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SELECTION OF SLOW DIFFUSION IN A REACTION DIFFUSION MODEL: LIMITING CASES

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Introduction. A common phenomenon, observed in a wide variety of models for the dispersal of organisms, is that dispersal rates tend to be lower if the environment is spatially heterogeneous [**10**]. In an attempt to understand this, Dockery et al. [**3**] proposed a reaction diffusion model for the evolution of n different phenotypes of a species, where the only phenotypic difference is in the diffusion rate. It is assumed that the per-capita net rate of increase of each phenotype, denoted by a, is not a constant. The diffusion rates are $d_1 < d_2 < \cdots < d_n$, the environment is a region $\Omega \subset \mathbf{R}^k$. It is assumed that Ω is a bounded domain with smooth boundary, across which there is no migration. In this model, the equation for the density $u_i(x,t)$ of phenotype i is:

$$\frac{\partial u_i}{\partial t} = d_i \Delta u_i + \left[a(x) - \sum_{j=1}^{n} u_j \right] u_i \quad \text{in } \Omega, \quad i = 1, \dots, n. \tag{1}$$

with homogeneous Neumann boundary condition: $\partial u_i / \partial \nu = 0$ and prescribed initial values $u_i(x,0)$ which are nonnegative functions in Ω.

One of the basic results of [**3**] is that the only nonnegative equilibria of this system are semi-trivial solutions, i.e., they have the form $\tilde{U}^i(x)$, where the jth component is zero for $j \neq i$ and the ith component $\tilde{U}^i_i(x)$ is the positive solution of

$$\begin{aligned} d_i \Delta u + [a(x) - u]\, u &= 0 \quad \text{in } \Omega \\ \frac{\partial u}{\partial \nu} &= 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{2}$$

It was also shown that $\tilde{U}^1(x)$ is linearly asymptotically stable and $\tilde{U}^i(x)$ is unstable for $i = 2, \dots, n$. Furthermore, if $n = 2$ and the

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first component of the initial condition is not identically zero, then the solution tends to $\tilde{U}^1(x)$ as $t \to \infty$. In other words, $\tilde{U}^1(x)$ is the global attractor for the set of initial conditions which lie in the interior of the positive cone.

In this sense, one sees that the spatial heterogeneity, $a(x)$ nonconstant, selects for the phenotype with the slowest diffusion rate. Dockery et al. conjectured that this phenomenon is true for all n. The purpose of this paper is to verify this conjecture in some special limiting cases.

We begin with the observation that the same techniques used in [**3**] apply to the more general setting where the diffusion rates are allowed to be spatially dependent. More precisely, we will consider equations of the form

$$\frac{\partial u_i}{\partial t} = \nabla.(d_i(x)\nabla u_i) + \left[a(x) - \sum_{j=1}^{n} u_j\right] u_i \tag{3}$$

defined on a bounded domain $\Omega \subset \mathbf{R}^k$ with smooth boundary and homogeneous Neumann boundary conditions. Throughout this work it is assumed that $a \in C^{2+\alpha}(\overline{\Omega})$ is not constant, $d_j \in C^{1+\alpha}(\overline{\Omega})$ for $j = 1, \dots, n$ with $0 < d_0 \leq d_1(x) \leq d_2(x) \leq \cdots \leq d_n(x)$ and unless explicitly stated otherwise, $d_i \neq d_j$ for $i \neq j$. We also assume $\int_\Omega a(x)\,dx > 0$. This condition refers to the quality of the environment and guarantees the existence of nonzero semi-trivial solutions for all diffusions $d_i(x)$ under consideration. We prove the following three results.

Theorem 2.1. *The only nonnegative equilibria of* (3) *are semi-trivial solutions* $\tilde{U}^i(x)$, *with* $\tilde{U}^i_i(x) \not\equiv 0$. *Furthermore,* $\tilde{U}^1(x)$ *is linearly stable and* $\tilde{U}^i(x)$ *is unstable for* $i = 2, \dots, n$.

Thus, the equilibrium structure is not changed by allowing the diffusion coefficients to be spatially dependent. It is easy to see that equation (3) reduces to a single equation in the case that $d_1(x) = d_2(x) = \cdots = d_n(x)$. Using this observation, one can verify the conjecture in the case that the diffusion coefficients are close to one of two values. An example of the type of result that can be proven is the following.

Theorem 4.2. *Let $n = 3$ and assume $|d_1(x) - d_2(x)|$ is sufficiently small for all $x \in \Omega$. Then, $\tilde{U}^1(x)$ is the global attractor for the set of initial conditions which lie in the interior of the positive cone.*

A biological interpretation of this result is as follows. Given two phenotypes u_2 and u_3 with diffusion rates $d_2 < d_3$, the results of [**3**] imply that u_2 will dominate. Theorem 4.2 implies that if u_2 undergoes a mutation that produces a phenotype u_1 which diffuses at a slightly smaller rate, then the slower diffuser u_1, in turn, becomes dominant.

In the proof, it will become clear that Theorem 4.2 is just a prototype of a variety of theorems that can be proven; however, they all require that the diffusion rates are appropriately clustered about two primary values.

At the other extreme is the case where the diffusion coefficients are quite different. A particular subset of these is where some of the diffusion coefficients are extremely large. Again, an example of the typical result that can be proven is the following.

Theorem 5.3. *Assume that $\inf_{x\in\Omega} d_i(x)$ are sufficiently large for $i = 3, \dots, n$. Then, $\tilde{U}^1(x)$ is the global attractor for the set of initial conditions which lie in the interior of the positive cone.*

An outline for the paper is as follows. In Section I we review some results for the single equation

$$\frac{\partial u}{\partial t} = \nabla.(d(x)\nabla u) + \big[a(x) - u\big]u \tag{4}$$

as these provide the basic information on the existence and uniqueness of stationary solutions, their stability properties and the large time behavior that will be used for the analysis of system (3). In Section II we study the special case of two phenotypes, for which we prove the convergence to the slowest equilibrium for all diffusions under consideration, and we construct a family of comparison functions that control the global dynamics. The proof of Theorem 4.2 is presented in Section IV. In Section V we prove Theorem 5.3. This involves the introduction of $u = u_1$, $v = u_2$, $w_i = u_{i+2}$ for $i = 1, \dots, n-2$, $\xi_i = \langle w_i \rangle$,

$w = \xi + z$, $\sigma = \sum_{j=1}^{n-2} \xi_j$ and the shadow system

$$
\begin{aligned}
\frac{\partial u}{\partial t} &= \nabla.(d_1(x)\nabla u) + [a(x) - (u+v) - \sigma]u \\
\frac{\partial v}{\partial t} &= \nabla.(d_2(x)\nabla v) + [a(x) - (u+v) - \sigma]v \\
\dot{\xi}_i &= \left[\frac{1}{|\Omega|}\int_\Omega \big(a(x) - (u+v)\big)\,dx - \sigma\right]\xi_i, \quad i = 1, \dots, n-2.
\end{aligned} \tag{5}
$$

The dynamics of this system can be described in detail and we shall show that it approximates the dynamics of (3) in the case that $d_i(x)$ is sufficiently large in all of Ω for $i = 3, \dots, n$.

