PERSISTENCE FOR A TWO STAGE REACTION-DIFFUSION SYSTEM

ROBERT STEPHEN CANTRELL[1], CHRIS COSNER[1] AND SALOMÉ MARTÍNEZ[2]

1. Department of Mathematics, University of Miami,
Coral Gables, FL 33124, USA

2. Departamento de Ingeniería Matemática, Universidad de Chile
Blanco Encalada 2120, 5° piso – Santiago, CHILE
and
Centro de Modelamiento Matemático, UMI 2807 CNRS-UChile
Universidad de Chile, Casilla 170 Correo 3 – Santiago, CHILE

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Abstract. In this article we study how the rates of diffusion in a reaction-diffusion model for a stage structured population in a heterogeneous environment affect the model's predictions of persistence or extinction for the population. In the case of a population without stage structure, faster diffusion is typically detrimental. In contrast to that we find that in a stage structured population it can be either detrimental or helpful. If the locations regions where adults can reproduce are the same as those where juveniles can mature, typically slower diffusion will be favored, but if those regions are separated then faster diffusion may be favored. Our analysis consists primarily of estimates of principal eigenvalues of the linearized system around $(0,0)$ and results on their asymptotic behavior for large or small diffusion rates. The model we study is not in general a cooperative system, but if adults only compete with other adults and juveniles with other juveniles then it is. In that case, the general theory of cooperative systems implies that when the model predicts persistence it has a unique positive equilibrium. We derive some results on the asymptotic behavior of the positive equilibrium for small diffusion and for large adult reproductive rates in that case.

1. Introduction

The question of how dispersal interacts with spatial heterogeneity to influence population dynamics and species interactions has been studied extensively in recent years, specifically from the viewpoint of reaction-diffusion systems and related models; see for example [6, 11, 18] and the references cited therein. Most work on that topic assumes that each population is structured only by space and has only one mode of dispersal. However, populations are often structured by age, stage, or other attributes, and there may be variation among individuals in their dispersal rates or patterns. Here we will examine how the presence of stage structure influences how diffusion rates influence population dynamics in a class of reaction-diffusion models for a population with two stages. In the case of a population with logistic growth, without age or stage structure, diffusing in a closed bounded spatially heterogeneous environment that is constant in time, it is well known that reaction-diffusion models predict that slower diffusion rates are advantageous relative to faster diffusion; see [13, 17]. The results in [17] also hold for patch models. More broadly, a wide class of models arising in population genetics, population dynamics, and related areas display some version of the reduction principle, which says that dispersal which causes faster mixing typically reduces the rate of population growth; see [1]. However, the situation seems to be quite different in the case of stage structured populations. In [15], the authors considered a discrete-time patch model for a structured population and found that in some cases there was no selection against faster dispersal. The goal of the present paper is to use a spatially explicit reaction-diffusion model to understand how the spatial distributions of habitats that are favorable for reproduction by adults and those that are favorable for survival and growth by juveniles affect whether faster diffusion is advantageous or harmful for a stage structured population. We will see that the answer depends on the details of the spatial distribution of favorable and unfavorable habitats.

The type of reaction-diffusion model we will study is

$$
\begin{cases}
\dfrac{\partial u}{\partial t} = d_1 \Delta u + r(x)v - s(x)u - a(x)u - b(x)u^2 - c(x)uv \ \text{ in } \Omega,\ t > 0,\\[2ex]
\dfrac{\partial v}{\partial t} = d_2 \Delta v + s(x)u - e(x)v - f(x)v^2 - g(x)uv \text{ in } \Omega,\ t > 0,\\[2ex]
\nabla u \cdot \nu = \nabla v \cdot \nu = 0 \ \text{ on } \partial\Omega,\ t > 0.
\end{cases}
\tag{1.1}
$$

where Ω is a bounded domain in $\mathbb{R}^N$ and ν is the outward unit normal to $\partial\Omega$, so that the system has Neumann boundary conditions, which are the no-flux boundary conditions for simple diffusion. In this system u and v represent the population densities of juveniles and individuals that have reached reproductive age, i.e. adults, respectively, of the same species. Thus, the term $s(x)$ represent the rate at which juveniles mature into adults, which is determined by the fraction of individuals that reach reproductive age and the rate at which they mature, while $r(x)$ accounts for the local fecundity of adults so that $r(x)v(x)$ describes that rate at which new juveniles are produced by an adult population with density v at location x. The terms $a(x)$, $b(x)$, $c(x)$, $e(x)$, $f(x)$, and $g(x)$ account for per-capita death rates and saturation factors due to logistic self-limitation. The diffusion coefficients d_1 and d_2 account for the the dispersal rates of juveniles and adults respectively. The coefficients are all assumed to be nonnegative and continuous in

$\overline{\Omega}$. This is the type of model for a stage structured population introduced in [3]. Related models with a different interpretation are discussed in [8, 9] and in the references in those papers. The model (1.1) is not an explicitly age structured model. It assumes that individuals in the juvenile stage mature at some spatially dependent rate but does not track the age of individuals within each stage. Explicitly age structured models are considered in [16, 22, 24]. A different way of modeling an age structured population, based on delayed reaction diffusion equations equations, is developed in [30]. Our focus here is on how spatial heterogeneity, dispersal, and stage structure interact, so we have chosen to use the simplest possible formulation of stage structure. In the case where $c = g = 0$ the system is cooperative and the methods and results of [25, 27] would apply to it. The linearization of (1.1) around $(0, 0)$ is cooperative, so the results of [25] apply to it; in particular, with a few technical assumptions they imply it has a principal eigenvalue.

The main questions we will address in this work are related to understanding the roles of the different functions and coefficients in (1.1) in the persistence of the species. For the remainder of the paper we will focus primarily on understanding how the principal eigenvalue of the linearization of (1.1) around $(0, 0)$ depends on the coefficients and what that dependence means biologically. We will see that whether faster diffusion is harmful or helpful for the persistence of the population depends on the details of the distribution of habitats that are favorable for adult reproduction and those that are favorable for juvenile survival and maturation. In some cases slower diffusion is still an advantage, but sometimes faster diffusion turns out to be helpful, and sufficiently fast diffusion may even be necessary for persistence. The spatial distribution of habitats favorable to adult reproduction ($r(x)$ large) relative to those favorable to juvenile development ($s(x)$ large) turns out to be important in some cases. Our analysis here is similar in spirit to the sorts of results obtained for diffusive Lotka-Volterra competition models in [5, 14, 18, 20]. In particular, we will examine the behavior of the system for small, large, and general diffusion rates. Related results for some epidemiological models are derived in [10, 26].

