \tilde{\varepsilon}_*$, there is $\mathbf{d}^{u,\varepsilon} \gg 1$ such that $\Lambda_{\max}(\cdot, \mathbf{u}_\varepsilon(\cdot, \mathbf{d}^{\mathbf{u}})) < 0$ for every $\mathbf{d}^{\mathbf{u}} > \mathbf{d}^{\mathbf{u},\varepsilon}$, in which case the faster competitor $\mathbf{u}_\varepsilon(\cdot, \mathbf{d}^{\mathbf{u}})$ is linearly stable and has a competitive advantage.

3.1.2 Case of $d_1^{\mathbf{u}}$ and $d_1^{\mathbf{v}}$ small

In this section we study the linear stability of the single species steady state solutions when the juveniles' diffusion rates $d_1^{\mathbf{u}}$ and $d_1^{\mathbf{v}}$ are either small or equal zero. Throughout this section, we shall always suppose that $(a+s)_{\min} > 0$. First, we shall fix $0 < d_2^{\mathbf{u}} < d_2^{\mathbf{v}}$ and then discuss two subcases: (i) $d_1^{\mathbf{u}}$ and $d_1^{\mathbf{v}}$ positive and small (see Theorem 3.4), and (ii) $d_1^{\mathbf{u}} = 0$ and $d_1^{\mathbf{v}} = 0$ (see Theorem 3.5). Second, we discuss the scenario where the juveniles move very slowly while the adults move very fast (see Theorem 3.6).

Let $0 < d_2^{\mathbf{u}} < d_2^{\mathbf{v}}$ be fixed and suppose that $\lambda(d_2^{\mathbf{v}}, \frac{rs}{a+s} - e) > 0$. Thanks to Lemma 2.11, there is $0 < d_{1,d_2^{\mathbf{v}}} \ll 1$ such that $\lambda_1^{\mathbf{d}^{\mathbf{v}}} > 0$ for every $0 < d_1^{\mathbf{v}} < d_{1,d_2^{\mathbf{v}}}$. And hence (2.1) has a positive steady state solution $\mathbf{v}(\cdot, \mathbf{d}^{\mathbf{v}})$ for all $\mathbf{d}^{\mathbf{v}} = (d_1^{\mathbf{v}}, d_2^{\mathbf{v}})$ with $0 < d_1^{\mathbf{v}} < d_{1,d_2^{\mathbf{v}}}$. Since $0 < \lambda(d_2^{\mathbf{v}}, \frac{rs}{a+s} - e) \le \lambda(d_2^{\mathbf{u}}, \frac{rs}{a+s} - e)$ by Lemma 2.8, then by Lemma 2.11 (i) and Theorem 2.13 (i), there is $d_{1,d_2^{\mathbf{u}}} > 0$ such that (2.1) has a positive steady state solution $\mathbf{u}(\cdot, \mathbf{d}^{\mathbf{u}})$ for all $\mathbf{d}^{\mathbf{u}} = (d_1^{\mathbf{u}}, d_2^{\mathbf{u}})$ with $0 < d_1^{\mathbf{u}} < d_{1,d_2^{\mathbf{u}}}$. Moreover, $\mathbf{u}(\cdot, \mathbf{d}^{\mathbf{u}}) \to \big(\frac{2rw(\cdot,d_2^{\mathbf{u}})}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}, w(\cdot, d_2^{\mathbf{u}})\big)$ (resp. $\mathbf{v}(\cdot, \mathbf{d}^{\mathbf{v}}) \to \big(\frac{2rw(\cdot,d_2^{\mathbf{v}})}{G(\cdot,w(\cdot,d_2^{\mathbf{v}}))}, w(\cdot, d_2^{\mathbf{v}})\big)$) as $d_1^{\mathbf{u}} \to 0^+$ (resp. $d_1^{\mathbf{v}} \to 0^+$) uniformly in $\overline{\Omega}$, where for each $d_2 \in \{d_2^{\mathbf{u}}, d_2^{\mathbf{v}}\}$, $w(\cdot, d_2)$ is the unique positive solution of the elliptic equation

$$\begin{cases} 0 = d_2\Delta w + \Big(\frac{2sr}{G(\cdot,w)} - e - \Big(f + \frac{2gr}{G(\cdot,w)}\Big)w\Big)w & x\in\Omega, \\ 0 = \partial_{\vec{n}} w & x\in\partial\Omega, \end{cases} \tag{3.10}$$

where the function G is defined by (2.32). It is clear from (3.10) that

$$\lambda\Big(d_2^{\mathbf{u}}, \frac{2sr}{G(\cdot, w(\cdot, d_2^{\mathbf{u}}))} - e - \Big(f + \frac{2gr}{G(\cdot, w(\cdot, d_2^{\mathbf{u}}))}\Big)w(\cdot, d_2^{\mathbf{u}})\Big) = 0.$$

As a result, by Lemma 2.8, if

$$\frac{2sr}{G(\cdot, w(\cdot, d_2^{\mathbf{u}}))} - e - \Big(f + \frac{2gr}{G(\cdot, w(\cdot, d_2^{\mathbf{u}}))}\Big) w(\cdot, d_2^{\mathbf{u}}) \not\equiv 0, \tag{3.11}$$

then

$$\lambda\Big(d_2^{\mathbf{v}}, \frac{2sr}{G(\cdot, w(\cdot, d_2^{\mathbf{u}}))} - e - \Big(f + \frac{2gr}{G(\cdot, w(\cdot, d_2^{\mathbf{u}}))}\Big) w(\cdot, d_2^{\mathbf{u}})\Big) < 0. \tag{3.12}$$

Similarly, it is clear from (3.10) that

$$\lambda\Big(d_2^{\mathbf{v}}, \frac{2sr}{G(\cdot, w(\cdot, d_2^{\mathbf{v}}))} - e - \Big(f + \frac{2gr}{G(\cdot, w(\cdot, d_2^{\mathbf{v}}))}\Big) w(\cdot, d_2^{\mathbf{v}})\Big) = 0.$$

As a result, by Lemma 2.8, if

$$\frac{2sr}{G(\cdot, w(\cdot, d_2^{\mathbf{v}}))} - e - \Big(f + \frac{2gr}{G(\cdot, w(\cdot, d_2^{\mathbf{v}}))}\Big) w(\cdot, d_2^{\mathbf{v}}) \not\equiv 0, \tag{3.13}$$

then

$$\lambda\Big(d_2^{\mathbf{u}}, \frac{2sr}{G(\cdot, w(\cdot, d_2^{\mathbf{v}}))} - e - \Big(f + \frac{2gr}{G(\cdot, w(\cdot, d_2^{\mathbf{v}}))}\Big) w(\cdot, d_2^{\mathbf{v}})\Big) > 0. \tag{3.14}$$

Theorem 3.4 *Suppose that* **(H2)** *holds and let* $0 < d_2^{\mathbf{u}} < d_2^{\mathbf{v}}$ *be fixed such that* $\lambda(d_2^{\mathbf{v}}, \frac{rs}{a+s} - e) > 0$. *Then*

$$\lim_{(d_1^{\mathbf{u}}, d_1^{\mathbf{v}}) \to \mathbf{0}} \lambda_1^{\mathbf{d}^{\mathbf{v}}}(\mathbf{u}(\cdot, \mathbf{d}^{\mathbf{u}})) = \lambda^*_{d_2^{\mathbf{u}}, d_2^{\mathbf{v}}}, \tag{3.15}$$

and

$$\lim_{(d_1^{\mathbf{u}}, d_1^{\mathbf{v}}) \to \mathbf{0}} \lambda_1^{\mathbf{d}^{\mathbf{u}}}(\mathbf{v}(\cdot, \mathbf{d}^{\mathbf{v}})) = \tilde{\lambda}^*_{d_2^{\mathbf{u}}, d_2^{\mathbf{v}}}, \tag{3.16}$$

where

$$\begin{aligned} \lambda^*_{d_2^{\mathbf{u}}, d_2^{\mathbf{v}}} = \inf \Big\{ \eta \in \Big(-\Big(\frac{G(\cdot, w(\cdot, d_2^{\mathbf{u}}))}{2}\Big)_{\min}, 0\Big) \\ : \lambda\Big(d_2^{\mathbf{v}}, \frac{rs}{\frac{G(\cdot, w(\cdot, d_2^{\mathbf{u}}))}{2} + \eta} - \Big(e + \eta + f w(\cdot, d_2^{\mathbf{u}}) + \frac{2grw(\cdot, d_2^{\mathbf{u}})}{G(\cdot, w(\cdot, d_2^{\mathbf{u}}))}\Big)\Big) < 0 \Big\} \end{aligned} \tag{3.17}$$

and

$$\tilde{\lambda}^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}} > 0 \quad \textit{satisfies} \quad \lambda\Big(d_2^{\mathbf{u}}, \frac{rs}{\tilde{\lambda}^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}} + \frac{G(\cdot,w(\cdot,d_2^{\mathbf{v}}))}{2}} - \Big(\tilde{\lambda}^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}} + e + fw(\cdot,d_2^{\mathbf{v}}) + \frac{2grw(\cdot,d_2^{\mathbf{v}})}{G(\cdot,w(\cdot,d_2^{\mathbf{v}}))}\Big)\Big) = 0. \tag{3.18}$$

