

# THE EVOLUTION OF SLOW DISPERSAL RATES: A REACTION DIFFUSION MODEL

Jack Dockery  
Department of Mathematical Sciences  
Montana State University  
Bozeman, Montana 59717  
U.S.A.

Vivian Hutson  
School of Mathematics and Statistics  
Sheffield University  
Sheffield, S3 7RH  
U.K.

Konstantin Mischaikow  
Center for Dynamical Systems and Nonlinear Studies  
School of Mathematics  
Georgia Institute of Technology  
Atlanta, GA 30332  
U.S.A.

and

Mark Pernarowski  
Department of Mathematical Sciences  
Montana State University  
Bozeman, Montana 59717  
U.S.A.

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## **Abstract**

We consider  $n$  phenotypes of a species in a continuous but heterogeneous environment. It is assumed that the phenotypes differ only in their diffusion rates. With haploid genetics and a small rate of mutation, it is shown that the only nontrivial equilibrium is a population dominated by the slowest diffusing phenotype. We also prove that if there are only two possible phenotypes, then this equilibrium is a global attractor and conjecture that this is true in general. Numerical simulations supporting this conjecture and suggesting that this is a robust phenomenon are also discussed.

**Key words.** Evolution of dispersal, migration modification, reaction-diffusion, monotone systems, perturbation of Morse decomposition

**Contact Address:** V. Hutson. FAX 114 2223739, E-mail: V.Hutson@sheffield.ac.uk

**1. Introduction.** Dispersal of organisms has important effects both from an ecological and genetic point of view in a variety of situations. These effects have been much studied recently; wide-ranging discussions of continuous models may be found in [30, 10, 27, 2] and of discrete models in [28]. However, the evolution of dispersal itself, although of obvious importance in this context, has received a great deal less attention, although over the last few years more research has been directed to its study. A recent review [21] contains a useful survey and additional discussion, and further references may, for example, be obtained from [31, 4, 24, 25].

A conclusion that is common to a large class of models (see [21]) is that variability in space tends to reduce dispersal rates. The purpose of the present investigation is to focus on the effect of spatial variability on its own by considering a haploid model of a species where the only phenotypic difference is the dispersal rate, thus excluding all other effects, and to enquire whether the above conclusion is confirmed. Although there are considerable differences in detail, a number of investigations that have a broadly similar direction and conclusion have been carried out; see for example [24, 25, 9, 22, 35, 36, 13]. The model adopted here is continuous in space and time, and the basic equations are of reaction-diffusion type. The general conclusion is that spatial variation on its own causes a reduction in dispersal rates both in the absence of mutation and with a small mutation rate, and the conclusion is robust in that it remains valid even when slow diffusers suffer a penalty in their birth rate.

We consider  $n$  phenotypes of a species with densities  $u_i(x, t)$ , respectively, at the point  $x$  in the bounded domain  $\Omega \subset \mathbf{R}^m$  at time  $t$ . Dispersal is modelled by a diffusion approximation, and phenotype  $i$  is assumed to have diffusion rate  $d_i$ , with  $0 < d_1 < d_2 < \dots < d_n$ . The per-capita rate of increase of each phenotype is identical, so phenotypes differ only in their diffusion rates, and we assume that at low densities this rate of increase is represented by the function  $a$ , which varies in space but is time independent. The genetics are assumed to be haploid, and mutation is represented by the matrix  $\epsilon M$ , where  $\epsilon$  is a small positive scalar. The structure of  $M$  is of course limited by biological constraints, but it turns out that our conclusions require only very weak conditions on  $M$  (see (H2) in section 2), which are certainly satisfied in almost any conceivable biological situation. The basic equations take the form

$$(1.1) \quad \frac{\partial u_i}{\partial t} = d_i \Delta u_i + u_i(a(x) - \sum_{j=1}^n u_j) + \epsilon \sum_{j=1}^n M_{ij} u_j \quad \text{on } \Omega \times \mathbf{R}_+ \quad (1 \leq i \leq n) \quad ,$$

where  $\Delta$  is the Laplacian. Zero Neumann conditions  $\partial u_i / \partial \nu = 0$  (where  $\partial / \partial \nu$  signifies differentiation in the direction of the outward normal) are imposed on the boundary  $\partial \Omega$  of  $\Omega$ , representing the condition of no migration across  $\partial \Omega$ . When  $\epsilon = 0$ , that is there is no mutation, we shall require that there be a so-called ‘semi-trivial’ equilibrium on each axis, that is a stationary solution  $U_i = (0, \dots, 0, \tilde{u}_i, 0, \dots, 0)$ , where  $\tilde{u}_i(x) > 0$  ( $x \in \bar{\Omega}$ ); conditions ensuring this are discussed in Section 2, where technical assumptions are given in detail.