I. The scalar equation. We begin with a review of some basic properties of solutions of the single equation

$$
\frac{\partial u}{\partial t} = \nabla.(d(x)\nabla u) + [a(x) - u]u \quad \text{in } \Omega \tag{6}
$$

with $\partial u/\partial \nu = 0$ on $\partial\Omega$ and $u(x, 0) = u_0(x) \geq 0$.

This equation is well understood in the case of a constant diffusion coefficient, see [1]. The case of a variable diffusion coefficient is similar and we include the proofs only for the sake of completeness. We begin by considering a general smooth function $a(x)$. At the end of the section we prove that the positivity of its integral implies the existence of a unique positive steady state of (6).

Let λ_0 be the first eigenvalue of the self-adjoint operator defined by

$$
L\phi = \nabla.(d(x)\nabla\phi) + a(x)\phi
$$

with zero Neumann boundary conditions, which is the linearization of the righthand side of (6) around $u \equiv 0$. If $\lambda_0 \leq 0$, then all solutions of (6) tend to 0 as $t \to \infty$, see Proposition 1.1 below. If $\lambda_0 > 0$, there exists a unique positive stationary solution which is the global attractor for the flow. This is the content of Proposition 1.2.

The result in [**1**] is stated in terms of an eigenvalue problem with a weight, which is equivalent to the formulation given in [**9**]. We have chosen to present a direct proof, as it gives information on the dynamics and the convergence to equilibrium. Moreover, we prove that under the assumption $\int_\Omega a(x)\,dx > 0$, there exists a positive stationary solution for *any* positive diffusion coefficient $d(x)$.

I.1. *Existence and uniqueness of a positive stationary solution.* The first observation is that the form of the reaction term guarantees uniqueness of positive stationary solutions of (6).

Lemma 1.1. *The elliptic problem*

$$\begin{aligned} \nabla.(d(x)\nabla u) + [a(x) - u]u &= 0 \quad \text{in } \Omega \\ \frac{\partial u}{\partial \nu} &= 0 \quad \text{on } \partial\Omega \end{aligned} \tag{7}$$

has at most one positive solution.

Proof. Note that if $u_1(x)$, $u_2(x)$ are any two solutions of (7), then

$$\int_\Omega d(x)\nabla u_1.\nabla u_2\,dx = \int_\Omega [a(x) - u_1]u_1u_2\,dx = \int_\Omega [a(x) - u_2]u_1u_2\,dx$$

from which it follows that

$$\int_\Omega u_1u_2(u_1 - u_2)\,dx = 0.$$

If, moreover $0 < u_1 \leq u_2$, then necessarily $u_1 = u_2$.

Now let $a^* := \max\{a(x) : x \in \overline{\Omega}\}$. Note that any nonnegative solution $u(x)$ of (7) must satisfy $u(x) \leq a^*$ for all $x \in \Omega$. Moreover, $\overline{u}(x) := a^*$ is an upper solution. Using the monotone iteration scheme starting at $\overline{u}$, we get a nonnegative solution $\tilde{u}(x)$. If $u(x) \geq 0$ is another solution of (7), then, by the maximum principle, $u(x) \leq \tilde{u}(x)$ in Ω. Therefore, $u(x) = \tilde{u}(x)$ for all $x \in \Omega$, which establishes the uniqueness. $\square$

Remark 1.1. The above argument works for reaction terms of the form $f(x,u)u$, such that $\partial f/\partial u(x,0) < 0$ (> 0) for all x and all u.

A sufficient condition for the existence of the positive stationary solution is stated in terms of λ_0, the first eigenvalue of the linear operator L defined above.

Lemma 1.2. *If $\lambda_0 > 0$, then equation* (7) *has a unique positive solution $\tilde{u}(x)$.*

Proof. By Lemma 1.1, it is enough to construct a strictly positive lower solution. We use the analogue of the comparison functions for the constant diffusion case, see [**1**].

Let ϕ_0 be the positive eigenfunction associated to λ_0, and take $r > 0$. Since

$$\nabla.(d(x)r\nabla\phi_0) + [a(x) - r\phi_0]r\phi_0 = r\phi_0(\lambda_0 - r\phi_0)$$

it follows that $\underline{u}(x) = r\phi_0(x)$ is a positive lower solution, provided r is small enough. $\square$

Finally, we state conditions that guarantee $\lambda_0 > 0$. The simplest way to achieve this is to assume that $a_* := \min\{a(x)\colon\ x \in \overline{\Omega}\} > 0$, since $\lambda_0 \geq a_*$. In this case the constant a_* is a positive lower solution.

In the case of zero Neumann boundary conditions, if $a(x)$ is allowed to become negative in some parts of the habitat, then substitution of $\phi(x) \equiv 1$ in the Rayleigh quotient in (8) yields $\lambda_0 \geq < a >$, so that by Lemma 1.2, the condition $\int_\Omega a(x)\,dx > 0$ guarantees the existence of a positive stationary solution.

I.2. *Behavior of eigenvalues and stationary solutions.* In the constant diffusion case, the first eigenvalue depends monotonically on the diffusion coefficient and on the potential. The limiting behavior of this eigenvalue, as the diffusion gets small or large, is known, see [**1**]. These results generalize to the case of a variable diffusion coefficient. The proofs are essentially the same.

Lemma 1.3. *Let $\lambda_0 = \lambda_0(d, q)$ be the first eigenvalue of the linear operator $L = L(d, q)$ defined by $L\phi = \nabla.(d(x)\nabla\phi) + q(x)\phi$, then*

(i) λ_0 *is a decreasing function of d if q is not a constant.*

(ii) λ_0 *is increasing in q.*

Proof. It is easily obtained from the variational principle

$$\lambda_0(d,q) = \sup\left\{ \frac{\int_\Omega \left[-d(x)|\nabla\phi|^2 + q(x)\phi^2 \right] dx}{\int_\Omega \phi^2(x)\,dx} : \phi \in H^1,\ \phi \neq 0 \right\}. \tag{8}$$

□

With the convention

$$\langle q\rangle := \frac{1}{|\Omega|}\int_\Omega q(x)\,dx,$$

and

$$q^* := \max\{q(x) : x \in \overline{\Omega}\},$$

the asymptotic behavior of the principal eigenvalue is as follows.

Lemma 1.4. (i) $\lambda_0(d,q) \to q^*$ *as* $d \to 0$ *uniformly on* $\overline{\Omega}$.

(ii) $\lambda_0(d,q) \to < q >$ *as* $d \to \infty$ *uniformly on* $\overline{\Omega}$.

Proof. (i) It is obtained from the variational principle (8), see [**4**].