Proof First, note that since **(H2)** holds, then (3.11) holds. Let $\varepsilon > 0$ and chose $0 < d^\varepsilon \ll 1$ such that

$$\Big\| b\Big(u_1(\cdot,\mathbf{d}^{\mathbf{u}}) - \frac{2rw(\cdot,d_2^{\mathbf{u}})}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}\Big) + c\Big(u_2(\cdot,\mathbf{d}^{\mathbf{u}}) - w(\cdot,d_1^{\mathbf{u}})\Big)\Big\|_\infty < \varepsilon$$

and

$$\Big\| f\Big(u_2(\cdot,\mathbf{d}^{\mathbf{u}}) - w(\cdot,d_1^{\mathbf{u}})\Big) + g\Big(u_1(\cdot,\mathbf{d}^{\mathbf{u}}) - \frac{2rw(\cdot,d_2^{\mathbf{u}})}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}\Big)\Big\|_\infty < \varepsilon \quad \forall\, 0 < d_1^u < d^\varepsilon.$$

Hence by (3.3),

$$\tilde{\lambda}_1^{\mathbf{d}^{\mathbf{v}}} - \varepsilon \le \lambda_1^{\mathbf{d}^{\mathbf{v}}} \le \tilde{\lambda}_1^{\mathbf{d}^{\mathbf{v}}} + \varepsilon, \tag{3.19}$$

where $\tilde{\lambda}_1^{\mathbf{d}^{\mathbf{v}}}$ is the principal eigenvalue of the cooperative system

$$\begin{cases} \lambda\psi_1 = d_1^{\mathbf{v}}\Delta\psi_1 - \Big(s + a + b\frac{2rw(\cdot,d_2^{\mathbf{u}})}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))} + cw(\cdot,d_2^{\mathbf{u}})\Big)\psi_1 + r\psi_2 & x \in \Omega, \\ \lambda\psi_2 = d_2^{\mathbf{v}}\Delta\psi_2 + s\psi_1 - \Big(e + fw(\cdot,d_2^{\mathbf{u}}) + g\frac{2rw(\cdot,d_2^{\mathbf{u}})}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}\Big)\psi_2 & x \in \Omega, \\ 0 = \partial_{\vec{n}}(d_i^{\mathbf{v}}\psi_i) & x \in \partial\Omega,\ i = 1,2. \end{cases} \tag{3.20}$$

Recalling from Proposition (2.10) that $\big(\frac{2rw(\cdot,d_2^{\mathbf{u}})}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}, w(\cdot,d_2)\big)$ is the unique positive steady state solution of (2.29), then

$$0 = rw(\cdot,d_2^{\mathbf{u}}) - \Big(a + s + \frac{2brw(\cdot,d_2^{\mathbf{u}})}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))} + cw(\cdot,d_2^{\mathbf{u}})\Big)\frac{2rw(\cdot,d_2^{\mathbf{u}})}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))},$$

which is equivalent to

$$a + s + \frac{2brw(\cdot,d_2^{\mathbf{u}})}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))} + cw(\cdot,d_2^{\mathbf{u}}) = \frac{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}{2}. \tag{3.21}$$

It then follows from (3.12) that

$$\begin{aligned} &\lambda\Big(d_2^{\mathbf{v}}, \frac{rs}{a + s + \frac{2brw(\cdot,d_2^{\mathbf{u}})}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))} + cw(\cdot,d_2^{\mathbf{u}})} - \Big(e + fw(\cdot,d_2^{\mathbf{u}}) + \frac{2grw(\cdot,d_2^{\mathbf{u}})}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}\Big)\Big) \\ = \ &\lambda\Big(d_2^{\mathbf{v}}, \frac{2rs}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))} - \Big(e + fw(\cdot,d_2^{\mathbf{u}}) + \frac{2grw(\cdot,d_2^{\mathbf{u}})}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}\Big)\Big) < 0. \end{aligned} \tag{3.22}$$

We can proceed as in the proof of Lemma 2.11 (iii) to conclude that $\lim_{d_1^{\mathbf{v}}\to 0^+}\tilde{\lambda}_1^{\mathbf{d}^{\mathbf{v}}} = \lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}$ where $\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}$ is given by (3.17). It is clear that (3.15) follows from (3.19) since ε is arbitrarily chosen. To see that (3.16) also holds, we can interchange the role of $\mathbf{d}^{\mathbf{u}}$ and $\mathbf{d}^{\mathbf{v}}$ in the above arguments, to obtain as in (3.3) that $\tilde{\lambda}_1^{\mathbf{d}^{\mathbf{u}}} - \varepsilon \le \lambda_1^{\mathbf{d}^{\mathbf{u}}} \le \tilde{\lambda}_1^{\mathbf{d}^{\mathbf{u}}} + \varepsilon$, where $\tilde{\lambda}_1^{\mathbf{d}^{\mathbf{u}}}$ is the principal eigenvalue of the cooperative system (3.20) where we interchanged the role of $\mathbf{d}^{\mathbf{u}}$ and $\mathbf{d}^{\mathbf{v}}$. Now, since (3.14) holds, we can proceed as in the proof of Lemma 2.8 (i) to conclude that $\lim_{d_1^{\mathbf{u}}\to 0^+}\tilde{\lambda}_1^{\mathbf{d}^{\mathbf{u}}} = \tilde{\lambda}^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}$ where $\tilde{\lambda}^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}} > 0$ and satisfies $\lambda\Big(d_2^{\mathbf{u}}, \frac{rs}{\tilde{\lambda}^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}} + \frac{G(\cdot,w(\cdot,d_2^{\mathbf{v}}))}{2}} - \Big(\tilde{\lambda}^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}} + e + fw(\cdot,d_2^{\mathbf{v}}) + \frac{2grw(\cdot,d_2^{\mathbf{v}})}{G(\cdot,w(\cdot,d_2^{\mathbf{v}}))}\Big)\Big) = 0.$ We now deduce that (3.16) holds since ε is arbitrarily chosen. □

Thanks to Theorem 3.4, when the juvenile diffusion rates are small, the species with the smaller adult diffusion rate is favored by competition in the sense that it cannot be invaded at equilibrium. Moreover, when rare, the species with the slower adult diffusion rate can invade the one with the faster adult diffusion rate. Observe that under the hypotheses of Theorem 3.4, by recalling the facts that (3.21) holds and w solves (3.10), we have that inequality (3.5) holds for at least some $x \in \Omega$ for both $\mathbf{u} = \mathbf{u}(\cdot,\mathbf{d}^{\mathbf{u}})$ and $\mathbf{u} = \mathbf{v}(\cdot,\mathbf{d}^{\mathbf{v}})$ when $0 < d_1^{\mathbf{u}}, d_1^{\mathbf{v}} \ll 1$. However, inequality (3.5) requires that the distributions of s and r to overlap significantly, which is the case that in general favors slow diffusion. A natural question is to ask whether this competition advantage is preserved in the extreme scenario that both species' juveniles do not move, that is $d_1^{\mathbf{u}} = d_1^{\mathbf{v}} = 0$. Our next result answers this question with an affirmation. However, note that in this scenario, the existence of a principal eigenvalue of (3.3) with a positive eigenfunction is not guaranteed due to the lack of compactness of the semiflow generated by solutions of the linear cooperative system

$$\begin{cases}\partial_t U_1 = -\Big(s + a + b\frac{2rw(\cdot,d_2^{\mathbf{u}})}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))} + cw(\cdot,d_2^{\mathbf{u}})\Big)U_1 + rU_2 & x\in\Omega,\ t>0,\\ \partial_t U_2 = d_2^{\mathbf{v}}\Delta U_2 + sU_1 - \Big(e + fw(\cdot,d_2^{\mathbf{u}}) + g\frac{2rw(\cdot,d_2^{\mathbf{u}})}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}\Big)U_2 & x\in\Omega,\ t>0,\\ 0 = \partial_{\vec{n}}U_2 & x\in\partial\Omega,\ t>0.\end{cases} \tag{3.23}$$