The linearization of (1.1) around $(0, 0)$ has a principal eigenvalue whose sign determines whether the model predicts persistence or extinction. Since the sign of the principal eigenvalue of the linearization of (1.1) around $(0, 0)$ determines the fate (1.1) predicts for the population it describes, we will study in detail the following problem:

$$\begin{cases} d_1\Delta\varphi + r(x)\psi - (s(x) + a(x))\varphi &= \lambda\varphi \ \text{ in } \Omega, \\ d_2\Delta\psi + s(x)\varphi - e(x)\psi &= \lambda\psi \ \text{ in } \Omega, \\ \nabla\varphi\cdot\nu = \nabla\psi\cdot\nu &= 0 \ \text{ on } \partial\Omega. \end{cases} \tag{1.2}$$

2. Basic properties

In this section we discuss some basic properties of (1.1). From now on we assume that $r, s, a, b, c, e, f, g \in C^{\alpha}(\bar{\Omega})$, $\partial\Omega$ is of class $C^{2,\alpha}$, and the following hypotheses:

(H1) $r(x), s(x) \geq 0$ in Ω, with $r(x_r) \neq 0$, $s(x_s) \neq 0$ for some $x_r, x_s \in \Omega$.

(H2) $a(x), c(x), e(x), g(x) \geq 0$ in Ω.
(H3) $b(x) > 0,\ f(x) > 0$ in $\overline{\Omega}$.

This model (1.1) has many mathematical features in common with the models discussed in [8, 9] for populations where individuals can switch between two different movement modes. A key feature is that the linear part of (1.1) is cooperative, so it will have a principal eigenvalue which determines the stability of the equilibrium $(0,0)$ and hence the persistence or extinction of the population. Another key feature of (1.1) is that the nonlinearity is subhomogeneous. The maximum principle and existence of principal eigenvalues for cooperative linear systems such as the linear part of the right side of (1.1) are derived in [25]. The general theory for systems such as (1.1) is developed in [27] for the fully cooperative case (where $c = g = 0$, so that adults only compete with other adults and juveniles with other juveniles) and in the general case in [3, 8, 9, 19]. As expected, the sign of the principal eigenvalue of the linearization of (1.1) around $(0,0)$ gives us the relevant information to study the persistence of the species. If it is positive, the population will persist. If it is nonpositive the population will go extinct. In the case where the coefficients of c and g in (1.1) are zero so that the system is cooperative, the results and methods of [27] imply that if the principal eigenvalue of the linear part is positive then the system has a unique globally attractive equilibrium. If those coefficients are small the methods of [8, 9] can be applied to show that (1.1) is asymptotically cooperative, and still has a unique globally attractive positive equilibrium. Combining results that are given in [3, 8, 9, 25, 27] or that follow directly by the same arguments used in those papers, we have the following:

Lemma 2.1. *The eigenvalue problem (1.2) has a unique principal eigenvalue λ_1 that is characterized by having a positive eigenvector (φ, ψ).*

Lemma 2.2. *If $\lambda_1 > 0$ then the system (1.1) is persistent and has at least one positive equilibrium. If $\lambda_1 \leq 0$ then $(0,0)$ is globally asymptotically stable in (1.1).*

Lemma 2.3. *If $\lambda_1 > 0$ and c and g are sufficiently small then the system (1.1) has a unique globally attracting positive equilibrium.*

Remark: In the case that $c = g = 0$ the system (1.1) is cooperative and hence generates a monotone semi-flow on appropriate spaces.

3. The case of d_1, d_2 small.

Following the approach in [23] we will establish the asymptotic behavior of the principal eigenvalue of (1.2) when $d_1,\ d_2$ are small, and in the fully cooperative case where $c \equiv g \equiv 0$ the profile of the nonnegative solutions of the corresponding steady state system for (1.1)

$$
\begin{cases}
d_1 \Delta u + r(x) v - s(x) u - a(x) u - b(x) u^2 = 0 \ \text{ in } \Omega, \\
d_2 \Delta v + s(x) u - e(x) v - f(x) v^2 = 0 \text{ in } \Omega, \\
\nabla u \cdot \nu = \nabla v \cdot \nu = 0 \ \text{ on } \partial\Omega,
\end{cases}
\tag{3.3}
$$

as well. Related results are derived in [27]. We observe that the associated kinetic system, which corresponds to (1.1), is given by

(3.4)
$$\begin{cases} u_t = r(x)V(x) - s(x)U(x) - a(x)U(x) - b(x)U^2(x) - c(x)U(x)V(x) = 0, \\ v_t = s(x)U(x) - e(x)V(x) - f(x)V^2(x) - g(x)U(x)V(x) = 0, \end{cases}$$

for each $x \in \Omega$.

For each x this system shares the same properties as (1.1) given in Lemmas 2.1, 2.2, and 2.3, which we state for convenience.

Lemma 3.1. *Set $x \in \Omega$. The linearization around (0,0) of* (3.4) *has a principal eigenvalue $\lambda_1(x)$. Moreover:*

i) *If $\lambda_1(x) \leq 0$ then all the solutions with nonnegative initial condition of* (3.4) *converge to (0,0) when $t \to \infty$.*
ii) *If $\lambda_1(x) > 0$ then* (3.4) *is persistent and has at least one positive equilibrium.*
iii) *If $c \equiv g \equiv 0$ and $\lambda_1(x) > 0$ then* (3.4) *is cooperative and admits a unique positive equilibrium which is the global attractor for all non-negative, non trivial solutions.*

Observe that when $d_1 = d_2 = 0$ the eigenvalues of the linearization around (0,0) of (3.4) are the roots of $\det(A(x) - \lambda I)$, with

$$A(x) = \begin{bmatrix} -(s(x) + a(x)) & r(x) \\ s(x) & -e(x) \end{bmatrix} \tag{3.5}$$

By a simple computation, we obtain that the maximum eigenvalue is given by

(3.6)
$$\Lambda(x) = \frac{1}{2}\left[-(s(x) + a(x) + e(x)) + \sqrt{(s(x) + a(x) - e(x))^2 + 4r(x)s(x)}\right],$$

which is positive provided that $(s(x) + a(x))e(x) - r(x)s(x) < 0$. Our first result, which is a direct application of Theorem 1.4 of [23], It states that this is indeed the necessary and sufficient condition to have a positive principal eigenvalue when d_1 and d_2 are small. (That theorem is stated in the Appendix to this paper.)

Proposition 3.2. *The principal eigenvalue λ_1 of* (1.2) *satisfies*

$$\lambda_1 \to \max_{x \in \overline{\Omega}} \Lambda(x) \text{ as } d_1, d_2 \to 0. \tag{3.7}$$

Thus, there exists a $\delta > 0$ such that if

$$\min_{x \in \overline{\Omega}}((s(x) + a(x))e(x) - r(x)s(x)) < 0, \tag{3.8}$$

the principal eigenvalue of (1.2) *is positive for all $0 < d_1, d_2 < \delta$, while if*

$$\min_{x \in \overline{\Omega}}((s(x) + a(x))e(x) - r(x)s(x)) > 0, \tag{3.9}$$

the principal eigenvalue is negative.

As a consequence of this result, if (3.9) holds, the unique nonnegative equilibrium of the system (3.3) is $(0, 0)$, and that equilibrium is globally attracting, whenever d_1, d_2 are small, while if (3.8) holds system (3.3) is persistent, and has a positive equilibrium for d_1, d_2 small. If (3.8) holds and

$c \equiv g \equiv 0$ there is a unique globally attracting positive equilibrium which we denote by (u_d, v_d) with $d = (d_1, d_2)$.