(ii) Let ϕ_0 be the principal eigenfunction, normalized by $\langle\phi_0\rangle = 1$, then $\phi_0 = 1+r$ with $\langle r\rangle = 0$. If $E(\phi;d,q)$ denotes the Rayleigh quotient in (8), then

$$\lambda_0(d,q) \geq E(1;d,q) = \langle q\rangle.$$

Moreover, $\int_\Omega q\phi^2/\int_\Omega \phi^2 \leq q^*$. It follows that the first term in $E(\phi_0;d,q)$ is bounded below and therefore $\int_\Omega |\nabla r|^2\,dx = O(1/d_*)$, where d_* denotes the minimum of d over $\overline{\Omega}$. By Rellich's Lemma, there exists a constant C such that $\int_\Omega r^2\,dx \leq C\int_\Omega |\nabla r|^2\,dx$. It follows that $r \to 0$ in the H^1-norm as $d_* \to \infty$. Therefore, $\phi_0 \to 1$ in H^1 and $\lambda_0(d,q) = E(\phi_0;d,q) = \langle q\rangle + O(1/d_*) \to \langle q\rangle$ as $d \to \infty$ uniformly on $\overline{\Omega}$. □

I.3. *Integral identities.* Integration of (7) yields $\int_\Omega [a(x)-\tilde{u}(x)]\tilde{u}(x)\,dx = 0$. Multiplication of (7) by $\tilde{u}$ followed by integration results in

$$\int_\Omega [a(x)-\tilde{u}(x)]\tilde{u}^2(x)\,dx = \int_\Omega d(x)|\nabla\tilde{u}(x)|^2\,dx.$$

An important identity is obtained upon division of (7) by $\tilde{u}$ and integration by parts:

$$\int_\Omega [a(x) - \tilde{u}(x)]\, dx = -\int_\Omega d(x) \frac{|\nabla \tilde{u}(x)|^2}{\tilde{u}^2(x)}\, dx. \tag{9}$$

I.4. *The dynamics.* The existence of solutions for a short time is straightforward. Let $X = L^2(\Omega)$, $3/4 < \alpha < 1$ and X^α be the usual fractional power space. We also assume that k, the space dimension, satisfies $k \leq 3$. With these choices, we have the inclusion $X^\alpha \subset H^1(\Omega) \cap L^\infty$ and, for any $u_0 \in X^\alpha$, there exists $T > 0$ such that the solution of (6) with $u(x,0) = u_0(x)$ is defined on $[0,T]$, it satisfies $u(.,t) \in H^2$ for $0 \leq t \leq T$ and it is continuous in (t, u_0). See [**7**].

By the maximum principle, $u(x,t) \geq 0$ for $0 \leq t \leq T$ if $u_0(x) \geq 0$. Hence, the positive cone $K^+ = \{u_0 \in X^\alpha : u_0 \geq 0\}$ is positively invariant under the flow. Moreover, if $M_0 = \max\{u_0(x) | x \in \Omega\}$ and $C = \max\{a^*, M_0\}$, then $u(x,t) \leq C$ for all $t \in [0,T]$. Therefore, any solution remains bounded in L^∞, uniformly in time, as long as it exists. From this it follows that solutions of (6) exist for all positive times for initial conditions in X^α.

From now on we shall restrict our attention to initial conditions in the positive cone K^+.

Equation (6) has a gradient structure, since it is of the form $\dot{u} = -\nabla\Phi(u)$, where the energy Φ is defined by

$$\Phi(u) = \int_\Omega \left[\frac{d(x)}{2} |\nabla u(x)|^2 - \frac{a(x)}{2} u^2(x) + \frac{1}{3} u^3(x) \right] dx.$$

The energy decreases along trajectories of (6):

$$\frac{d}{dt}\Phi(u(.,t)) = -\int_\Omega u_t^2(x,t)\, dx \leq 0$$

and it is constant only along stationary solutions.

It follows that the only possible ω-limit points of trajectories corresponding to nonnegative initial values are $u \equiv 0$ and $\tilde{u}(x)$.

We claim that in the case $\lambda_0 > 0$, there are no trajectories in K^+ which converge to 0. Indeed, the positive eigenfunctions $\{r\phi_0\}$, for r sufficiently small, form a family of stationary lower solutions of (6) which act as barriers in the sense that given any $u_0 \in K^+$, by the strong maximum principle, $u(x,1;u_0) > 0$ for all $x \in \overline{\Omega}$ and, therefore, there exists a positive value of $r = r(u_0)$ such that $r\phi_0(x) < u(x,1;u_0)$. This allows us to conclude that $u(x,t;u_0) \to \tilde{u}(x)$ as $t \to \infty$. Hence, all solutions corresponding to nonnegative initial conditions converge to $\tilde{u}(x)$ as $t \to \infty$.

Our final task is to verify that the global dynamics is controlled by the sign of λ_0, the leading eigenvalue of the linearization around the zero solution. In particular, we prove that the condition $\int_\Omega a(x)\,dx > 0$ guarantees the existence of a positive stationary solution of (6) which is the global attractor of the nonlinear flow.

Proposition 1.1. *If $\lambda_0 \le 0$, then $u(x,t) \to 0$ as $t \to \infty$.*

Proof. Take $r > 0$, and $\phi_0 > 0$ a fixed eigenfunction corresponding to λ_0, then $r\phi_0$ is an upper solution:

$$\nabla.(d(x)r\phi_0) + [a - r\phi_0]r\phi_0 = r\phi_0[\lambda_0 - r\phi_0] \le -r^2\phi_0^2 < 0.$$

Let $u(x,t;r)$ be the solution with $u(x,0;r) = r\phi_0(x)$. By the maximum principle, $u(x,t;r)$ decreases to a nonnegative stationary solution.

We claim that $u(x,t;r)$ decreases to zero. Assume contrariwise that there exists a positive stationary solution $\overline{u}(x)$ and $r > 0$ such that $u(x,t;r) \to \overline{u}(x)$ as $t \to \infty$. Define $r^* := \inf\{r > 0 : \overline{u}(x) < r\phi_0(x)\}$, then $r^* > 0$. Since $\overline{u}(x) \le r^*\phi_0(x)$ in Ω, it follows that $u(x,t;r^*) \to \overline{u}(x)$. On the other hand, there exists $x_0 \in \Omega$ such that $\overline{u}(x_0) = r^*\phi_0(x_0)$. Since $u_t(x_0,0;r^*) < 0$, it follows that $u(x,t;r^*) \to 0$. This contradiction proves the claim and it establishes the result. $\square$

Proposition 1.2. *If $\int_\Omega a(x)\,dx > 0$, then*

(i) *there exists a positive stationary solution $\tilde{u}(x)$ of* (6)

(ii) $\lambda_0 > 0$

(iii) *$\tilde{u}$ is the global attractor for initial conditions in the positive cone.*

Proof. (i) If α is a constant, then

$$\Phi(\alpha) = -\frac{\alpha^2}{2}\int_\Omega a(x)\,dx + \frac{1}{3}|\Omega|\alpha^3 = \frac{\alpha^2|\Omega|}{3}\left[\alpha - \frac{3}{2}\langle a\rangle\right]$$

and this quantity is negative if $0 < \alpha < 3/2\langle a\rangle$. Thus, the solution $u(x,t;\alpha)$ cannot converge to 0. It follows that there exists a positive stationary solution $\tilde{u}(x)$ to which $u(x,t;\alpha)$ converges as $t \to \infty$.

(ii) Fix $\phi_0 > 0$ an eigenfunction corresponding to λ_0, then for any $r > 0$,

$$\nabla.(d(x)r\phi_0) + [a - r\phi_0]r\phi_0 = r\phi_0[\lambda_0 - r\phi_0].$$

Assume $\lambda_0 \le 0$, then $r\phi_0$ is an upper solution of (7). Now choose r small enough so that $r\phi_0(x) < \tilde{u}(x)$ in Ω, then $u(x,t;r\phi_0)$ decreases to 0 as $t \to \infty$. But this contradicts part *i*), as we can find a positive value of $\alpha < r\phi_0$ such that $E(\alpha) < 0$. Therefore, $\lambda_0 > 0$.