To handle the stability question of the trivial solution $\mathbf{0}$ of system (3.23), when $d_2^{\mathbf{u}} < d_2^{\mathbf{v}}$, we first introduce the set $\mathcal{M}_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}$, defined as the collection of all real numbers η such that there exist $(\psi_1,\psi_2) \in C(\overline{\Omega})\times[C^2(\Omega)\cap C^1(\overline{\Omega})]$ with $\psi_{i,\min} > 0, i = 1,2,$ satisfying

$$\begin{cases}\eta\psi_1 \ge -\Big(s + a + b\frac{2rw(\cdot,d_2^{\mathbf{u}})}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))} + cw(\cdot,d_2^{\mathbf{u}})\Big)\psi_1 + r\psi_2 & x\in\Omega,\\ \eta\psi_2 \ge d_2^{\mathbf{v}}\Delta\psi_2 + s\psi_1 - \Big(e + fw(\cdot,d_2^{\mathbf{u}}) + g\frac{2rw(\cdot,d_2^{\mathbf{u}})}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}\Big)\psi_2 & x\in\Omega,\\ 0 = \partial_{\vec{n}}\psi_2 & x\in\partial\Omega.\end{cases} \tag{3.24}$$

Observe that with $\psi_1 = \psi_2 \equiv 1$, system of inequalities (3.24) is satisfied for any positive number $\eta > \|s\|_\infty + \|r\|_\infty + \|s + a + b\frac{2rw(\cdot,d_2^{\mathbf{u}})}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))} + cw(\cdot,d_2^{\mathbf{u}})\|_\infty + \|e + fw(\cdot,d_2^{\mathbf{u}}) + g\frac{2rw(\cdot,d_2^{\mathbf{u}})}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}\|_\infty$, hence $\mathcal{M}_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}$ is nonempty. Observe also that if $\inf \mathcal{M}_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}} < 0$, then the trivial solution $\mathbf{0}$ is exponentially stable and hence every solution of the initial value problem decays exponentially. Thus, if $\inf \mathcal{M}_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}} < 0$, then the steady state solution $\mathbf{u}(\cdot, d_2^{\mathbf{u}}) = \left(\frac{2rw(\cdot,d_2^{\mathbf{u}})}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}, w(\cdot, d_2^{\mathbf{u}})\right)$ is linearly stable when $d_1^{\mathbf{u}} = d_1^{\mathbf{v}} = 0$ and $d_2^{\mathbf{u}} < d_2^{\mathbf{v}}$. The following result holds.

Theorem 3.5 *Suppose that* **(H2)** *holds and take* $d_1^{\mathbf{u}} = d_1^{\mathbf{v}} = 0$. *Let* $d_2^{\mathbf{u}} < d_2^{\mathbf{v}}$ *be given such that* $\lambda\left(d_2^{\mathbf{v}}, \frac{rs}{a+s} - e\right) > 0$. *The following conclusions hold.*

(i) *Let* $w(\cdot, d_2^{\mathbf{u}})$ *be the unique positive solution of* (3.10) *and* $\mathbf{u}(\cdot, d_2^{\mathbf{u}}) = \left(\frac{2rw(\cdot,d_2^{\mathbf{u}})}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}, w(\cdot, d_2^{\mathbf{u}})\right)$ *be the unique positive steady state solution of* (2.29). *Let* $\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}$ *be defined by* (3.17). *Then* $\inf \mathcal{M}_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}} = \lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}$, *and hence* $\mathbf{u}(\cdot, d_2^{\mathbf{u}})$ *is linearly stable. Furthermore, if* $\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}} > -(\frac{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}{2})_{\min}$, *then* $\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}$ *is an eigenvalue of* (3.3) *with a positive eigenfunction.*

(ii) *Let* $w(\cdot, d_2^{\mathbf{v}})$ *be the unique positive solution of* (3.10) *and* $\mathbf{u}(\cdot, d_2^{\mathbf{v}}) = \left(\frac{2rw(\cdot,d_2^{\mathbf{v}})}{G(\cdot,w(\cdot,d_2^{\mathbf{v}}))}, w(\cdot, d_2^{\mathbf{v}})\right)$ *be the unique positive steady state solution of* (2.29). *Let* $\tilde{\lambda}^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}$ *be the positive number given by* (3.18) *of Theorem 3.4. Then* $\tilde{\lambda}^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}$ *is an eigenvalue of* (3.3) *with a positive eigenfunction. Therefore,* $\mathbf{v}(\cdot, d_2^{\mathbf{v}})$ *is unstable.*

Proof (i) For every $\eta > -\left(\frac{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}{2}\right)_{\min}$, let $\lambda^\eta := \lambda\left(d_2^{\mathbf{v}}, \frac{rs}{\eta+\frac{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}{2}} - \left(\eta + e + fw(\cdot, d_2^{\mathbf{u}}) + \frac{2grw(\cdot,d_2^{\mathbf{u}})}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}\right)\right)$. It is clear that the function $\eta \mapsto \lambda^\eta$ is strictly decreasing. Recall also from (3.21) that $s + a + b\frac{2rw(\cdot,d_2^{\mathbf{u}})}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))} + cw(\cdot, d_2^{\mathbf{u}}) = \frac{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}{2}$. Next, let $\eta \in (\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}, 0)$. Hence $\lambda^\eta < 0$. So, we can choose $0 < \varepsilon \ll 1$ such that

$$\lambda^{\eta,\varepsilon} := \lambda\left(d_2^{\mathbf{v}}, \frac{(r+\varepsilon)s}{\frac{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}{2} + \eta} - \left(e + \eta + fw(\cdot, d_2^{\mathbf{u}}) + \frac{2rgw(\cdot, d_2^{\mathbf{u}})}{G(\cdot, w(\cdot, d_2^{\mathbf{u}}))}\right)\right) < 0.$$

Let $\psi_2^{\eta,\varepsilon}$ be the principal eigenfunction of $\lambda^{\eta,\varepsilon}$ with $\psi^{\eta,\varepsilon}_{2,\max} = 1$ and set $\psi_1^{\eta,\varepsilon} = \frac{(r+\varepsilon)\psi_2^{\eta,\varepsilon}}{\frac{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}{2}+\eta}$. Hence, $\psi^{\eta,\varepsilon}_{i,\min} > 0$ for each $i = 1, 2$ and

$$\begin{cases} \eta\psi_1^{\eta,\varepsilon} = -\left(s + a + b\frac{2rw(\cdot,d_2^{\mathbf{u}})}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))} + cw(\cdot, d_2^{\mathbf{u}})\right)\psi_1^{\eta,\varepsilon} + (r+\varepsilon)\psi_2^{\eta,\varepsilon} & x \in \Omega, \\ \eta\psi_2^{\eta,\varepsilon} = d_2^{\mathbf{v}}\Delta\psi_2^{\eta,\varepsilon} + s\psi_1^{\eta,\varepsilon} - \lambda^{\eta,\varepsilon}\psi_2^{\eta,\varepsilon} - \left(e + \eta + fw(\cdot, d_2^{\mathbf{u}}) + \frac{2rgw(\cdot,d_2^{\mathbf{u}})}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}\right)\psi_2^{\eta,\varepsilon} & x \in \Omega, \\ 0 = \partial_{\vec{n}}\psi_2^{\eta,\varepsilon} & x \in \partial\Omega. \end{cases}$$

Since $\varepsilon > 0$ and $-\lambda^{\eta,\varepsilon} > 0$, we have that $\eta \in \mathcal{M}_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}$, and hence $\eta \geq \inf \mathcal{M}_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}$. It then follows that $\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}} \geq \inf \mathcal{M}_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}$ since $\eta \in (\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}, 0)$ is arbitrarily chosen. It remains to show that $\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}} \leq \inf \mathcal{M}_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}$. To this end, we distinguish two cases.