Throughout the remainder of this section we will assume that $c \equiv g \equiv 0$ in Ω, in which case the system (1.1) is cooperative.

The next result establishes the convergence of (u_d, v_d) to the unique non-negative steady state $(U(x), V(x))$ of the kinetic system, which satisfies:

$$\begin{aligned} &(U(x),V(x)) \text{ is positive where } (s(x)+a(x))e(x) - r(x)s(x) < 0, \\ &(U(x),V(x)) = 0 \text{ where } (s(x)+a(x))e(x) - r(x)s(x) \geq 0. \end{aligned} \tag{3.10}$$

Theorem 3.3. *Suppose that* (3.8) *holds. Set*

$$\Omega_0 = \{x \in \Omega \ / \ (s(x)+a(x))e(x) - r(x)s(x) < 0\}.$$

Then $(u_d, v_d) \to (U, V)$ *as* $d \to 0$ *locally uniformly in* $\Omega_0 \cup \Omega \setminus \bar{\Omega}_0$.

To prove this theorem we follow the proof of Theorem 1.5 of [23]., specifically their Proposition 5.2 (Theorem 1.5 of [23] and its hypotheses, which are listed in [23] as (A1)-(A4), are stated in the Appendix.) We should point out that assumptions (A2) and (A3) of [23] do not hold in our case, so we cannot apply that result directly. The difference is that we allow situations where the kinetic system (3.4) has a positive equilibrium for some values of $x \in \bar{\Omega}$ but not for others, whereas condition (A2) requires a positive equilibrium for the kinetic system for all x. For that reason we need to construct a version of the arguments in [23] that is local in x. Condition (A3) in [23] is used only to prove the existence of a nontrivial subsolution for a system corresponding to (3.3) which is independent of $d_1,\ d_2$. We show the existence of the analogous local subsolutions we need in our case in the next lemma.

Lemma 3.4. *Suppose that* $\tilde{x} \in \Omega_0$ *. Then there exists* $d_0 > 0$*,* $\rho_0 > 0$ *and a function* $\underline{w}^0 > 0$ *in* $B(\tilde{x}, \rho) \subset \Omega_0$ *which is a subsolution of* (3.3) *for all* $0 < d_1,\ d_2 < d_0$*.*

Proof. Let $p = (p_1, p_2)$ a positive eigenvector of $A(\tilde{x})$ with $p_1 + p_2 = 1$, associated to its principal eigenvalue $\tilde{\sigma} > 0$. Set $\varepsilon > 0$ small. We can choose $\rho > 0$ such that $\overline{B(\tilde{x}, \rho)} \subset \Omega_0$ and

$$\begin{aligned} &|a(x) - \tilde{a}| < \varepsilon,\ |r(x) - \tilde{r}| < \varepsilon, \\ &|s(x) - \tilde{s}| < \varepsilon \text{ and } |e(x) - \tilde{e}| < \varepsilon \text{ for all } x \text{ in } \overline{B(\tilde{x}, \rho)}, \end{aligned} \tag{3.11}$$

where $\tilde{a} = a(\tilde{x})$, $\tilde{r} = r(\tilde{x})$, $\tilde{s} = s(\tilde{x})$ and $\tilde{e} = e(\tilde{x})$. Set $\eta > 0$ as the principal eigenfunction associated to $\lambda > 0$, the principal eigenvalue of

$$\Delta\eta + \lambda\eta = 0 \text{ in } B(\tilde{x}, \rho),\ \eta = 0 \text{ on } \partial B(\tilde{x}, \rho), \tag{3.12}$$

with $\max_{B(\tilde{x},\rho)} \eta = 1$. We claim that we can choose $\delta, \varepsilon, \rho, d_0 > 0$ such that $\delta\eta p$ is a subsolution of (3.3) for all $d_1,\ d_2 < d_0$. For simplicity and to keep the notation consistent with that in [23], we define $F(x, u, v) = (F_1(x, u, v), F_2(x, u, v))$, with

$$F_1(x,u,v) = rv - su - au - bu^2 \text{ and } F_2(x,u,v) = su - ev - fv^2 = 0, \tag{3.13}$$

where we have omitted the variable x in a, b, e, r, s, f to shorten the expressions. Observe that

$$\begin{aligned} F_1(x,\delta\eta p) &= \delta\eta(\tilde{\sigma}p_1 + (r-\tilde{r})p_2 - (s-\tilde{s})p_1 - (a-\tilde{a})p_1 - b\delta p_1^2\eta) \\ F_2(x,\delta\eta p) &= \delta\eta(\tilde{\sigma}p_2 + (s-\tilde{s})p_1 - (e-\tilde{e})p_2 - f\delta p_2^2\eta), \end{aligned}$$

and using (3.11), we obtain that if we choose $\varepsilon > 0$ and δ small, we have that

$$\begin{aligned} F_1(x,\delta\eta p) &\geq \delta\eta(\tilde{\sigma}p_1 - \varepsilon p_2 - 2\varepsilon p_1 - b\delta p_1^2\eta) > \delta\eta\frac{\tilde{\sigma}}{2}p_1 \\ F_2(x,\delta\eta p) &\geq \delta\eta(\tilde{\sigma}p_2 - \varepsilon p_1 - \varepsilon p_2 - f\delta p_2^2) > \delta\eta\frac{\tilde{\sigma}}{2}p_2, \end{aligned} \tag{3.14}$$

Therefore, replacing these inequalities in (3.3) we obtain

$$\begin{aligned} d_1\delta p_1\Delta\eta + F_1(x,\delta\eta p) &\geq \delta\eta\left(-d_1p_1\lambda + \frac{\tilde{\sigma}}{2}p_1\right) \\ d_2\delta p_2\Delta\eta + F_2(x,\delta\eta p) &\geq \delta\eta\left(-d_2p_2\lambda + \frac{\tilde{\sigma}}{2}p_2\right), \end{aligned}$$

hence, if we set $d_0 = \frac{\tilde{\sigma}}{2\lambda}$ we obtain the desired result. □

Using this lemma we can follow the proof of Proposition 5.2 in [23]. To facilitate our exposition, we will use the same notation. Set the operators $D = \operatorname{diag}(d_1, d_2)$, $\mathcal{L} = \operatorname{diag}(\Delta, \Delta)$. Regarding the hypothesis of Proposition 5.2, we can easily check that (1.1) and F satisfy the hypothesis (A1) and (A4) in [23]. Regarding (A2), the kinetic dynamics are as stated except that the equilibrium might be 0 as stated in (3.10), but this is enough for the result to hold. To prove Theorem 3.3 we will state the needed lemmas, discussing their relationships with the lemmas in [23] leading to the proof of Proposition 5.2.

Suppose that (3.8) holds, setting $\underline{w}^0 = \eta\delta p$ as in (3.4), and $\overline{w}^0 = M$ where $M > 0$ are given in (A4) so that $F_1(x,u,v) \leq -cu$, $F_2(x,u,v) \leq -cv$ for all $0 \leq u, v \leq M$ and $x \in \Omega$, with $c > 0$ fixed. Set $K > 0$ so that $K + \partial_u F_1(x,u,v) > 0$ and $K + \partial_v F_2(x,u,v) > 0$ for all $0 \leq u, v \leq M$, and we define $z = \overline{w}^k$ as the unique solution of

$$\begin{cases} -D\mathcal{L}z + Kz = Ku + F(x,u) \text{ in } \Omega, \\ \nabla z \cdot \nu = 0 \quad \text{on } \partial\Omega, \end{cases}$$

for $u = \overline{w}^{k-1}$.