(iii) Given $u_0 \in K^+$, choose α small so that $0 < \alpha < u(x,1;u_0)$ in $\overline{\Omega}$; then, by the maximum principle, $u(x,t;u_0) \to \tilde{u}(x)$ as $t \to \infty$. □

From now on, we assume that the function $a(x)$ satisfies the hypothesis of Proposition 1.2.

Remark 1.2. In this case, the rate of convergence to the positive steady state is exponential, as the linearized operator around $\tilde{u}$ is given by

$$L(d, a - 2\tilde{u})\phi = \nabla.(d(x)\nabla\phi) + [a - 2\tilde{u}]\phi$$

and $\lambda_0(d, a - 2\tilde{u}) < \lambda_0(d, a - \tilde{u}) = 0$.

An interesting property of equation (6) is that the one-parameter family of functions $\alpha\tilde{u}$ for $0 < \alpha < 1$ are lower solutions. This follows from

$$\nabla.(d(x)\alpha\nabla\tilde{u}) + (a - \alpha\tilde{u})\alpha\tilde{u} = \alpha(1-\alpha)\tilde{u}^2.$$

Note that we get upper solutions for $\alpha > 1$ and for $\alpha < 0$.

An important problem is to determine the behavior of the flow away from the stationary solutions. Our next result is a step in this direction, as it gives an upper bound on the time that a solution can spend in an order interval of the form $[\alpha\tilde{u}, \beta\tilde{u}]$, for $0 < \alpha < \beta < 1$. The bound is given in terms of λ_0, the first eigenvalue of $L = L(d, a - (1+\alpha)\tilde{u})$, which satisfies $\lambda_0(\alpha) \sim \alpha$.

Proposition 1.3. *Let $0 < \alpha < \beta < 1$, and λ_0 as defined in the preceding paragraph. Consider a solution $u(x,t)$ such that $\alpha\tilde{u}(x) \leq u(x,t) \leq \beta\tilde{u}(x)$ in Ω for $0 \leq t \leq T$, then*

$$T \leq T^* := \frac{-1}{\lambda_0} \ln\left(\frac{1-\alpha}{1-\beta}\right).$$

Moreover, $u(x,t) > \beta\tilde{u}(x)$ in some part of Ω for $t > T^*$.

Proof. In terms of $p = \tilde{u} - u$, equation (6) becomes

$$p_t = \nabla.(d(x)\nabla p) + [a - 2\tilde{u}]p + p^2. \tag{10}$$

For the solutions under consideration we have

$$p_t \leq \nabla.(d(x)\nabla p) + [a - (1+\alpha)\tilde{u}]p$$

Moreover, $\dot{f}(t) \leq 2\lambda_0 f(t)$ for

$$f(t) = \frac{1}{2}\int_\Omega p^2(x,t)\,dx.$$

Since $(1-\beta)\tilde{u}(x) \leq p(x,t) \leq (1-\alpha)\tilde{u}(x)$, we get

$$\frac{1}{2}\int_\Omega (1-\beta)^2\tilde{u}^2(x)\,dx \leq f(t) \leq f(0)e^{2\lambda_0 t} \leq \frac{1}{2}\Big[\int_\Omega (1-\alpha)^2\tilde{u}^2(x)\,dx\Big]e^{2\lambda_0 t}$$

from which the estimate is obtained.

The rest of the statement follows from the fact that $\alpha\tilde{u}$ are upper solutions of (10) for $0 \leq \alpha \leq 1$. $\square$

Since $T^* = \ln(1+(\beta-\alpha/1-\beta))$ and $\lambda_0 \sim \alpha$, it follows that $T^* \sim 1/\alpha$ as $\alpha \to 0$ and $T^* \sim \ln(1/1-\beta)$ as $\beta \to 1$.

II. Basic properties of the full system.

II.1. *Determination of nonnegative stationary solutions.* In the constant diffusion case, it was shown in [**3**] that the only nonnegative stationary solutions of (1) are the zero solution and the semi-trivial solutions $\tilde{U}^i = \tilde{u}_i \vec{e}_i$, where $\tilde{u}_i$ is the positive solution of (2). In that paper it was also shown that $\tilde{U}^1$ is linearly stable and $\tilde{U}^i$ is unstable for $i = 2, \dots, n$. The results for the case of diffusion coefficients with spatial dependence are the same.

Theorem 2.1. *If* $0 < d_1(x) \le \cdots \le d_n(x)$*, then the only nonnegative equilibria of* (3) *are the zero solution and the semi-trivial solutions* $\tilde{U}^i = \tilde{u}_i \vec{e}_i$*, for* $i = 1, \dots, n$*, where* $\tilde{u}_i$ *is the positive solution of* (7) *with* $d = d_i$*.*

Proof. Assume $(u_1, \dots, u_n)$ is a nonnegative stationary solution of (3), and let $q(x) = a(x) - \sum_{j=1}^n u_j(x)$, then u_i is a nonnegative solution of $\nabla.(d_i(x)\nabla u_i) + q(x)u_i = 0$. We claim that $q(x)$ is not a constant. To see this, assume contrariwise that $q(x) \equiv \mu$, and take i such that $u_i \not\equiv 0$, then $u_i > 0$ and $\nabla.(d(x)\nabla u_i) = -\mu u_i$ which forces $\mu = 0$ and u_i constant. Combining these two facts we get $a(x) = \sum_{j=1}^n u_j$ is a constant, a contradiction. It follows from Lemma 1.1 that the principal eigenvalue $\lambda_0(d, q)$ is a strictly decreasing function of d. Therefore, $u_i \not\equiv 0$ for at most one value of i, and if there is such a value, $\tilde{u}_i$ is the required positive stationary solution. □

When all diffusion coefficients $d_1, \dots, d_n$ are the same, the set of nonnegative stationary solutions is an $n-1$-dimensional manifold.

Theorem 2.2. *If the diffusion coefficients in* (3) *are equal, then any stationary solution is of the form* $\tilde{u}\Lambda$*, where* $\tilde{u}$ *is the positive solution of* (7)*,* $\Lambda = (\lambda_1, \dots, \lambda_n)$*, with* $0 \le \lambda_i \le 1$ *for* $i = 1, \dots, n$*, and* $\sum_{i=1}^n \lambda_i = 1$*.*

Proof. Assume $(u_1, \dots, u_n)$ is a nonnegative stationary solution of (3) and let $v = \sum_{j=1}^n u_j$. Then, v is a nonnegative stationary solution of (7). By uniqueness, either $v \equiv 0$ or $v = \tilde{u}$, the positive stationary solution. In the former case, each $u_i \equiv 0$.

If $v = \tilde{u}$, then each u_i is a nonnegative solution of

$$\nabla.(d(x)\nabla\phi) + [a - \tilde{u}]\phi = 0.$$

Therefore, each u_i must be of the form $u_i = \lambda_i \tilde{u}$ with $\lambda_i \geq 0$ and $\sum_{i=1}^{n} \lambda_i = 1$. $\square$

II.2. *Linear stability analysis.* The linearization of (3) around $\tilde{U}^i$ is determined by the operator $\mathcal{L}^i$ defined by

$$\begin{aligned} \mathcal{L}_i^i(\Phi) &= \nabla.(d_i(x)\nabla\phi_i) + [a - 2\tilde{u}_i]\phi_i - \left(\sum_{j\neq i}\phi_j\right)\tilde{u}_i \\ \mathcal{L}_k^i(\Phi) &= \nabla.(d_k(x)\nabla\phi_k) + [a - \tilde{u}_i]\phi_k \quad \text{for } k \neq i \end{aligned} \tag{11}$$

The spectrum of $\mathcal{L}^i$ consists of the values of $\lambda \in \mathcal{C}$ for which there exists a bounded nontrivial solution $\Phi = (\phi_1, \dots, \phi_n)$ of $\mathcal{L}^i(\Phi) = \lambda\Phi$.