Case 1. $\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}} = -\left(\frac{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}{2}\right)_{\min}$. Let $\eta \in \mathcal{M}_{d_2^{\mathbf{u}},d_2\mathbf{v}}$ and chose (ψ_1, ψ_2) positive functions satisfying (3.24). Hence $\eta \geq -\left(\frac{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}{2}\right)_{\min} = \lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}$, since $r\psi_2 \geq 0$ and $\psi_1 > 0$. This shows that $\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}} \leq \inf \mathcal{M}_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}$.

Case 2. $\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}} > -\left(\frac{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}{2}\right)_{\min}$. In this case we have that $\lambda^{\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}} = 0$. Let $\psi_2^{\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}}$ denote the eigenfunction of $\lambda^{\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}}$ with $\psi_{2,\max}^{\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}} = 1$ and set $\psi_1^{\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}} = \frac{2rs}{G(\cdot,d_2^{\mathbf{u}})}\psi_2^{\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}}$. Then

$$\begin{cases} \lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}\psi_1^{\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}} = -\left(s+a+b\frac{2rw(\cdot,d_2^{\mathbf{u}})}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}+cw(\cdot,d_2^{\mathbf{u}})\right)\psi_1^{\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}} + r\psi_2^{\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}} & x\in\Omega,\\ \lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}\psi_2^{\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}} = d_2^{\mathbf{v}}\Delta\psi_2^{\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}} + s\psi_1^{\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}} - \left(e+fw(\cdot,d_2^{\mathbf{u}})+\frac{2grw(\cdot,d_2^{\mathbf{u}})}{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}\right)\psi_2^{\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}} & x\in\Omega\\ 0=\partial_{\vec{n}}\psi_2^{\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}} & x\in\partial\Omega. \end{cases} \tag{3.25}$$

It then follows that $\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}} \le \inf\mathcal{M}_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}$. Observe in this case that $\lambda_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}} = \lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}$ is an eigenvalue with a positive eigenfunction $(\psi_1^{\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}}, \psi_2^{\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}})$.

(ii) In the current situation, since $\lambda\left(d_2^{\mathbf{u}}, \frac{rs}{\tilde{\lambda}^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}+\frac{G(\cdot,w(\cdot,d_2^{\mathbf{v}}))}{2}} - \left(\tilde{\lambda}^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}+e+fw(\cdot,d_2^{\mathbf{v}})+\frac{2grw(\cdot,d_2^{\mathbf{v}})}{G(\cdot,w(\cdot,d_2^{\mathbf{v}}))}\right)\right) = 0$, we can interchange the role $d_2^{\mathbf{u}}$ and $d_2^{\mathbf{v}}$ and replace $\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}$ with $\tilde{\lambda}^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}$ in (3.25), and let $\tilde{\psi}_2$ be the unique positive solution of (3.25) satisfying $\tilde{\psi}_{2,\max} = 1$. Setting also $\tilde{\psi}_1 = \frac{2r\tilde{\psi}_2}{G(\cdot,w(\cdot,d_2^{\mathbf{v}}))+2\tilde{\lambda}^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}}$, then $(\tilde{\psi}_1,\tilde{\psi}_2)$ is a positive eigenfunction corresponding to the eigenvalue $\tilde{\lambda}^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}$, and hence $\tilde{\lambda}^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}$ is an eigenvalue of (3.3) with a positive eigenfunction. Since $\tilde{\lambda}^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}} > 0$, we deduce that $\mathbf{v}(\cdot,d_2^{\mathbf{v}})$ is unstable. □

Recall from Remark 2.12 that if the parameters in (2.1) are Lipschitz continuous (which implies that $G(\cdot,w(\cdot,d_2^{\mathbf{u}}))$ is also Lipchitz) and $(rs)_{\min} > 0$, then $\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}} > -\left(\frac{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}{2}\right)_{\min}$. The assumption $(rs)_{\min} > 0$ indicates that at every location, both adults and juveniles are able to reproduce and attain maturity stage respectively. When $(rs)_{\min} = 0$, it is interesting to ask whether $\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}} > -\left(\frac{G(\cdot,w(\cdot,d_2^{\mathbf{u}}))}{2}\right)_{\min}$. Our next result shows that $\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}} \to 0$ as $d_2^{\mathbf{u}} \to \infty$.

Theorem 3.6 *Suppose that* $\overline{\frac{rs}{a+s}} > \overline{e}$.

(i) *There is* $D > 0$ *such that for every* $\max\{d_1^{\mathbf{u}}, d_1^{\mathbf{v}}\} < \frac{1}{D}$ *and* $\min\{d_2^{\mathbf{u}}, d_2^{\mathbf{v}}\} > D$, (2.1) *has single species positive steady state solutions* $\mathbf{u}(\cdot,\mathbf{d}^{\mathbf{u}})$ *and* $\mathbf{v}(\cdot,d^{\mathbf{v}})$. *Furthermore, it holds that*

$$\lim_{\max\{d_1^{\mathbf{u}},d_1^{\mathbf{v}}\}\to 0,\ \min\{d_2^{\mathbf{u}},d_2^{\mathbf{v}}\}\to\infty} \lambda_1^{\mathbf{d}^{\mathbf{v}}}(\mathbf{u}(\cdot,\mathbf{d}^{\mathbf{u}})) = \lim_{\max\{d_1^{\mathbf{u}},d_1^{\mathbf{v}}\}\to 0,\ \min\{d_2^{\mathbf{u}},d_2^{\mathbf{v}}\}\to\infty} \lambda_1^{\mathbf{d}^{\mathbf{u}}}(\mathbf{v}(\cdot,\mathbf{d}^{\mathbf{v}})) = 0. \tag{3.26}$$

(ii) *For every* $d_2^{\mathbf{u}} < d_2^{\mathbf{v}}$, *let* $\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}$ *be given by* (3.17). *Then* $\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}} \to 0$ *as* $d_2^{\mathbf{u}} \to \infty$. *Hence, there is* $d_2^* \gg 1$ *such that* $\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}} > -\left(\frac{G(\cdot,\mu^*)}{2}\right)_{\min}$ *whenever* $d_2^* < d_2^{\mathbf{u}} < d_2^{\mathbf{v}}$.

(iii) *For every* $d_2^{\mathbf{u}} < d_2^{\mathbf{v}}$, *let* $\tilde{\lambda}^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}}$ *be given by* (3.18). *Then* $\tilde{\lambda}^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}} \to 0$ *as* $d_2^{\mathbf{u}} \to \infty$.

Proof (i) The existence of $D \gg 1$ such that for every $\max\{d_1^{\mathbf{u}}, d_1^{\mathbf{v}}\} < \frac{1}{D}$ and $\min\{d_2^{\mathbf{u}}, d_2^{\mathbf{v}}\} > D$, (2.1) has single species positive steady state solutions $\mathbf{u}(\cdot, \mathbf{d}^{\mathbf{u}})$ and $\mathbf{v}(\cdot, \mathbf{d}^{\mathbf{v}})$ follows from Theorem 2.20 (i). Moreover, $\mathbf{u}(\cdot, \mathbf{d}^{\mathbf{u}})$ (resp. $\mathbf{v}(\cdot, \mathbf{d}^{\mathbf{v}})$) converge to $(\frac{2r\mu^*}{G(\cdot,\mu^*)}, \mu^*)$ as $\min\{\frac{1}{d_1^{\mathbf{u}}}, d_2^{\mathbf{u}}\} \to \infty$ (resp. $\min\{\frac{1}{d_1^{\mathbf{v}}}, d_2^{\mathbf{v}}\} \to \infty$) uniformly in Ω, where μ^* is the positive constant uniquely determined by 2.100. As a result, to deduce that (3.26) holds, it is equivalent to showing that the principal eigenvalue λ_1^* of the cooperative system

$$\begin{cases} \lambda\psi_1 = d_1\Delta\psi_1 - (s + a + \frac{2br\mu^*}{G(\cdot,\mu^*)} + c\mu^*)\psi_1 + r\psi_2 & x \in \Omega, \\ \lambda\psi_2 = d_2\Delta\psi_2 + s\psi_1 - (e + f\mu^* + \frac{2gr\mu^*}{G(\cdot,\mu^*)})\psi_2 & x \in \Omega \\ 0 = \partial_{\vec{n}}\psi_i & x \in \overline{\Omega},\ i = 1, 2. \end{cases} \tag{3.27}$$

satisfies $\lambda_1^* \to 0$ as $\min\{\frac{1}{d_1}, d_2\} \to \infty$. But observe that (2.100) is equivalent to

$$\int_\Omega \Big(\frac{2rs}{G(\cdot,\mu^*)} - \Big(e + f\mu^* + \frac{2gr\mu^*}{G(\cdot,\mu^*)}\Big)\Big) = 0.$$