Lemma 3.5. *Suppose that* (3.8) *holds. For every k we have $\underline{w}^0 < \overline{w}^{k+1} < \overline{w}^k$, and as $k \to \infty$, $\overline{w}^k$ converges uniformly to the unique positive solution w of* (3.3)*, which satisfies $\underline{w}^0 < w < \overline{w}^k$ in Ω for all $k \geq 0$.*

Proof. We will prove that $\underline{w}^0 < \overline{w}^k$ by induction. Suppose this is true for k. Observe that $\underline{w}^0 < \overline{w}^0$ by construction. In the set $B(\tilde{x},\rho) \subset \Omega_0$ as in Lemma 3.4 $\overline{w}^{k+1}$ satisfies

$$-D\mathcal{L}(\overline{w}^{k+1} - \underline{w}^0) + K(\overline{w}^{k+1} - \underline{w}^0) = K(\overline{w}^k - \underline{w}^0) + F(x,\overline{w}^k) - F(\underline{w}^0),$$

in $B(\tilde{x},\rho)$. By the induction hypothesis $\underline{w}^0 < \overline{w}^k$, whence $K\overline{w}^k + F(x,\overline{w}^k) > 0$, hence by the strong maximum principle applied to each component, we have that $\overline{w}^{k+1} > 0$ in $\bar{\Omega}$. Thus we have

$$\begin{cases} -D\mathcal{L}(\overline{w}^{k+1} - \underline{w}^0) + K(\overline{w}^{k+1} - \underline{w}^0) > 0 \text{ in } B(\tilde{x},\rho), \\ \overline{w}^{k+1} - \underline{w}^0 > 0 \text{ in } \partial B(\tilde{x},\rho), \end{cases}$$

so that we have that $\overline{w}^{k+1} - \underline{w}^0 > 0$ in $\overline{B(\tilde{x},\rho)}$. The remainder of the proof is a standard monotone iteration argument, just as in the proof of Lemma 5.3 of [23]. We observe that

$$\begin{cases} -D\mathcal{L}(\overline{w}^1 - \overline{w}^0) + K(\overline{w}^1 - \overline{w}^0) = K\overline{w}^0 + F(x,\overline{w}^0) - K\overline{w}^0 < 0 \text{ in } \Omega, \\ \nabla[\overline{w}^1 - \overline{w}^0]\cdot\nu = 0 \text{ on } \partial\Omega, \end{cases}$$

so by the strong maximum principle we have $\overline{w}^1 < \overline{w}^0$.

Similarly, if $\overline{w}^k < \overline{w}^{k-1}$ then

$$\begin{cases} -D\mathcal{L}(\overline{w}^{k+1} - \overline{w}^k) + K(\overline{w}^{k+1} - \overline{w}^k) = \\ K\overline{w}^k + F(x,\overline{w}^k) - K\overline{w}^{k-1} - F(x,\overline{w}^{k-1}) < 0 \text{ in } \Omega, \\ \nabla[\overline{w}^{k+1} - \overline{w}^k]\cdot\nu = 0 \text{ on } \partial\Omega, \end{cases}$$

By induction, the sequence $\{\{\overline{w}^k\}\}$ is decreasing , and it is bounded below by $max\{0,\underline{w}^0(x)\}$, so by standard elliptic theory it converges to a nonnegative nontrivial solution of (3.3). Since by Lemma 2.3 the nontrivial nonnegative solution of (3.3) is unique, it coincides with the one constructed as the limit of the sequence $\{\{\overline{w}^k\}\}$.

□

Define $\overline{W}^0 = \overline{w}^0$ and $\overline{W}^{k+1} = \overline{W}^k + F(x,\overline{W}^k)$ in Ω. Following the proof of Lemmas 5.6 and 5.7 in [23] we can prove the following result.

Lemma 3.6. *Suppose that* (3.8) *holds. For every k we have*

$$\underline{w}^0 < \overline{W}^{k+1} < \overline{W}^k,$$

$\overline{W}^k$ *converges uniformly to W^∞, a nonnegative equilibrium of the kinetic system* (3.4)*, as $k \to \infty$, and $\underline{w}^0 \le W^\infty < \overline{W}^k$ in Ω for all $k \ge 0$.*

Observe that by (3.10) we have that

$$W^\infty(x) = 0 \text{ where } (s(x) + a(x))e(x) - r(x)s(x) \ge 0,$$

and $W^\infty(x) = (U(x),V(x))$ the kinetic equilibrium which is positive in $B(\tilde{x},\rho)$.

Lemma 3.7. *For each k, as $d_1,\ d_2 \to 0$ we have that $\overline{w}^k$ converges to $\overline{W}^k$ uniformly in $\bar{\Omega}$.*

The proof of this result is the same as the one of Lemma 5.5 in [23].

Proof. (*Theorem 3.3*). Observe that as a consequence of Lemma (3.7) the unique positive solution w of (3.3) converges to W_∞ as $d_1, d_2 \to \infty$ and W_∞ is positive in $B(\tilde{x},\rho)$. Since the point $\tilde{x}$ is arbitrary in the region where $(s(x) + a(x))e(x) - r(x)s(x) < 0$ we obtain the desired result. □

4. The case of d_1 and d_2 large

We will start by giving a proof of a result that is well known as a "folk theorem." It is stated in slightly more generality than is needed for the specific application. For $i = 1, \ldots, N$, let L^i denote the operator

$$L^i u = \nabla \cdot \mu_i(x)[\nabla u - u\nabla\alpha_i(x)] \quad \text{for} \quad x \in \Omega \tag{4.15}$$

with no-flux boundary conditions

$$[\nabla u - u\nabla\alpha_i] \cdot \nu = 0 \quad \text{for} \quad x \in \partial\Omega. \tag{4.16}$$

Assume that $\mu_i(x) \geq \mu_0 > 0$ on $\bar{\Omega}$ for all i. Let $A = (a_{ij}(x))$ be an $N \times N$ irreducible matrix with $a_{ij} \geq 0$ if $i \neq j$. Consider the eigenvalue problem

$$d_i L^i \varphi_i + \sum_{j=1}^{N} a_{ij}\varphi_j = \lambda\varphi_j, \quad i = 1 \ldots N \tag{4.17}$$

where $d_i > 0$ for all i and φ_i satisfies the boundary condotion (4.16) for each i. Note that if we let $\Phi_i = exp(-\alpha_i(x))\varphi_i$ then Φ_i satisfies Neumann boundary conditions so that the system (4.17) rewritten in terms of the variables Φ_i is still cooperative. Because of the classical boundary conditions the usual results on elliptic regularity and on maximum principles for cooperative systems from [25, 23] can be applied to the system for the Φ_i's, so that system and hence (4.17) will have a principal eigenvalue under suitable conditions on the domain Ω and the coefficients. This idea has been used in models for single populations without age structure or competing pairs of such populations; see for for example [7, 11].