The following result corresponds to Theorem 3.2 of [**3**].

Theorem 2.3. *Under the assumptions of Theorem* 2.1*, we have*

(i) $\tilde{U}^1$ *is linearly stable*

(ii) $\tilde{U}^i$ *is unstable for* $i = 2, \dots, n$.

Proof. (i) If $\lambda \in \sigma(\mathcal{L}^1)$, then either $\lambda \in \sigma(L(d_k, a - \tilde{u}_1)$ for some $k \geq 2$ or $\lambda \in \sigma(L(d_1, a - 2\tilde{u}_1)$. Since the first eigenvalue of $L(d_1, a - \tilde{u}_1)$ is $\lambda_0(d_1, a - \tilde{u}_1) = 0$, it follows from the monotonocity that $\lambda_0(d_1, a - 2\tilde{u}_1) < 0$. Hence all eigenvalues of $\mathcal{L}^1$ are negative.

(ii) For $i \in \{2, \dots, n\}$ and $j \in \{1, \dots, i-1\}$, any positive eigenvalue of $L(d_j, a - \tilde{u}_i)$ is also an eigenvalue of $\mathcal{L}^i$, therefore it is an unstable mode of $\tilde{U}^i$. $\square$

An important consequence of identity (9) and part *i*) above is the uniform control on the first eigenvalue of $\mathcal{L}^1$ if we fix d_1 and d_2, and let $d_i \to \infty$ uniformly in Ω for $i = 3, \dots, n$. Indeed, for such values of i we have

$$\lambda_0(d_i, a - \tilde{u}_1) \to \langle a - \tilde{u}_1 \rangle = -\frac{1}{|\Omega|}\int_\Omega \frac{d_1(x)|\nabla\tilde{u}_1(x)|^2}{\tilde{u}_1^2(x)}\,dx \quad \text{as } d_i \to \infty.$$

Therefore, the first eigenvalue of $\mathcal{L}^1$ remains uniformly bounded away from zero as $d_i \to \infty$ in Ω for $i = 3, \ldots, n$.

In the case of equal diffusions, all stationary solutions have similar stability properties.

Theorem 2.4. *If $d_i(x) = d(x)$ for $i = 1, \ldots, n$, then the first eigenvalue of the linearization of* (3) *around $\tilde{u}\Lambda$ is $\mu = 0$. All other eigenvalues are negative.*

Proof. If $\mathcal{L}_{\tilde{u}\Lambda}$ is the linearized operator, then the eigenvalue equation is

$$\nabla.(d(x)\nabla\phi_i) + [a - \tilde{u}]\phi_i - \left(\sum_{j=1}^{n} \phi_j\right)\lambda_i \tilde{u} = \mu\phi_i \quad i = 1, \ldots, n. \tag{12}$$

It follows that $S = \sum_{j=1}^{n} \phi_j$ is a solution of $\nabla.(d(x)\nabla S) + [a - 2\tilde{u}]S = \mu S$. Then, either $S \not\equiv 0$ or $S \equiv 0$. In the former case, $\mu \in \sigma(L(d, a - 2\tilde{u}))$, hence $\mu < 0$. In the latter case, $\mu \in \sigma(L(d, a - \tilde{u}))$. Moreover, one can see from the structure of (11) that each $\mu \in \sigma(L(d, a - \tilde{u}))$ is an eigenvalue of the linearized operator. Therefore, $\mu = 0$ is the top eigenvalue. $\square$

II.3. *Global existence, uniform bounds and the global attractor.* The existence of solutions of (3) proceeds as in I.4, with $X = (L^2(\Omega))^n$, and the norm being the sum of the norms of the components. In the present situation, the initial condition U_0 belongs to $(X^\alpha)^n$. The solution satisfies $U(., t; U_0) \in (H^2)^n$ and it is C^1 in t and continuous in U_0, as long as it exists.

A simple application of the maximum principle shows that the positive cone $(K^+)^n$ is positively invariant under the flow.

From
$$\frac{\partial u_i}{\partial t} \le \nabla.(d_i(x)\nabla u_i) + [a(x) - u_i]u_i,$$
we conclude that each component is bounded above by the solution of the scalar equation (6) with diffusion $d_i(x)$ and initial value $u_i(x, 0)$, if U_0 is in the positive cone.

Therefore, solutions of (3) exist for all time and are bounded in L^∞. The existence of a compact global attractor is standard, see [**5**].

Moreover, each function $(u_1, \dots, u_n)$ in the global attractor satisfies $0 \le u_i \le \tilde{u}_i$, for $i = 1, \dots, n$, that is, each component is bounded above by the corresponding steady state.

II.4. 0 *is a repelling equilibrium.* We shall verify that in K^+ there is a neighborhood $\mathbf{N}$ of the trivial solution of (3) with the property that every trajectory starting in $\mathbf{N}$ leaves this set in finite time.

Indeed, let $A := \langle a \rangle$ and define $\mathcal{N} := \{U = (u_1, \dots, u_n) : ||U|| < A/2\}$. For any $t > 0$ and any $i \in \{1, \dots, n\}$ we have

$$\begin{aligned}\frac{d}{dt}\int_\Omega \ln(u_i(x,t))\,dx = \int_\Omega d_i(x)\frac{|\nabla u_i(x,t)|^2}{u_i^2(x,t)}\,dx \\ + \int_\Omega \Big[a(x) - \sum_{j=1}^n u_j(x,t)\Big]\,dx.\end{aligned}$$

Therefore, the lefthand side is bounded below by $A/2$ as long as the solution $U(x,t)$ remains in $\mathcal{N}$. Since $u_i(x,t)$ is bounded in L^∞, it follows that $U(x,t)$ leaves $\mathcal{N}$ in finite time.

III. The system of two phenotypes. The case of two phenotypes is special: the corresponding system is monotone. Here we use the notation $u_1 = u$ and $u_2 = v$, so that the system becomes

$$\begin{aligned} u_t &= \nabla.(d_1(x)\nabla u) + [a - (u+v)]u \\ v_t &= \nabla.(d_2(x)\nabla v) + [a - (u+v)]v. \end{aligned} \tag{13}$$

The stationary solutions are denoted by $\tilde{U} = (\tilde{u}, 0)$ and $\tilde{V} = (0, \tilde{v})$. The monotonicity of the system means that if $u_1(x,0) \ge u_2(x,0)$ and $v_1(x,0) \le v_2(x,0)$, then $u_1(x,t) \ge u_2(x,t)$ and $v_1(x,t) \le v_2(x,t)$ for all $t > 0$. This defines the order in $(X^\alpha)^2$ that is preserved by the flow. The verification of the monotonicity is straightforward.