This means that $\overline{\frac{rs}{\frac{G(\cdot,\mu^*)}{2}}} = \overline{e + f\mu^* + \frac{2gr\mu^*}{G(\cdot,\mu^*)}}$. Recalling from (3.21) that $s + a + c\mu^* + \frac{2br\mu^*}{G(\cdot,\mu^*)} = \frac{G(\cdot,\mu^*)}{2}$, we can infer from Lemma 2.19 to conclude that $\lambda_1^* \to 0$ as $\min\{\frac{1}{d_1}, d_2\} \to \infty$. Hence, the result follows.

(ii) The fact that $\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}} \to 0$ as $d_1^{\mathbf{u}} \to \infty$ follows from (i). Next, since $\|w(\cdot, d_2^{\mathbf{u}}) - \mu^*\|_\infty \to 0$ as $d_2^{\mathbf{u}} \to \infty$ by Theorem 2.20 (i) and $\Big(\frac{G(\cdot,\mu^*)}{2})\Big)_{\min} > 0$, then there is $d_2^* \gg 1$ such that $\lambda^*_{d_2^{\mathbf{u}},d_2^{\mathbf{v}}} > -\Big(\frac{G(\cdot,\mu^*)}{2})\Big)_{\min}$ whenever $d_2^* < d_2^{\mathbf{u}} < d_2^{\mathbf{v}}$.

(iii) The result follows from (i). □

3.1.3 Case of $d_1^{\mathbf{u}}$ and $d_1^{\mathbf{v}}$ large

In this subsection, we study the stability of the single species steady state solutions when the adults diffusion rates are fixed while that of the juveniles are sufficiently large. To this end, we take advantage of the results established in subsection 2.1.3. First consider, the system of ODE's,

$$\begin{cases} 0 = \overline{r}u_2 - (\overline{a} + \overline{s} + \overline{b}u_1 + \overline{c}u_2)u_1 & x \in \Omega, \\ 0 = s(x)u_1 - (e(x) + f(x)u_2 + g(x)u_1)u_2 & x \in \Omega. \end{cases} \tag{3.28}$$

obtained by formally setting $d_2 = 0$ in (2.78). We then introduce the following hypothesis which will be of help when stating our main result in this section.

(**H3**) System (3.28) has no positive constant solution.

Hypothesis **(H3)** implies that the ODE system (2.4) has no positive constant solution. Observe also that hypothesis **(H3)** implies hypothesis **(H2)**. Note that hypothesis **(H3)** is equivalent to saying that the nonlocal elliptic equation (2.84) has no positive constant solution. Under some addition assumptions on the model parameters, hypothesis **(H3)** will help us to determine the sign of principal eigenvalue when $d_1^{\mathbf{u}}$ and $d_1^{\mathbf{v}}$ are sufficiently large.

Let $0 < d_2^{\mathbf{u}} < d_2^{\mathbf{v}}$ be fixed. Next, let $s_{d_2^{\mathbf{u}}}$ and $s_{d_2^{\mathbf{v}}}$ denote the unique positive solutions of (2.64) when $d_2 = d_2^{\mathbf{u}}$ and $d_2 = d_2^{\mathbf{v}}$. Thanks to Lemma 2.16, the **u**-species (resp. **v**-species) steady state solution exists for large juvenile diffusion rate if and only if $\overline{rs_{d_2^{\mathbf{u}}}} > \overline{a+s}$ (resp. $\overline{rs_{d_2^{\mathbf{v}}}}$). Hence, in the current section, we shall suppose that $\min\{\overline{rs_{d_2^{\mathbf{u}}}}, \overline{rs_{d_2^{\mathbf{v}}}}\} > \overline{a+s}$ so that there $d_1^* \gg 1$ such that for every $d_1^{\mathbf{u}} > d_1^*$ (resp. $d_1^{\mathbf{v}} > d_1^*$) (2.1) has a positive steady state solution $\mathbf{u}(\cdot, \mathbf{d}^{\mathbf{u}})$ for $\mathbf{d} = \mathbf{d}^{\mathbf{u}}$ (resp. $\mathbf{v}(\cdot, \mathbf{d}^{\mathbf{v}})$ for $\mathbf{d} = \mathbf{d}^{\mathbf{v}}$). Furthermore, by Theorem 2.17, there is $\mathbf{u}^{\infty}(\cdot, d_2^{\mathbf{u}}) = (u_1^{\infty}, u_2^{\infty})(\cdot, d_2^{\mathbf{u}})$ (resp. $\mathbf{v}^{\infty}(\cdot, d_2^{\mathbf{v}}) = (v_1^{\infty}, v_2^{\infty})(\cdot, d_2^{\mathbf{v}})$) a positive solution of (2.78) with $d_2 = d_2^{\mathbf{u}}$ (resp. $d_2 = d_2^{\mathbf{v}}$) such that $\mathbf{u}(\cdot, \mathbf{d}^{\mathbf{u}}) \to \mathbf{u}^{\infty}(\cdot, d_2^{\mathbf{u}})$ (resp. $\mathbf{v}(\cdot, \mathbf{d}^{\mathbf{v}}) \to \mathbf{v}^{\infty}(\cdot, d_2^{\mathbf{v}})$) as $d_1^{\mathbf{u}} \to \infty$ (resp. $d_1^{\mathbf{v}} \to \infty$) uniformly in Ω. Now, we can state our main result of this subsection.

Theorem 3.7 *Assume that $e \not\equiv 0$ and let $0 < d_2^{\mathbf{u}} < d_2^{\mathbf{v}}$ be fixed and suppose that $\min\{\overline{rs_{d_2^{\mathbf{u}}}}, \overline{rs_{d_2^{\mathbf{v}}}}\} > \overline{a+s}$.*

(i) *There is $d_1^* \gg 1$ such that for every $d_1^{\mathbf{u}} > d_1^*$, (2.1) has a positive steady state solution $\mathbf{u}(\cdot, \mathbf{d}^{\mathbf{u}})$ for $\mathbf{d}^{\mathbf{u}} = (d_1^{\mathbf{u}}, d_2^{\mathbf{u}})$ satisfying $\mathbf{u}(\cdot, \mathbf{d}^{\mathbf{u}}) \to \mathbf{u}^{\infty}(\cdot, d_2^{\mathbf{u}})$ as $d_1^{\mathbf{u}} \to \infty$ uniformly in Ω, where $\mathbf{u}^{\infty}(\cdot, d_2^{\mathbf{u}}) = (u_1^{\infty}, u_2^{\infty})(\cdot, d_2^{\mathbf{u}})$ is a positive steady state solution of (2.78). Furthermore, with $\mathbf{d}^{\mathbf{v}} = (d_1^{\mathbf{v}}, d_2^{\mathbf{v}})$ for every $d_1^{\mathbf{v}} > d_1^*$, it holds that*

$$\lim_{\min\{d_1^{\mathbf{v}}, d_1^{\mathbf{u}}\} \to \infty} \lambda_1^{\mathbf{d}^{\mathbf{v}}}(\mathbf{u}(\cdot, \mathbf{d}^{\mathbf{u}})) = \lambda^* \tag{3.29}$$

where λ^* is the unique number $\lambda^* > \lambda(d_2^{\mathbf{v}}, -(e + fu_1^{\infty}(\cdot, d_2^{\mathbf{u}}) + gu_2^{\infty}(\cdot, d_2^{\mathbf{u}})))$ for which there is a positive solution ψ of the system

$$\begin{cases} \lambda^* \psi = d_2^{\mathbf{v}} \Delta \psi - (e + fu_1^{\infty}(\cdot, d_2^{\mathbf{u}}) + gu_2^{\infty}(\cdot, d_2^{\mathbf{u}}))\psi + s & x \in \Omega, \\ 0 = \partial_{\vec{n}} \psi & x \in \partial\Omega, \\ \lambda^* |\Omega| + \overline{a + s + bu_1^{\infty}(\cdot, d_2^{\mathbf{u}}) + cu_2^{\infty}(\cdot, d_2^{\mathbf{u}})} - \overline{r\psi} = 0. \end{cases} \tag{3.30}$$