Furthermore, we have $L^i(exp(\alpha_i(x)) = 0$ so that the principal eigenvalue of L^i is zero and the eigenfunction is a multiple of $exp(\alpha_i)$. Let $\overline{A}$ be the matrix defined by

$$\overline{A}_{ij} := \frac{\displaystyle\int_\Omega a_{ij} exp(\alpha_i)dx}{\displaystyle\int_\Omega exp(\alpha_i)dx}. \tag{4.18}$$

Denote the principal eigenvalue of (4.17) as $\lambda_1(\vec{d})$ where $\vec{d} = (d_1, \ldots, d_N)$. Denote the principal eigenvalue of $\overline{A}$ as $\overline{\Lambda}$.

Lemma 4.1. *Suppose that for some $\gamma \in (0,1)$ the coefficients of (4.17) satisfy $\alpha \in C^{2,\gamma}(\overline{\Omega})$, $\mu \in C^{1,\gamma}(\overline{\Omega})$,*

and $a_{ij} \in C^{\gamma}(\overline{\Omega})$ for $i, j = 1 \ldots N$, and that $\partial\Omega$ is of class $C^{2,\gamma}$. Suppose further that $\overline{A}$ is irreducible. If $min\{d_i : i = 1, \ldots N\} \to \infty$ then $\lambda_1(\vec{d}) \to \overline{\Lambda}$.

Proof. Choose any sequence $\vec{d_n} = (d_{1n}, \ldots d_{Nn})$ such that $min\{d_{in} : i = 1, \ldots N\} \to \infty$. Choose any subsequence, then renumber it as $\vec{d_n}$. Let λ_n be the principal eigenvalue of (4.17) corresponding to $\vec{d_n}$ and let $\varphi_{in}(x) > 0$ be the ith component of the eigenvector, where the eigenvector is normalized by $max\{\varphi_{in}(x) : x \in \overline{\Omega},\ i = 1, \ldots, N\} = 1$. Integrating the ith equation of

(4.17) over Ω and summing over i yields

$$\lambda_n \int_\Omega \sum_{i=1}^N \varphi_{in}(x)dx = \int_\Omega \sum_{i,j=1}^N a_{ij}(x)\varphi_{jn}(x)dx \le A_1 \int_\Omega \sum_{i=1}^N \varphi_{in}(x)dx$$

where A_1 is a constant depending only on A. It follows that λ_n is uniformly bounded from above. Similarly, λ_n is uniformly bounded from below. Thus, any subsequence of λ_n itself has a convergent subsequence. It then follows from dividing the ith equation of (4.17) by d_{in} that $L^i\varphi_{in}$ is uniformly bounded, and $L_i\varphi_{in} \to 0$ as $n \to \infty$. By elliptic regularity the sequence φ_{in} is uniformly bounded in $W^{2,p}(\Omega)$ for any $p < \infty$, then by Sobolev embedding it has a subsequence that is convergent in $C^1(\overline{\Omega})$ and weakly convergent in $W^{2,p}(\Omega)$. This will be true for any i. Taking a further subsequence if necessary and renumbering again, we obtain a sequence where $\lambda_n \to \lambda^*$ for some λ^* and $\varphi_{in} \to \varphi_i^*$ for all i, with $L_i\varphi_i^* = 0$. We then must have $\varphi_i^* = c_i exp(\alpha_i)$ for some nonnegative constant c_i, and with $max\{\varphi_i^*(x) : x \in \overline{\Omega},\ i = 1 \dots N\} = 1$. Integrating (4.17) over Ω and using the no-flux boundary conditions gives

$$\sum_{j=1}^N \left[\int_\Omega a_{ij}(x)\varphi_j^*(x)dx\right] = \lambda^* \int_\Omega \varphi_i^*, \quad i = 1 \dots N, \tag{4.19}$$

so that

$$\sum_{j=1}^N \left[\frac{\displaystyle\int_\Omega a_{ij}(x)exp(\alpha_j(x))dx}{\displaystyle\int_\Omega exp(\alpha_i(x))dx}\right] c_j = \lambda^* c_i, \quad i = 1 \dots N. \tag{4.20}$$

It follows that $(c_1, \dots, c_N)$ must be a nontrivial nonnegative eigenvector of $\overline{A}$ with the normalization prescribed by $max\{c_i exp(\alpha_i(x)) : x \in \overline{\Omega},\ i = 1, \dots N\} = 1$. These last conditions uniquely determine the limits of the subsequence of the original subsequence $\{\lambda(d_n), \vec{\varphi}_n\}$. Since every subsequence of the original sequence $\{\lambda(d_n), \vec{\varphi}_n\}$ has a subsequence converging to the values determined by (4.20), the same must be true for the original sequence. Since the original sequence of values $\{\vec{d_n}\}$ could be any increasing sequence that approaches infinity as $n \to \infty$, the conclusion of the lemma follows.

□

In the specific system (1.1) that we consider, $L^i = \Delta$, so that α_i and μ_i are constants. In that case we have $\overline{A}_{ij} = \overline{a}_{ij}$, where $\overline{a}_{ij}$ is the average of a_{ij} over Ω. Denote the averages of the coefficients in (1.1) by $\bar{r}$, $\bar{s}$, etc. Calculations analogous to those in (3.5),(3.6) and the related discussion then yield the following:

Corollary 4.2. *Suppose that the hypotheses of Lemma 4.1 are satisfied. There exists a $D > 0$ such that if*

$$\bar{e}(\bar{s} + \bar{a}) - \bar{r}\bar{s} < 0,$$

the principal eigenvalue λ_1 of(1.2)is positive for all $d_1, d_2 > D$, while if

$$\bar{e}(\bar{s} + \bar{a}) - \bar{r}\bar{s} > 0,$$

the principal eigenvalue is nonpositive.

Remark: In the ODE system corresponding to (1.1) with coefficients averaged over Ω, one can compute R_0 as $\bar{r}\bar{s}/[\bar{e}(\bar{s}+\bar{a})]$ via the methods of [29]. The first inequality in Corollary 4.2 is equivalent to $R_0 > 1$ while the second is equivalent to $R_0 < 1$. By writing $R_0 = [\bar{r}/(\bar{s}+\bar{a})][\bar{s}/\bar{e}]$ we can interpret the condition for persistence as a saying that that products of the ratios of the growth terms over the loss terms for adults and juveniles should be greater than 1 for persistence.