Theorem 3.1. *If* $0 < d_1(x) \le d_2(x)$ *but* $d_1 \ne d_2$, *then* $\tilde{U} = (\tilde{u}, 0)$ *is the global attractor for the set of solutions with positive initial conditions.*

Proof. The result for initial conditions in the order interval $I := [\tilde{U}, \tilde{V}]$ follows from Proposition 2.4 in [**8**] since there are no stationary solutions in the interior of the positive cone, the origin is a repelling equilibrium and an extreme point of I. These properties guarantee the existence of a connecting orbit $\gamma(t)$ which is decreasing in t and such that $\gamma(-\infty) = \tilde{V}$, and $\gamma(+\infty) = \tilde{U}$.

Each function on the connecting orbit is a comparison function and each initial condition in the order interval is bounded above by one of these comparison functions.

The estimates in II.3 show that the ω-limit set of every positive initial condition lies in the order interval I. Moreover, no trajectory in the positive cone can converge to $\tilde{V}$, otherwise, in any neighborhood of $\tilde{V}$ there would be an open set of initial conditions on the stable manifold of $\tilde{V}$, but this contradicts the fact that the local center-stable manifold of $\tilde{V}$ has codimension at least 1. $\square$

Our next task is to find explicit comparison functions. To this end, notice that the principal eigenvalue λ_0 of

$$\nabla.(d_1(x)\nabla\phi) + [a - \tilde{v}]\phi = \lambda\phi,$$

is positive. If, in addition, ϕ_0 denotes the corresponding eigenfunction, then λ_0 is also the first eigenvalue of the linearization of (13) around $\tilde{V}$ and the corresponding eigenfunction is $(\phi_0, 0)$.

The comparison functions (or lower-upper solutions) for (13) are $(r\phi_0, \beta\tilde{v})$. If we normalize ϕ_0 by the condition $||\phi_0||_\infty = 1$, then it is enough to require $0 < r \leq \lambda_0$. The restriction on β is that $1-\beta \leq m_0 r$, where $m_0 = \inf\{\phi_0(x)/\tilde{v}(x)\}$.

These comparison functions provide explicit invariant regions of the form

$$\{(u_0, v_0) : u_0 \geq r\phi_0,\ v_0 \leq \beta\tilde{v}\}.$$

In this situation we see that the difference in the diffusion rates plays a role in the construction of comparison functions, as λ_0 is very small if d_1 and d_2 are very close.

It is clear from Theorems 2.2 and 2.4 that if the diffusion coefficients are different but very close, then the flow on the perturbed invariant manifold is very slow. Thus, if there is an estimate for the time that a solution spends in an order interval determined by comparison functions, that is, the extension of Proposition 1.2 to systems, then the estimate will depend on the difference in the diffusions.

IV. Dynamics in the nearly equal diffusions case. When all diffusion coefficients in (3) are the same, $d_i(x) = d(x)$ for $i = 1, \dots, n$, system (3) reduces to a scalar equation. Indeed, $v = \sum_{i=1}^n u_i$ is a solution of

$$\frac{\partial v}{\partial t} = \nabla.(d(x)\nabla v) + [a - v]v.$$

More generally, we can consider the case where

$$d_k(x) = d_{k+1}(x) = \dots = d_{k+l}(x). \tag{14}$$

(Since by assumption $d_k(x) \leq d_{k+1}(x)$ for all $k = 1, \dots, n-1$ the above statement follows from assuming $d_k(x) = d_{k+l}(x)$.) This degeneracy results in an l-dimensional family of equilibria. In particular, let $\tilde{u}$ be the positive equilibrium for (4) when $d(x) = d_k(x)$, then the set of equilibria corresponding to the degeneracy of (14) is given by

$$S(k, \dots, k+l) := \left\{ \sum_{i=k}^{l} \lambda_i \tilde{u}\vec{e_i} \mid \sum_{i=k}^{l} \lambda_i = 1 \right\}.$$

It follows from the result in I.4 that $v(x,t) \to \tilde{u}(x)$ as $t \to \infty$, at an exponential rate. We shall prove that all trajectories of (3) with initial conditions in the positive cone converge to a stationary solution, which, by Theorem 2.2, is of the form $\tilde{u}\Lambda$.

In this case we get a Morse decomposition, which will persist for small perturbations of the diffusion coefficients, yielding the equilibrium U^1 as the global attractor of the perturbed system. In the case of two phenotypes, system (3) is monotone. From this property, we can extend the previous result to the case of systems whose diffusion coefficients are clustered about two primary values.

IV.1. *Dynamics in the equal diffusion case.* Consider the system

$$\frac{\partial u_i}{\partial t} = \nabla.(d(x)\nabla u_i) + \left[a(x) - \sum_{j=1}^{n} u_j\right] u_i \quad \text{for } i = 1, \dots, n. \tag{15}$$

The main result in this part is that all solutions of (15) starting in the positive cone converge to a stationary solution, the form of which is described in Theorem 2.2.

Theorem 4.1. *Any solution of* (15) *with initial condition in* K^+ *converges to a stationary solution of the form* $\tilde{u}\Lambda$*, where* $\Lambda = (\lambda_1, \dots, \lambda_n)$ *with* $0 \leq \lambda_i \leq 1$ *and* $\sum_{i=1}^n \lambda_i = 1$.

Proof. Note that $v(x,t) := \sum_{i=1}^n u_i \to \tilde{u}(x)$ as $t \to \infty$, at an exponential rate.

The next step is to show that each component has a limit as $t \to \infty$. Let L_0 be the linear operator $L_0 = L(d, a - \tilde{u})$, then for each $t > 0$ we have the representation

$$u_i(x,t) = \mathrm{e}^{tL_0} u_i(x,0) + \int_0^t \mathrm{e}^{(t-s)L_0}[\tilde{u}(x) - v(x,s)]u_i(x,s)\,ds.$$

The first term in the above expression converges to the projection of the ith component of the initial condition onto the positive steady state $\tilde{u}$. The integral term has two contributions, one coming from the projection onto the span of $\tilde{u}$ and one from the projection onto the orthogonal complement. Because of the exponential rate of convergence of v to $\tilde{u}$, the first contribution converges to $\int_0^\infty \alpha_i(s)\,ds\tilde{u}$, where $\alpha_i(s)$ is the projection of $[\tilde{u} - v(s)]u_i(s)$ onto $\tilde{u}$. The second term decays to zero at an exponential rate. Therefore,

$$\lim_{t\to\infty} u_i(x,t) = \left(\mu_i + \int_0^\infty \alpha_i(s)\,ds\right)\tilde{u}(x).$$

Let $\lambda_i = \mu_i + \int_0^\infty \alpha_i(s)\,ds$, then $\lambda_i \geq 0$ by the maximum principle and clearly $\sum_{i=1}^n \lambda_i = 1$. $\square$

IV.2. *The clustered diffusion case.* Consider the system

$$(16)\qquad \begin{aligned} \frac{\partial u_i}{\partial t} &= \nabla.(\mu(x)\nabla u_i) + \Big[a(x) - \sum_{j=1}^n u_j\Big]u_i \quad \text{for } i = 1, \dots, m, \\ \frac{\partial u_i}{\partial t} &= \nabla.(\nu(x)\nabla u_i) + \Big[a(x) - \sum_{j=1}^n u_j\Big]u_i \quad \text{for } i = m+1, \dots, n. \end{aligned}$$

where $0 < \mu(x) \leq \nu(x)$ and $\mu \neq \nu$. Setting

$$v = \sum_{i=1}^{m} u_i \quad \text{and} \quad w = \sum_{i=m+1}^{n} u_i$$

allows one to rewrite (16) as

$$\begin{aligned} \frac{\partial v}{\partial t} &= \nabla.(\mu(x)\nabla v) + \Big[a(x) - v - w\Big]v, \\ \frac{\partial w}{\partial t} &= \nabla.(\nu(x)\nabla w) + \Big[a(x) - v - w\Big]w. \end{aligned} \tag{17}$$

As was indicated in Section II, the global dynamics for this system is completely understood. However, to treat the case of perturbations from (16) we need to introduce some additional ideas, see [**2**] for further details.