Moreover, $\lambda^* > -\frac{\overline{a+s+bu_1^{\infty}(\cdot,d_2^{\mathbf{u}})+cu_2^{\infty}(\cdot,d_2^{\mathbf{u}})}}{|\Omega|}$ and

$$\lambda^* \begin{cases} < 0 & \text{if } \overline{rp_{d_2^{\mathbf{v}}}} < \overline{a + s + bu_1^{\infty}(\cdot, d_2^{\mathbf{u}}) + cu_2^{\infty}(\cdot, d_2^{\mathbf{u}})}, \\ = 0 & \text{if } \overline{rp_{d_2^{\mathbf{v}}}} = \overline{a + s + bu_1^{\infty}(\cdot, d_2^{\mathbf{u}}) + cu_2^{\infty}(\cdot, d_2^{\mathbf{u}})}, \\ > 0 & \text{if } \overline{rp_{d_2^{\mathbf{v}}}} > \overline{a + s + bu_1^{\infty}(\cdot, d_2^{\mathbf{u}}) + cu_2^{\infty}(\cdot, d_2^{\mathbf{u}})}, \end{cases} \tag{3.31}$$

where $p_{d_2^{\mathbf{v}}}$ is the unique positive solution of the elliptic equation

$$\begin{cases} 0 = d_2^{\mathbf{v}} \Delta p_{d_2^{\mathbf{v}}} - (e + fu_1^{\infty}(\cdot, d_2^{\mathbf{u}}) + gu_2^{\infty}(\cdot, d_2^{\mathbf{u}}))p_{d_2^{\mathbf{v}}} + s & x \in \Omega, \\ 0 = \partial_{\vec{n}} p_{d_2^{\mathbf{v}}} & x \in \partial\Omega. \end{cases} \tag{3.32}$$

In particular, if **(H3)** *holds and* $r = c_0 s$ *for some positive constant* c_0*, then* $\lambda^* < 0$.

(ii) *There is* $d_1^* \gg 1$ *such that for every* $d_1^{\mathbf{v}} > d_1^*$, (2.1) *has a positive steady state solution* $\mathbf{v}(\cdot, \mathbf{d}^{\mathbf{v}})$ *for* $\mathbf{d}^{\mathbf{v}} = (d_1^{\mathbf{v}}, d_2^{\mathbf{v}})$ *satisfying* $\mathbf{v}(\cdot, \mathbf{d}^{\mathbf{v}}) \to \mathbf{v}^{\infty}(\cdot, d_2^{\mathbf{v}})$ *as* $d_1^{\mathbf{v}} \to \infty$ *uniformly in* Ω*, where* $\mathbf{v}^{\infty}(\cdot, d_2^{\mathbf{v}}) = (v_1^{\infty}, v_2^{\infty})(\cdot, d_2^{\mathbf{v}})$ *is positive steady state solution of* (2.78)*. Furthermore, with* $\mathbf{d}^{\mathbf{u}} = (d_1^{\mathbf{u}}, d_2^{\mathbf{u}})$ *for every* $d_1^{\mathbf{u}} > d_1^*$*, it holds that*

$$\lim_{\min\{d_1^{\mathbf{v}}, d_1^{\mathbf{u}}\} \to \infty} \lambda_1^{\mathbf{d}^{\mathbf{v}}}(\mathbf{v}(\cdot, \mathbf{d}^{\mathbf{v}})) = \tilde{\lambda}^* \tag{3.33}$$

where $\tilde{\lambda}^*$ *is the unique number* $\tilde{\lambda}^* > \lambda(d_2^{\mathbf{u}}, -(e + f v_1^{\infty}(\cdot, d_2^{\mathbf{v}}) + g v_2^{\infty}(\cdot, d_2^{\mathbf{v}})))$ *for which there is a positive solution* ψ *of the system*

$$\begin{cases} \tilde{\lambda}^* \psi = d_2^{\mathbf{u}} \Delta \psi - (e + f v_1^{\infty}(\cdot, d_2^{\mathbf{v}}) + g v_2^{\infty}(\cdot, d_2^{\mathbf{v}}))\psi + s & x \in \Omega, \\ 0 = \partial_{\vec{n}} \psi & x \in \partial\Omega, \\ \tilde{\lambda}^* |\Omega| + \overline{a + s + b v_1^{\infty}(\cdot, d_2^{\mathbf{v}}) + c v_2^{\infty}(\cdot, d_2^{\mathbf{v}})} - \overline{r\psi} = 0. \end{cases} \tag{3.34}$$

Moreover, $\tilde{\lambda}^* > -\frac{\overline{a+s+bv_1^{\infty}(\cdot, d_2^{\mathbf{v}})+cv_2^{\infty}(\cdot, d_2^{\mathbf{v}})}}{|\Omega|}$ *and*

$$\tilde{\lambda}^* \begin{cases} < 0 & \text{if } \overline{r p_{d_2^{\mathbf{u}}}} < \overline{a + s + b v_1^{\infty}(\cdot, d_2^{\mathbf{v}}) + c v_2^{\infty}(\cdot, d_2^{\mathbf{v}})}, \\ = 0 & \text{if } \overline{r p_{d_2^{\mathbf{u}}}} = \overline{a + s + b v_1^{\infty}(\cdot, d_2^{\mathbf{v}}) + c v_2^{\infty}(\cdot, d_2^{\mathbf{v}})}, \\ > 0 & \text{if } \overline{r p_{d_2^{\mathbf{u}}}} > \overline{a + s + b v_1^{\infty}(\cdot, d_2^{\mathbf{v}}) + c v_2^{\infty}(\cdot, d_2^{\mathbf{v}})}, \end{cases} \tag{3.35}$$

where $p_{d_2^{\mathbf{u}}}$ *is the unique positive solution of the elliptic equation*

$$\begin{cases} 0 = d_2^{\mathbf{u}} \Delta p_{d_2^{\mathbf{u}}} - (e + f v_1^{\infty}(\cdot, d_2^{\mathbf{v}}) + g v_2^{\infty}(\cdot, d_2^{\mathbf{v}})) p_{d_2^{\mathbf{u}}} + s & x \in \Omega, \\ 0 = \partial_{\vec{n}} p_{d_2^{\mathbf{u}}} & x \in \partial\Omega. \end{cases} \tag{3.36}$$

In particular, if **(H3)** *holds and* $r = c_0 s$ *for some positive constant* c_0*, then* $\tilde{\lambda}^* > 0$.