5. General diffusion rates

Case1: Persistence or extinction for all diffusion rates

Proposition 5.1. *If*

$$\int_\Omega \sqrt{rs}\,dx - \frac{1}{2}\int_\Omega (s+a+e)dx > 0 \tag{5.21}$$

then $\lambda_1 > 0$ *for all positive diffusion rates.*

If

$$min_{x\in\overline{\Omega}}[4(s(x)+a(x))e(x) - (r(x)+s(x))^2] > 0 \tag{5.22}$$

then $\lambda_1 < 0$ *for all positive diffusion rates.*

Proof. If we divide the first equation in (1.2) by φ and integrate over Ω, using Green's formula to integrate the term $\Delta\varphi/\varphi$, we obtain the inequality

$$|\Omega|\lambda_1 \geq \int_\Omega r\left(\frac{\psi}{\varphi}\right)dx - \int_\Omega (s+a)dx. \tag{5.23}$$

Similarly, if we divide the second equation by ψ and integrate we obtain

$$|\Omega|\lambda_1 \geq \int_\Omega s\left(\frac{\varphi}{\psi}\right)dx - \int_\Omega e\,dx. \tag{5.24}$$

If we add (5.23) and (5.24) and divide by 2 we obtain

$$\lambda_1 \geq \frac{1}{2|\Omega|}\left(\int_\Omega \left[r\left(\frac{\psi}{\varphi}\right) + s\left(\frac{\varphi}{\psi}\right)\right]dx - \int_\Omega (s+a+e)dx\right). \tag{5.25}$$

By Cauchy's inequality, $rz + sz^{-1} \geq 2\sqrt{rs}$ for all $z > 0$, so from (5.25) we obtain

$$\lambda_1 \geq \frac{1}{|\Omega|}\left[\int_\Omega \sqrt{rs}\,dx - \frac{1}{2}\int_\Omega (s+a+e)dx\right] \tag{5.26}$$

so $\lambda_1 > 0$ if (5.21) holds, so the first part of Proposition 5.1 holds. Going in the other direction, if we multiply the first equation of (1.2) by φ and integrate, using integration by parts on the $\varphi\Delta\varphi$ term, and similarly multiply the second equation by ψ and integrate, then add the results, we get

$$\lambda_1 \int_\Omega (\varphi^2 + \psi^2)dx \leq \int_\Omega [-(s+a)\varphi^2 + (r+s)\varphi\psi - e\psi^2)dx]. \tag{5.27}$$

The integrand on the right side of (5.27) is a quadratic form in φ and ψ, which will be negative definite if

$$4(s+a)e > (r+s)^2, \tag{5.28}$$

so $\lambda_1 < 0$ if (5.22) holds, which proves the second part of Proposition 5.1. □

Remarks: Note that the first integral in (5.21) is what appears in the formula for the Bhattacharyya coefficient [2, 12], which is used to compare how well probability distributions match each other. Specifically, if two probability distributions P and Q have probability density functions $p(x)$ and $q(x)$ for $x \in U \subset \mathbb{R}^n$, the Bhattacharyya coefficient is

$$BC(P,Q) = \int_U \sqrt{p(x)q(x)}dx.$$

For any P and Q, $0 \leq BC(P,Q) \leq 1$. If $BC(P,Q) = 1$ then P and Q are the same, that is, $p = q$ a.e. If $BC(P,Q) = 0$ then the supports of p and q are disjoint. If we write $r(x) = r_0\rho(x)$ and $s(x) = s_0\sigma(x)$ so that $\int_\Omega \rho(x) = \int_\Omega \sigma(x) = 1$, then we can compute $r_0 = \bar{r}|\Omega|$ and $s_0 = \bar{s}|\Omega|$. We can treat ρ and σ as if they were probability density functions for distributions R and S. We then have

$$\int_\Omega \sqrt{rs}dx = |\Omega|\sqrt{\bar{r}\bar{s}}BC(R,S). \tag{5.29}$$

The maximum of $BC(R,S)$ is 1, corresponding to the case where r and s are multiples of each other, and the minimum is 0, corresponding to the case where the supports of r and s are disjoint. Thus, the degree to which ρ and σ match each other has a strong impact on the estimate for λ in (5.26).

Using (5.29) and the fact that $BC(R,S) \leq 1$ in (5.21) shows that (5.21) implies $2\sqrt{\bar{r}\bar{s}} > [(\bar{s}+\bar{a}) + \bar{e}]$. Squaring both sides and using Cauchy's inequality implies $\bar{e}(\bar{s}+\bar{a}) - \bar{r}\bar{s} < 0$ as in the first case of Corollary 4.2. Similarly, if (5.21) holds then $2\sqrt{r(x)s(x)} > (s(x)+a(x)) + e(x)$ for some $x \in \Omega$, and it then follows in the same way that the inequality in the first case of Proposition 3.2 holds. If (5.22) hplds then (5.28) holds, and then by Cauchy's inequality the second case of Proposition 3.2 holds. Thus, the conditions (5.21), (5.22) in Proposition 5.1, which imply $\lambda_1 > 0$ or $\lambda_1 < 0$ for all diffusion rates, also imply some of the corresponding conditions we have obtained for either large or small diffusion rates.

In the situation where the spatial distributions of habitat quality r for reproduction by adults and s for survival and maturation of juveniles into adults are perfectly correlated, so that $r(x) = r_1 s(x)$ for some constant r_1, the eigenvalue problem (1.2) can be rewritten as a weighted symmetric eigenvalue problem by multiplying the second equation of (1.2) by r_1, which yields

$$\begin{aligned} &d_1\Delta\varphi(x) - (s(x)+a(x))\varphi + r(x)\psi = \lambda\varphi \\ &d_2 r_1 \Delta\psi + r(x)\varphi - r_1 e(x)\psi = \lambda r_1 \psi. \end{aligned} \tag{5.30}$$

The principal eigenvalue for (5.30) has a variational characterization of λ_1 as

(5.31)
$$\lambda_1 = \max_{\varphi,\psi \in W^{1,2}(\Omega)} \frac{\displaystyle\int_\Omega (-d_1|\nabla\varphi|^2 - d_2 r_1|\nabla\psi|^2 - (s+a)\varphi^2 + 2r\varphi\psi - r_1 e\psi^2)dx}{\displaystyle\int_\Omega (\varphi^2 + r_1\psi^2)dx}.$$

It follows in that case that λ_1 is decreasing in both d_1 and d_2, so that slower diffusion is advantageous.

Case 2: Asymptotic behavior for large reproductive rates

Suppose that $r(x) = nr_0(x)$ and that $s(x)r_0(x) > 0$ for $x \in \Omega_0$ with $\Omega_0 \neq \emptyset$, so there is a region where both the adult reproduction rate and the juvenile maturation rate are positive. The factor n scales the reproductive rate of adults in regions where $r_0(x) > 0$. For any fixed diffusion rates it turns out that for sufficiently large values of the scaling coefficient n the principal eigenvalue of (1.2) is positive so the system (1.1) is persistent. We will characterize the asymptotic behavior of the principal eigenvalue as $n \to \infty$. If we make the further assumption that $g \equiv c \equiv 0$ then the system (1.1) is cooperative, so for n large enough that the principal eigenvalue of (1.2) is positive, (1.1) has a unique positive equilibrium, and we will characterize the behavior of that equilibrium as $n \to \infty$ as well in that case.

Let λ_1^n denote the principal eigenvalue for (1.2) with $r(x) = nr_0(x)$. Observe that since $s(x)r_0(x) > 0$ for $x \in \Omega_0$ and $\Omega_0 \neq \emptyset$, Proposition 5.1 implies that $\lambda_1^n > 0$ for n sufficiently large, and in fact by (5.26), $\lambda_1^n \to \infty$ as $n \to \infty$. The following proposition states the asymptotic behavior of λ_1^n as $n \to \infty$.