Let Inv.K^+ denote the set of bounded solutions in K^+. The alpha and omega limit sets of a point u are denoted by $\alpha(u)$ and $\omega(u)$, respectively. A finite collection of disjoint compact invariant subsets of $\operatorname{Inv} K^+$,

$$\{M(p) \subset \operatorname{Inv} K^+ \mid p = 1, \dots P\}$$

is a *Morse decomposition* if there exists a partial ordering $>$ on the indexing set $\{1, \dots, P\}$ such that for every

$$u \in \operatorname{Inv} K^+ \setminus \bigcup_{p=1}^{P} M(p)$$

there exists p for which $\omega(u) \subset M(p)$ and for each full trajectory in backwards time through u there exists q such that $q > p$ and $\alpha(u) \subset M(q)$.

In the case of the dynamics generated by (17) the Morse decomposition is given by

$$M(3) = (0,0), \quad M(2) = (0, \tilde{w}), \quad M(1) = (\tilde{v}, 0)$$

or equivalently in the context of (16) one has that

$$M(3) = (0,0), \quad M(2) = S(m+1, \dots n), \quad M(1) = S(1, m).$$

An important property of Morse decompositions is that they are robust with respect to perturbations. In the context of these equations this implies the following. Given $\varepsilon > 0$, there exists a $\delta > 0$ such that if for all $x \in \Omega$,

$$\begin{aligned} |d_i(x) - \mu(x)| &< \delta, \quad \text{for } i = 1, \dots m \\ |d_i(x) - \nu(x)| &< \delta, \quad \text{for } i = m+1, \dots n, \end{aligned}$$

then there is a Morse decomposition $\{M'(3), M'(2), M'(1)\}$ of $\operatorname{Inv} K^+$ for the perturbed system and in the Hausdorff metric on compact sets

$$d(M(k), M'(k)) < \varepsilon, \quad k = 1, 2, 3.$$

Thus, one immediately has the following proposition.

Proposition 4.1. *Consider system* (3) *under the additional assumption that* $|d_1(x) - d_m(x)| < \delta$ *and* $|d_{m+1}(x) - d_n(x)| < \delta$ *for all* $x \in \Omega$ *and* $\delta > 0$ *sufficiently small. Then, if* $u \in \operatorname{Inv}^+ K$ *such that* $u_k(x) \neq 0$ *for some* $k < m$,

$$\omega(u) \subset B_\varepsilon(S(1, \dots, m)).$$

If we impose the additional assumption that $m = 2$ then obviously $\omega(u) \subset B_\varepsilon(S(1,2))$. However, since in the perturbed system, $d_1 \neq d_2$ the dynamics on $S(1,2)$ is determined by Theorem 3.1. Thus, in the special case of $n = 3$ and $|d_1(x) - d_2(x)|$ small, we obtain Theorem 4.2.

V. Large diffusions. In this section we consider equation (3) in the case when at least $n-2$ diffusion coefficients are large in Ω. We shall prove that the slow equilibrium is the global attractor of initial conditions in the interior of the positive cone, if d_i is sufficiently large in Ω for $i = 3, \dots, n$. This result is based on the corresponding result for the associated shadow system (5), and the fact that the dynamics of (3) is approximated by that of the shadow system.

As a motivation, we begin with the case of two equations having constant diffusion rates. In this section we use the notation $u_1 = u$ and $u_2 = v$.

Let $d_2 = 1/\varepsilon$, with $0 < \varepsilon \ll 1$. We look for solutions of (3) of the form

$$u(x,t;\varepsilon) = u_0(x,t)+\varepsilon u_1(x,t)+\dots,\ v(x,t;\varepsilon) = v_0(x,t)+\varepsilon v_1(x,t)+\dots.$$

The equations to order ε^0 are

$$\begin{aligned}\frac{\partial u_0}{\partial t} &= d_1\Delta u_0 + (a-u_0)u_0 - u_0v_0\\ 0 &= \Delta v_0.\end{aligned}$$

The boundary condition implies that v_0 is a function of t only, $v_0 = v_0(t) = \langle v(.,t)\rangle$.

The equation for v to order ε is

$$\dot v_0 = \Delta v_1 + [a-(u_0+v_0)]v_0,$$

which has solutions if and only if $\dot v_0 = \langle a-u_0\rangle v_0 - (v_0)^2$. It follows that the shadow system is

$$\begin{aligned}\frac{\partial u}{\partial t} &= d_1\Delta u + [a-(u+v)]u\\ \dot v &= [\langle a-u\rangle - v]v.\end{aligned}$$

When the diffusion coefficients are allowed to vary in space and $n-2$ of them are large, the shadow system is (5). The first step in the analysis of (5) is the determination of the stationary solutions in the positive cone.

Theorem 5.1. *The only nonnegative stationary solutions of* (5) *are the zero solution,* $\hat U = (\tilde u, 0, 0)$, $\hat V = (0,\tilde v,0)$, $(0,0,\alpha\langle a\rangle)$, *where* $\alpha = (\alpha_1,\dots,\alpha_{n-2})$ *with* $0\le\alpha_i\le 1$ *and* $\sum_{i=1}^{n-2}\alpha_i = 1$.

Proof. The system for stationary solutions (u,v,ξ) of (5) is

$$\begin{aligned}&\nabla.(d_1(x)\nabla u) + [a(x)-(u+v+\sigma)]u = 0\\ &\nabla.(d_2(x)\nabla v) + [a(x)-(u+v+\sigma)]v = 0\\ &[\langle a-(u+v)\rangle - \sigma]\xi_i = 0\end{aligned}\tag{18}$$

where $\sigma = \sum_{j=1}^{n-2} \xi_j$.

The stationary solutions of (18) in the positive cone satisfy either $\xi_i = 0$ for $i = 1, \dots, n-2$, or $\langle a - (u+v) \rangle = \sigma$. In the first case, we get the semi-trivial solutions $\hat{U}$, $\hat{V}$ as well as the zero solution. In the second case, if u is not identically zero, then $u > 0$ in Ω, so that we can divide the first equation in (18) by u and integrate by parts to get

$$\int_\Omega d_1(x) \frac{|\nabla u(x)|^2}{u^2(x)}\, dx = -\int_\Omega (a - u - v - \sigma)\, dx = 0.$$

Hence, u is constant in Ω. Similarly, if $v \not\equiv 0$, then v is a constant. Since $a(x)$ is not a constant, there are no solutions to the first equation in (18) for which u and v are constants in space. This contradiction shows that $u \equiv 0$, $v \equiv 0$ and $\xi = \langle a \rangle \alpha$. $\square$

Existence of solutions of (18) for all positive times is established in the space $(X^\alpha)^2 \times \mathbf{R}^{n-2}$, the argument is similar to the one given for the full system in Section II. The a priori bounds of solutions and the existence of the global attractor are entirely analogous. The only new element is the estimate of the norm in $(X^\alpha)^2$ in terms of the L^2-norm as in [**7**].