Proof (i) The existence of $d_1^* > 0$ such that for every $d_1^{\mathbf{u}} > d_1^*$, (2.1) has a positive steady state solution $\mathbf{u}(\cdot, \mathbf{d}^{\mathbf{u}})$ for $\mathbf{d}^{\mathbf{u}} = (d_1^{\mathbf{u}}, d_2^{\mathbf{u}})$ satisfying $\mathbf{u}(\cdot, \mathbf{d}^{\mathbf{u}}) \to \mathbf{u}^{\infty}(\cdot, d_2^{\mathbf{u}})$ as $d_1^{\mathbf{u}} \to \infty$ uniformly in Ω, where $\mathbf{u}^{\infty}(\cdot, d_2^{\mathbf{u}}) = (u_1^{\infty}, u_2^{\infty})(\cdot, d_2^{\mathbf{u}})$ is a positive steady state solution of (2.78) is proved in the discussion preceding the statement of the theorem. Next, let $\varepsilon > 0$ be fixed and chose $d_{1,\varepsilon} \gg 1$ such that

$$\|(bu_1 + cu_2) - (bu_1^{\infty} + cu_2^{\infty})\|_{\infty} + \|(fu_2 + gu_1) - (fu_2^{\infty} + gu_1^{\infty})\|_{\infty} < \varepsilon \quad \forall d_1^{\mathbf{u}} > d_{1,\varepsilon}. \tag{3.37}$$

For every $\mathbf{d}^{\mathbf{v}}$ and $d_1^{\mathbf{u}} > d_{1,\varepsilon}$, let $\lambda_1^{\mathbf{d}^{\mathbf{v}}}(\mathbf{u}(\cdot, \mathbf{d}^{\mathbf{u}}))$ be the principal eigenvalue of (3.3). By (3.37), it holds that

$$\tilde{\lambda}_1^{\mathbf{d}^{\mathbf{v}}}(\mathbf{u}(\cdot, \mathbf{d}^{\mathbf{u}})) - \varepsilon \le \lambda_1^{\mathbf{d}^{\mathbf{v}}}(\mathbf{u}^{\infty}(\cdot, \mathbf{d}^{\mathbf{u}})) \le \tilde{\lambda}_1^{\mathbf{d}^{\mathbf{v}}}(\mathbf{u}^{\infty}(\cdot, \mathbf{d}^{\mathbf{u}})) + \varepsilon \tag{3.38}$$

where $\tilde{\lambda}_1^{\mathbf{d^v}}(\mathbf{u}^\infty(\cdot,\mathbf{d^u}))$ is the principal eigenvalue of the cooperative system

$$\begin{cases}\lambda\psi_1 = d_1^{\mathbf{v}}\Delta\psi_1 - (s+a+bu_1^\infty + cu_2^\infty)\psi_1 + r\psi_2 & x\in\Omega,\\ \lambda\psi_2 = d_2^{\mathbf{v}}\Delta\psi_2 + s\psi_1 - (e+fu_2^\infty + gu_1^\infty)\psi_2 & x\in\Omega\\ 0=\partial_{\vec{n}}\psi_i & x\in\overline{\Omega},\ i=1,2.\end{cases} \tag{3.39}$$

Now, since $\tilde{\lambda}_1^{\mathbf{d^v}}(\mathbf{u}^\infty(\cdot,\mathbf{d^u}))$ is the principal eigenvalue of (3.39), thanks to Lemma 2.16, it holds that $\tilde{\lambda}_1^{\mathbf{d^v}}(\mathbf{u}^\infty(\cdot,\mathbf{d^u}))\to\lambda^*$ as $d_1^{\mathbf{v}}\to\infty$, where λ^* is given as in the statement of the result. In view of (3.38) and the fact that ε is arbitrarily chosen, we conclude that $\lambda_1^{\mathbf{d^v}}(\mathbf{u}(\cdot,\mathbf{d^u}))\to\lambda^*$ as $\min\{d_1^{\mathbf{u}},d_1^{\mathbf{v}}\}\to\infty$. To complete the proof of (ii), we suppose that (**H2**) holds and that $r=c_0s$ for some positive number c_0, and then show that $\lambda^*<0$. To this end, for every $d>0$, let p_d denote the unique positive solution of

$$\begin{cases}0=d\Delta p-(e+fu_1^\infty(\cdot,d_2^{\mathbf{u}})+gu_2^\infty(\cdot,d_2^{\mathbf{u}}))p+s & x\in\Omega,\\ 0=\partial_{\vec{n}}p & x\in\partial\Omega.\end{cases} \tag{3.40}$$

By the implicit function theorem, we have that the function $(0,\infty)\ni d\mapsto p_d\in C^{2,\nu}$ is continuously differentiable. Denoting by $\dot{p}=\partial_d p$, it follows that

$$\begin{cases}0=d\Delta\dot{p}+\Delta p-(e+fu_1^\infty(\cdot,d_2^{\mathbf{u}})+gu_2^\infty(\cdot,d_2^{\mathbf{u}}))\dot{p} & x\in\Omega,\\ 0=\partial_{\vec{n}}\dot{p} & x\in\partial\Omega.\end{cases} \tag{3.41}$$

By multiplying (3.40) by $\dot{p}$ and (3.41) by p, integrating the resulting equations over Ω, and taking the difference side by side of the resulting equations, we obtain

$$\int_\Omega s\dot{p}_d = -\int_\Omega |\nabla p_d|^2. \tag{3.42}$$

Now, we claim that $\int_\Omega|\nabla p_d|^2>0$ for all $d>0$. Suppose to the contrary that this is not true. Hence there is some $d_0>0$ such that p_{d_0} is a positive constant. It follows from (3.40) that

$$0=s-(e+fu_1^\infty(\cdot,d_2^{\mathbf{u}})+gu_2^\infty(\cdot,d_2^{\mathbf{u}}))p_{d_0}\quad\forall x\in\Omega.$$

Multiplying this equation by u_1^∞, we get

$$0=u_1^\infty s-(e+fu_1^\infty(\cdot,d_2^{\mathbf{u}})+gu_2^\infty(\cdot,d_2^{\mathbf{u}}))u_1^\infty p_{d_0}\quad\forall x\in\Omega.$$

This shows that $(u_1^\infty,u_1^\infty p_{d_0})$ is also a positive solution of (2.78) with $d_2=d_2^{\mathbf{u}}$. By the uniqueness of solution of (2.78) when d_2 and u_1^∞ are fixed, we obtain that

$u_2^\infty = u_1^\infty p_{d_0}$. Recalling that (u_1^∞, u_2^∞) also satisfies (2.83), we obtain that

$$\begin{cases} 0 = \overline{r}u_2^\infty - (\overline{a} + \overline{s} + b\overline{u}_1^\infty + \overline{b}u_2^\infty)u_1^\infty & x \in \Omega, \\ 0 = s(x)u_1^\infty - (e(x) + f(x)u_2^\infty + g(x)u_1^\infty)u_2^\infty & x \in \Omega. \end{cases} \tag{3.43}$$

Hence, (u_1^∞, u_2^∞) is a positive constant solution of (3.28), which contradicts with hypothesis **(H3)**. Therefore, $\int_\Omega |\nabla p_d|^2 > 0$ for all $d > 0$. This together with (3.42) implies that the function $(0, \infty) \ni d \mapsto \int_\Omega sp_d$ is strictly decreasing. In particular

$$\overline{sp_{d_2^{\mathbf{v}}}} < \overline{sp_{d_2^{\mathbf{u}}}}$$

since $d_2^{\mathbf{u}} < d_2^{\mathbf{v}}$. Multiplying this inequality by c_0 and using the fact that $r = c_0 s$, we obtain

$$\overline{rp_{d_2^{\mathbf{v}}}} < \overline{rp_{d_2^{\mathbf{u}}}} \tag{3.44}$$

Now, by observing that $p_{d_2^{\mathbf{u}}} = \frac{u_2^\infty}{u_1^\infty}$ since (u_1^∞, u_2^∞) solves (2.78) with $d_2 = d_2^{\mathbf{u}}$, we get from (2.83) that

$$\overline{rp_{d_2^{\mathbf{u}}}} = \overline{a + s + bu_1^\infty + cu_2^\infty},$$

which together with (3.44) yields $\overline{rp_{d_2^{\mathbf{v}}}} < \overline{a + s + bu_1^\infty + cu_2^\infty}$. Therefore, $\lambda^* < 0$ by (3.35).