Proposition 5.2. *If $r(x) = nr_0(x)$ and $s(x)r_0(x) > 0$ for $x \in \Omega_0$ with $\Omega_0 \neq \emptyset$, then*
$$\lim_{n\to\infty} \frac{\lambda_1^n}{\sqrt{n}} \to \max_{x\in\overline{\Omega}}(\sqrt{r_0(x)s(x)}).$$

Proof. We start by noting that if λ_1^n, (φ_n, ψ_n) are the principal eigenvalue and corresponding eigenfunction of (1.2) for $r(x) = nr_0(x)$, then $\lambda_1^n/\sqrt{n}$, $\widehat{\varphi}_n = \varphi_n$, $\widehat{\psi}_n = \sqrt{n}\psi_n$ are the principal eigenvalue and eigenfunction of the problem

(5.32)
$$\begin{cases} \dfrac{d_1}{\sqrt{n}}\Delta\widehat{\varphi} - \dfrac{(s(x)+a(x))}{\sqrt{n}}\widehat{\varphi} + r_0(x)\widehat{\psi} &= \widehat{\lambda}\widehat{\varphi} \ \text{ in } \Omega, \\ \dfrac{d_2}{\sqrt{n}}\Delta\widehat{\psi} - \dfrac{e(x)}{\sqrt{n}}\widehat{\psi} + s(x)\widehat{\varphi} &= \widehat{\lambda}\widehat{\psi} \ \text{ in } \Omega, \\ \nabla\widehat{\varphi}\cdot\nu = \nabla\widehat{\psi}\cdot\nu &= 0 \ \text{ on } \partial\Omega. \end{cases}$$

Considering the elliptic operators $L_1 u = d_1\Delta u - (s(x) - a(x))u$ and $L_2 v = d_2\Delta v - e(x)v$, $D = \operatorname{diag}\left(\frac{1}{\sqrt{n}}, \frac{1}{\sqrt{n}}\right)$ and $\mathcal{L} = \operatorname{diag}(L_1, L_2)$ the system (5.32) satisfies the hypothesis of Theorem 1.4 of [23]. Thus as $n \to \infty$

$$\frac{\lambda_1^n}{\sqrt{n}} \to \max_{x \in \overline{\Omega}} \lambda(A(x)),$$

where

$$A(x) = \begin{pmatrix} 0 & r_0(x) \\ s(x) & 0 \end{pmatrix},$$

which has eigenvalues $\pm\sqrt{r_0(x)s(x)}$, from whence the result follows. □

In the case where $g \equiv c \equiv 0$ so that (1.1) is cooperative, Lemma 2.3 implies that (1.1) has a unique positive equilibrium if the principal eigenvalue of (1.2) is positive. The next result states the asymptotic behavior of the unique positive equilibrium of (1.1) for n large in that case.

Proposition 5.3. *Suppose the hypotheses of Proposition 5.2 are satisfied and that $g \equiv c \equiv 0$. Let (u_n, v_n) be the unique positive solution of* (3.3)*. Then $n^{-\frac{2}{3}}(u_n, v_n) \to (U^\infty, V^\infty)$ uniformly in $\bar{\Omega}$ where*

(5.33)

$$U^\infty(x) = \frac{r_0(x)^{\frac{2}{3}}}{b(x)^{\frac{2}{3}}}\frac{s(x)^{\frac{1}{3}}}{f(x)^{\frac{1}{3}}}, \quad V^\infty(x) = \frac{s(x)^{\frac{2}{3}}}{f(x)^{\frac{2}{3}}}\frac{r_0(x)^{\frac{1}{3}}}{b(x)^{\frac{1}{3}}} \text{ when } s(x)r_0(x) > 0$$

$$U^\infty(x) = 0, V^\infty(x) = 0 \text{ when } s(x)r_0(x) = 0.$$

Proof. To prove this result we use a different scaling. After some simple computations we obtain that

$$(w_n, z_n) = \left(u_n n^{-\frac{2}{3}}, v_n n^{-\frac{1}{3}}\right),$$

is the unique positive solution of the scaled system

$$\text{(5.34)} \qquad \begin{cases} n^{-\frac{2}{3}}[d_1\Delta w - (s(x)+a(x))w] + r_0(x)z - b(x)w^2 = 0 \ \text{ in } \Omega, \\ \\ n^{-\frac{1}{3}}[d_2\Delta z - e(x)z] + s(x)w - f(x)z^2 = 0 \ \text{ in } \Omega, \\ \nabla w \cdot \nu = \nabla z \cdot \nu = 0 \ \text{ on } \partial\Omega. \end{cases}$$

We set the operators

$$L_1 w = d_1\Delta w - (s(x)+a(x))w \text{ and } L_2 z = d_2 \Delta z - e(x)z,$$

$$D = \operatorname{diag}\left(n^{-\frac{2}{3}}, n^{-\frac{1}{3}}\right) \text{ and } \mathcal{L} = (L_1, L_2), \text{ and}$$

$$F(x, w, z) = (r_0(x)z - b(x)w^2, s(x)w - f(x)z^2).$$

To prove the proposition we can follow the same steps as in the proof of Theorem (3.3). Indeed, the principal eigenvalue of the linearization around $(0,0)$ of the associated kinetic system of (5.34) is $\sqrt{s(x)r_0(x)}$, and when it is positive, the kinetic equilibrium is given by the right hand side of (5.33). This concludes the proof.

□

6. Conclusions

The most fundamental conclusion from our analysis is that reaction-diffusion models for populations with stage structure in spatially heterogeneous environments do not necessarily predict that slower diffusion is advantageous for persistence. This is in contrast to the case where populations are structured only by spatial location, where a version of the reduction principle [1] applies, and in a competition between otherwise identical populations with different diffusion rates the prediction is that "the slower diffuser wins" [13, 17]. The mechanism underlying this observation is that in our structured model, the regions where it is possible for adults to produce offspring may be separated from those where juveniles can survive and mature into adults. The conditions we find that imply persistence generally require that the product $r(x)s(x)$ of the reproductive rate of adults and the maturation rate of juveniles be sufficiently large relative to their death rates. For slow diffusion, the condition for persistence is that $r(x)s(x) > e(x)(s(x) + (a(x))$ at some point $x \in \Omega$. For fast diffusion it is $\bar{r}\bar{s} > \bar{e}(\bar{s} + \bar{a})$ where $\bar{r}, \bar{s}, \bar{e}$ and $\bar{a}$ are the spatial averages of those quantities. If the spatial distributions of r and s are closely correlated and are large in a few places but small in most, so that the maximum of rs is large but the averages $\bar{r}$ and $\bar{s}$ are small, the condition for persistence with slow diffusion may be satisfied while the condition with fast diffusion may fail. In that type of environment slow diffusion is clearly favored. Furthermore, if r and s are perfectly correlated in the sense that they are multiples of each other, the principal eigenvalue determining the growth rate of the population at low density is decreasing with respect to the diffusion rates, as in the case of unstructured populations in heterogeneous environments. On the other hand, if both r and s are large on some regions but very small outside of them, and the regions where they are large are disjoint (that is, separated from each other) then the product rs could be small everywhere but the averages $\bar{r}$ and $\bar{s}$ could be large. In that case, the condition for persistence with small diffusion may fail but the condition with fast diffusion may be satisfied, so that fast diffusion is favored.