An important tool in the description of the dynamics of the shadow system is the existence of a Lyapunov function in the interior of the positive cone K^+:

$$\Phi(u(.), v(.), \xi) = -\frac{1}{|\Omega|} \int_\Omega [\ln(u(x)) + \ln(v(x))]\, dx + 2 \sum_{i=1}^{n-2} \ln(\xi_i).$$

Indeed, along a trajectory $(u(.,t), v(.,t), \xi(t))$ of (5) starting in the interior of the positive cone we have

$$\begin{aligned} &\frac{d}{dt}\, \Phi(u(.,t), v(.,t), \xi(t)) \\ &\qquad = -\frac{1}{|\Omega|} \int_\Omega d_1(x)\, \frac{|\nabla u(x,t)|^2}{u^2(x,t)} + d_2(x)\, \frac{|\nabla v(x,t)|^2}{v^2(x,t)}\, dx. \end{aligned}$$

This energy decreases along orbits of (5) which lie in $\operatorname{int}(K^+)$ and it is strictly decreasing along such orbits, since there are no solutions of (18) in the interior of the positive cone for which u and v remain independent of x during an interval of time.

Theorem 5.2. *The stationary solution* $\hat{U} = (\tilde{u}, 0, 0)$ *is the global attractor of the shadow system* (5) *for the set of initial conditions which lie in the interior of the positive cone.*

Proof. Take a point $p_0 = (u_0, v_0, \xi_0)$ in the interior of K^+, and a point $q = (u_1, v_1, \xi_1)$ in the ω-limit set $\omega(p_0)$. The Lyapunov function and Theorem 5.1 guarantee that q lies on the boundary $\partial(K^+)$, and by the maximum principle, at least one of the components of q must be zero.

Since $\Phi(u_1, v_1, \xi_1) = \infty$ if $\sigma_1 > 0$ and either $u_1 \equiv 0$ or $v_1 \equiv 0$, then necessarily, $\xi_1 = 0$. Hence, the global attractor lies on the subspace $\xi = 0$. Moreover, $\xi(t) \to 0$ as $t \to \infty$. It follows that every trajectory starting in the interior of the positive cone converges to either $\hat{U}$ or $\hat{V}$.

On the subspace $\xi = 0$, the dynamics corresponds to system (3) with $n = 2$. One can verify that the shadow system is order preserving in the sense of the hypotheses of [8]. From Theorem 2.3 (i), the fact that each component of a point in the global attractor is bounded above by the corresponding equilibrium, and Theorem B of [**8**], we conclude that the slow equilibrium $(\tilde{u}, 0)$ is the global attractor for initial conditions in the interior of the positive cone.

Relative to (5), the center, if any, and stable directions of $\hat{V}$ are contained in the subspace $u \equiv 0$. Therefore, the center-stable manifold is also contained in that subspace. □

In the constant diffusion case, the basic facts about shadow systems and attractors for systems of reaction-diffusion equations have been established by Hale and Sakamoto [**6**]: if the shadow system has a compact attractor $\mathcal{A}(d_1, d_2)$ for all d_1 and d_2 sufficiently large, then for d_i sufficiently large, $i = 3, \dots, n$, the full system has a compact attractor $\mathcal{A}(d_1, d_2, \dots, d_n)$ which is upper semi-continuous at $d_i = \infty$, $i = 3, \dots, n$.

In (2.5) of [**6**], the full system is expressed as a perturbation of a system consisting of the shadow system and a system of linear heat equations, with diffusion constants d_i, in the subspace of functions with mean zero. From this and Gronwall's inequality, one concludes that orbits of the shadow system are uniformly close to the corresponding orbits of the full system, over finite intervals of time. See the proof of Theorem 1 in [**6**] for details.

With the conventions established in the introduction, the unperturbed system is

$$\begin{aligned}
\frac{\partial u}{\partial t} &= \nabla.(d_1(x)\nabla u) + [a(x) - (u + v + \sigma)]u \\
\frac{\partial v}{\partial t} &= \nabla.(d_2(x)\nabla v) + [a(x) - (u + v + \sigma)]v \\
\dot{\xi}_i &= [\langle a - (u + v)\rangle - \sigma]\xi_i \\
\frac{\partial z_i}{\partial t} &= \nabla.(d_i(x)\nabla z_i) \quad i = 1, \dots, n-2.
\end{aligned}$$

The perturbation is obtained from (3) and (5).

The estimates can be extended to the type of diffusion coefficients we are considering. Indeed, the key ingredient is the exponential bound (2.7) in [**6**] for the fundamental solution of the linear heat equation on the subspace of functions with mean zero. In our case, the basic linear operator is $\nabla.(d(x)\nabla u)$ and its first nonzero eigenvalue is bounded above by the first nonzero eigenvalue of $d_*\Delta$, where d_* is the minimum of d over $\overline{\Omega}$. The estimates in the proof of the next theorem are omitted, as they are straightforward extensions of the estimates used in the proof of Theorem 1 in [**6**].

Theorem 5.3. *Assume that d_i in* (3) *are sufficiently large for $i = 3, \dots, n$. Then, $U^1 = \tilde{u}_1\vec{e}_1$ is the global attractor for the set of initial conditions which lie in the interior of the positive cone.*

Proof. Let λ_0 be the top eigenvalue of the linearization of (3) around U^1. In Section II we verified that λ_0 remains uniformly bounded away from zero as $d_i \to \infty$ uniformly in Ω for $i = 3, \dots, n$. Hence, there exist $r > 0$ and $D > 0$ such that if $d_i > D$ in Ω for $i = 3, \dots, n$, then all trajectories of the full system (3) starting in $B(U^1, r)$ converge to U^1 as $t \to \infty$.

Let $\mathcal{A}(d_1, d_2, \dots, d_n)$ be the global attractor of (3) for initial conditions in the interior of the positive cone. By the second estimate in (2.10) of [**6**], the full system is a small ($O(D^{\alpha-1})$) perturbation of the shadow system when we take initial conditions on the attractor $\mathcal{A}(d_1, d_2, \dots, d_n)$.

By compactness of the flow, there exists $t_0 > 0$ such that the trajectory of the shadow system starting at $(\overline{u}, \overline{v}, \overline{w}) \in \mathcal{A}(d_1, d_2, \dots, d_n)$ remains in $B(U^1, (r/2))$ for $t \geq t_0$. By choosing D so that the size of the perturbation satisfies $O(D^{\alpha-1}) < (r/2t_0)$, we can guarantee that the solution of the full system starting at $(\overline{u}, \overline{v}, \overline{w})$ differs from the solution of the shadow system by less than $(r/2)$ for $0 \leq t \leq t_0$. It follows that the trajectory of the full system enters $B(U^1, r)$ at time t_0, hence it approaches U^1 as $t \to \infty$.

Therefore, $\mathcal{A}(d_1, d_2, \dots, d_n) = U^1$. $\square$

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