(ii) The follows from a proper modification of the proof of (i). □

4 Conclusion

The conditions for persistence in (2.1) describe some types of diffusion rates that are compatible with certain types of spatial distributions of habitat quality for juveniles and adults. They extend the results of (Cantrell et al. 2020) by allowing more general combinations of diffusions rates, so where juveniles diffuse slowly and adults rapidly, or vice-versa. Also, we show that the model is well posed even if either the juveniles or adults do not disperse, and obtain asymptotic profiles of equilibria as each diffusion rate goes to zero. In (Cantrell et al. 2020) it was shown that having both d_1 and d_2 small is compatible with a habitat distribution satisfying $(rs - (a+s)e)_{\max} > 0$, which is equivalent to $(\frac{rs}{(a+s)} - e)_{\max} > 0$, $(\frac{rs}{e} - (a+s))_{\max} > 0$, etc. It was also shown that having both d_1 and d_2 large is compatible with $\overline{r} \cdot \overline{s} - (\overline{s} + \overline{a})\overline{e} > 0$, equivalently $\frac{\overline{r} \cdot \overline{s}}{(\overline{s} + \overline{a})} - \overline{e} > 0$, etc. In the case of both d_1 and d_2 small it is crucial that the supports of r and s overlap and r and s are both sufficiently large at some point, while when both d_1 and d_2 are large, only the integrals (or equivalently averages) of the coefficients are relevant. In the cases considered in the present paper where one of the diffusion coefficients is large and the other is small, or one is large or small and the other is fixed, the conditions for persistence typically involve the integrals of combinations of the parameters or more complicated sorts of quantities involving the parameters. There is a certain amount of symmetry between the cases of d_1 large and d_2 small and

d_2 large and d_1 small. By Theorem 2.13, when d_2 is fixed but d_1 is small, the condition for persistence for small d_1 is $\lambda(d_2, \frac{rs}{(a+s)} - e) > 0$, where $\lambda(d_2, \frac{rs}{(a+s)} - e)$ is the principal eigenvalue of (2.35), which depends nonlocally on $\frac{rs}{a+s}$ and e. As $d_2 \to 0$, we have $\lambda(d_2, \frac{rs}{(a+s)} - e) \to (\frac{rs}{(a+s)} - e)_{\max}$ so we recover the condition from (Cantrell et al. 2020). However, as $d_2 \to \infty$, we have $\lambda(d_2, \frac{rs}{(a+s)} - e) \to \frac{1}{|\Omega|}(\overline{\frac{rs}{(a+s)}} - \overline{e})$. Thus, the condition for d_1 small and d_2 large involves what amounts to a weighted average of $\frac{rs}{(a+s)}$ which converges to the ordinary average as $d_2 \to \infty$. Hence, the condition for large d_2 requires that the regions where r is large and where $s/(a+s)$ is not too small must overlap, but only the average of e is relevant and not its spatial distribution. The case of d_1 fixed and d_2 small is somewhat analogous, see Theorem 2.15. For fixed d_2 and large d_1 the condition for persistence is $\overline{rs_{d_2,e}} > (\overline{a} + \overline{s})$, where $s_{d_2,e}$ depends nonlocally on s and e according to (2.64). For d_2 small and d_1 large this leads to a condition analogous to that for d_1 small and d_2 large, but the roles of e and $a + s$ are reversed for large d_1. Specifically, the condition for fixed d_1 as $d_2 \to 0$ is $\lambda(d_1, \frac{rs}{e} - (a + s)) > 0$, which if $d_1 \to \infty$ leads to the condition $\overline{\frac{rs}{e}} - (\overline{s} + \overline{a}) > 0$. The situations with one of d_1 and d_2 fixed or large and the other is small are different from those obtained in (Cantrell et al. 2020) when d_1 and d_2 are both large or small, since they involve integrals (or averages) of combinations of parameters.

It is interesting to examine how the predictions of persistence and invasion, or the failure of those, depend on the parameters in the model. The quantity $\frac{rs}{(a+s)} - e$ turns out to be important in several cases. For persistence when d_2 is arbitrary and d_1 is small, the condition is

$$\lambda(d_2, \frac{rs}{(a+s)} - e) > 0 \tag{4.1}$$

where λ is the principal eigenvalue defined in (2.36). A necessary condition for (4.1) is that $(\frac{rs}{a+s} - e))_{max} > 0$. That condition is sufficient for persistence if d_1 and d_2 are both sufficiently small. If $\int_\Omega (\frac{rs}{a+s} - e) > 0$ then (4.1) holds for any fixed d_2 . However, if $\int_\Omega (\frac{rs}{(a+s)} - e) < 0$ but $(\frac{rs}{(a+s)} - e))_{\max} > 0$, then the problem

$$\begin{cases} 0 = \Delta\varphi + \gamma(\frac{rs}{a+s} - e)\varphi & x \in \Omega, \\ 0 = \partial_{\vec{n}}\varphi & x \in \partial\Omega \end{cases}$$

has a positive principal eigenvalue γ_1, and (4.1) holds if and only if $d_2 < 1/\gamma_1$; see (Brown and Lin 1980) and (Cantrell and Cosner 2003), Section 2.2. We have $\lambda(d_2, \frac{rs}{(a+s)} - e) \to (\frac{rs}{a+s} - e)_{max}$ as $d_2 \to 0$.

In the case of two competing populations, it turns out that when $\Lambda(x)$ is nonconstant and is positive for some x, $0 < d_2^{\mathbf{u}} < d_2^{\mathbf{v}}$, and (4.1) holds for $d_2 = d_2^{\mathbf{v}}$, then for $d_1^{\mathbf{u}}$, $d_1^{\mathbf{v}}$ sufficiently small or zero, the single species equilibrium $\mathbf{u}(\cdot, \mathbf{d}^{\mathbf{u}})$ is stable relative to invasion by $\mathbf{v}$, but $\mathbf{v}(\cdot, \mathbf{d}^{\mathbf{v}})$ is unstable relative to invasion by $\mathbf{u}$. Thus, in this case, the slower diffuser has an advantage. Cases where one diffusion coefficient is large but the other is small, for example where $\max\{d_1^{\mathbf{u}}, d_1^{\mathbf{v}}\} \to 0$, $\min\{d_2^{\mathbf{u}}, d_2^{\mathbf{v}}\} \to \infty$, seem more subtle. In such cases the eigenvalues determining invasibility of single species equibria can go to zero in the limit, even if $\overline{\frac{rs}{a+s}} - \overline{e} > 0$. Even when it is possible to obtain criteria for the stability or instability of single species equilibria in limiting cases, those are somewhat complicated and implicit. However, it is possible to draw some conclusions in special cases. In particular, when $d_1^{\mathbf{u}}$ and $d_1^{\mathbf{v}}$ are large, the ODE system (2.4) has no constant equilibria, and $r = c_0 s$ for some constant c_0, then having $d_2^{\mathbf{u}} < d_2^{\mathbf{v}}$ implies $\mathbf{u}(\cdot, \mathbf{d^u})$ is stable but $\mathbf{v}(\cdot, \mathbf{d^v})$ is unstable. On the other hand, when $r(x)s(x)$ is small, it is possible to have $\mathbf{u}(\cdot, \mathbf{d^u})$ stable for sufficiently large $\mathbf{d^u}$. Our results give considerable support to the general trend that if r (the reproductive rate of adults) is large in some region where s (the survival and maturation rate of juveniles) is not too small, so that rs is large in some sense, then slower diffusion is advantageous. In that case the model behaves in the same way as the models for unstructured populations (Hastings 1983; Dockery et al. 1998; Altenberg 2012; Cantrell and Lam 2020). However, if rs is small but $\overline{r}$ and $\overline{s}$ are large, there are cases where faster diffusion is advantageous. Our results in that situation are less complete or harder to interpret than in cases where rs is large. What we can say is that if there is any region Ω_1, no matter how small, where the product $r(x)s(x)$ is large enough that the nonspatial model has a positive equilibrium for all $x \in \Omega_1$, then the spatial model will have a positive equilibrium if the diffusion rates of both adults and juveniles are sufficiently small. On the other hand, if the regions where $r(x)$ and $s(x)$ are positive are disjoint, there is no positive equilibrium when both diffusion rates are small, but there may be one if the averages of $r(x)$ and $s(x)$ and the diffusion rates of both adults and juveniles are all sufficiently large. In general, the conditions for the existence of a positive equilibrium when one diffusion rate is large and the other is small are more subtle, and we do not yet have a complete understanding their interpretation in those cases. There remain many open questions, especially in the cases where $r(x)s(x)$ is small for all x or where one of d_1 and d_2 is large and the other is small. Those cases are important biologically because in many populations only adults or only juveniles disperse. Although we do not have as clear an understanding of those cases as we do of those where adults and juveniles have similar dispersal characteristics, our results on the asymptotic behavior of solutions as diffusion rates go to zero should be useful for further research.

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