We found that a sufficient condition for persistence for all diffusion rates is

$$\int_\Omega \sqrt{rs}\, dx - \frac{1}{2}\int_\Omega (s + a + e)dx > 0.$$

The first term can be written as $\sqrt{\bar{r}\bar{s}}|\Omega|BC(r(x)/\bar{r}, s(x)/\bar{s})$ where BC denotes the Bhattacharrya coefficient (see [2, 12]), which measures how closely probability densities match each other. For distributions that are equal to each other $BC = 1$ but for distributions that are mutually exclusive in the sense that the regions where they are positive do not intersect, $BC = 0$. This observation again shows that the degree to which the spatial distributions of r and s match each other is significant in determining the predictions of the model (1.1).

Finally, we found that if we scale the adult reproductive rate as $r(x) = nr_0(x)$ and there is some overlap between the distributions of r and s so that $s(x)r_0(x) > 0$ on some subset of Ω with positive measure, then for any fixed diffusion rates the system (1.1) will be persistent if n is sufficiently large. That means a population with any diffusion rates can persist if there is even a modest overlap between the regions where adults can reproduce and where juveniles can mature, provided that the reproductive rate of adults is sufficiently large. We characterized the asymptotic behavior as $n \to \infty$ of the principal eigenvalue of (1.2). In the cooperative case where $g \equiv c \equiv 0$ the system (1.1) will have a unique positive equilibrium if it is persistent, and in that case we also characterized the asymptotic behavior as $n \to \infty$ of the equilibrium.

There are several directions for further research on the general topic of this paper. It would be of interest to take the approach of [13] and consider competition between two stage structured populations described by systems such as (1.1) that differ only in their diffusion rates. That would be somewhat challenging because it would involve systems of four equations, but at least in the cooperative case where $c = g = 0$ the general theory of monotone dynamical systems and some of the ideas and methods of [9] would apply. It would also be interesting to consider models with explicit age structure, as introduced in [16] and studied in [22, 24]. Finally, it would be interesting but challenging to consider the case of time-periodic environments with spatial heterogeneity. Temporal variation alone is sufficient to cause faster diffusion to be favored in such environments in some cases (see [21]) but even without stage structure the time dependent case is challenging and there are many open questions.

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7. Appendix

In [23] the authors considered the equilibria and dynamics of the system

$$\begin{cases} \dfrac{\partial u}{\partial t} = D\mathcal{L}u + F(x,u) \ \text{ in } \Omega \times (0,\infty), \\ \\ \mathcal{B}u = 0 \ \text{ on } \partial\Omega \times (0,\infty) \end{cases} \tag{7.35}$$

where $u = (u_1, \dots, u_n)^T$ is a vector of smooth functions, Ω is a bounded domain in $\mathbb{R}^N$ with smooth boundary, $u = (u_1(x), \dots u_n)^T$ is a vector of smooth functions, $D = diag(d_1, \dots d_n)$ is a diagonal matrix of positive constants, $\mathcal{L} = diag(L^1, \dots L^n)$ is a diagonal matrix of second order uniformly strongly elliptic operators of the form

$$L^i = \sum_{j,k=1}^{N} \alpha^i_{jk} \frac{\partial^2}{\partial x_j \partial x_k} + \sum_{j=1}^{N} \beta^i_j \frac{\partial}{\partial x_j} + \gamma^i$$

with smooth coefficients, , and $\mathcal{B} = (B_1, \dots B_n)$ where for each i, B_i defines a Dirichlet, Neumann, or Robin boundary condition. (They include Neumann as a case of Robin.) They also considered the associated linearized problem, which they wrote as

$$\begin{cases} D\mathcal{L}\phi + Au\phi = -\lambda\phi \ \text{ in } \Omega, \\ \\ B\phi = 0 \ \text{ on } \partial\Omega, \end{cases} \tag{7.36}$$

where $A = ((a_{ij}))$ iis an $n \times n$ matrix of smooth functions with $a_{ij} \geq 0$ for $i \neq j$ and $\phi = (\phi_1(x), \dots \phi_n(x))^T$ is a vector of smooth functions.

NOTE: In our notation we use the opposite sign convention to the one used in [23], so that what they denote as $-\lambda$, we denote as λ.

For details on the specific smoothness assumptions requires see [23]. Under those assumptions, by the Perron-Frobenius theorem, for each $x \in \Omega$ the matrix A has a principal eigenvalue which in our notation we denote as $\Lambda(x)$. The first major result of [23] is their Theorem 1.4, which can be stated as

Theorem 7.1. *(Theorem 1.4 of* [23]*) The principal eigenvalue* λ_1 *of the system* (7.36) *with Dirichlet, Neumann,or Robin boundary conditions satisfies*

$$\lim_{max\{d_1,\ldots,d_n\}\to 0} \lambda_1 = -\max_{x\in\bar{\Omega}} \Lambda(x).$$

Except for the adjustments needed for our different notation, that theorem applies directly to our system in all cases.

The second major result of [23] gives conditions under which the system (7.35) with small diffusion rates has the same dynamics as the kinetic system

$$\frac{dU_i}{dt} = F_i(x, U_1, \ldots, U_n) \text{ for } i = 1, \ldots, n. \tag{7.37}$$

The conditions can be stated as
(A1) $\partial F_i/\partial U_j \geq 0$ (i.e. systems (7.35) and (7.37) are cooperative),
(A2) For each $x_0 \in \bar{\Omega}$ the system (7.37) has a unique positive equilibrium $\alpha(x_0)$ which is globally asymptotically stable among positive solutions and is locally linearly stable, and $\alpha(x)$ depends continuously on x,
(A3) There exists $\delta_0 > 0$ such that for $j = 1, \ldots, n$, $F_j(x, U)/U_j > \delta_0$ for all $x \in \bar{\Omega}$ provided $0 < U_i \leq \delta_0$ for $i = 1, \ldots, n$,
(A4) There exist $\delta_0', M > 0$ such that for $j = 1, \ldots, n$, $F_j(x, U)/U_j < -\delta_0'$ for all $x \in \bar{\Omega}$ provided $U_i \geq M$ for $i = 1, \ldots, n$.

The second main theorem of [23] is their Theorem 1.5, which can be stated as

Theorem 7.2. *(Theorem 1.5 of* [23]*) Under conditions (A1)-(A4), if* $max_{1\leq i\leq n}\{d_i\}$ *is sufficiently small,* (7.35) *has a unique positive steady state* $\tilde{w}$ *which is globally asymptotically stable among nontrivial nonnegative solutions. Furthermore,* $\tilde{w}(x) \to \alpha(x)$ *uniformly on* $\bar{\Omega}$ *as* $max_{1\leq i\leq n}\{d_i\} \to 0$*, where* $\alpha(x)$ *is the positive equilibrium of* (7.37)*.*