In outline, the aims of the analysis are as follows. We wish to show that if  $\epsilon = 0$ , the phenotype with the smallest diffusion rate, that is, the first, will be favored. In terms of the system (1.1) this means that  $U_1$  is a global attractor for all interior orbits, that is, for orbits with non-negative values none of which is identically zero. We wish further to show that this broad conclusion remains basically unaltered for small mutation rates, the precise meaning of this statement being clarified below. From the point of view of the mathematical theory of reaction-diffusion systems, this raises interesting questions because the form of the reaction terms are such that they do not favor one phenotype over another. Thus, it is the difference in the diffusion rates that principally drives the dynamics of the system.

The plan of this paper is as follows. In Section 2, the basic assumptions are given in detail and certain background results are stated. In Section 3, the case  $\epsilon = 0$  is first considered, and the key result that lies at the heart of the analysis is established:  $U_1$  is asymptotically stable, whereas all the  $U_i$  ( $i \geq 2$ ) are unstable. Remarkably, this result holds independent of the form of  $a(x)$ , so long as it is not constant. This result suggests that the interior orbits are globally

attracted to  $U_1$ , with the consequence from a biological point of view that evolution always favors the slowest diffuser. This conclusion is in accordance with the tenor of the remarks in the introductory paragraphs. The main thrust of the analysis that follows is first to attempt to show that the local stability results are essentially unmodified when small mutation acts. We show broadly that the equilibrium  $U_1$  perturbs into the positive cone - that is, the biologically feasible region - yielding an equilibrium  $U_1(\epsilon)$ , say, and that  $U_1(\epsilon)$  is asymptotically stable, whereas the other  $U_i$  do not enter the feasible region. We also consider in detail (Theorem 3.7 and Corollary 3.8) how the form of  $U_1(\epsilon)$  depends on the mutation matrix.

The second main object, considered in Section 4, is to see how far global conclusions may be drawn. Using results from the theory of monotone dynamical systems (see [19, 17, 32] for a general discussion) we first show that if  $\epsilon = 0$ , then  $U_1(0) = U_1$  is globally stable in the case of two phenotypes. For  $n > 2$ , this question appears to present a difficult mathematical problem. We conjecture, but are unable to prove, that this result remains true. We then consider the global stability of  $U_1(\epsilon)$ . Using a result based on the perturbation of a Morse decomposition, we show that for small  $\epsilon$ ,  $U_1(\epsilon)$  is globally stable whenever  $U_1(0)$  has this property. Therefore, global stability holds when  $n = 2$ , and also if the conjecture is valid.

Section 5 contains a computational investigation partly undertaken to confirm the global convergence discussed above. However, the main question we consider concerns the robustness of the result. The question discussed is the strength of the evolutionary force, that is whether or not a small penalty for slow diffusers, as might be caused by a lower birth rate, would reverse the conclusions. Numerical studies are described in detail, and we show that the evolutionary force is rather strong: a considerable penalty is allowed without modification of the results. In Section 6, the results are summarized and some further directions of research on elaborations of the model are discussed.

**2. Preliminaries.** Here the basic assumptions are listed and some well known results that will be used later are recalled. The reaction-diffusion system (1.1) is first rewritten in more convenient form. Let  $U = (u_1, \dots, u_n)$  and define the  $n \times n$  matrix  $D = \text{diag}\{d_1, \dots, d_n\}$ . Put  $\mathbf{1} = (1, \dots, 1)$  and let  $\langle, \rangle$  be the scalar product in  $\mathbf{R}^n$ . Then (1.1) may be compactly written in the following form:

$$(2.2) \quad \begin{aligned} U_t &= D\Delta U + [a(x) - \langle \mathbf{1}, U \rangle]U + \epsilon MU, \\ \partial U / \partial \nu &= 0 \quad (x \in \partial\Omega), \end{aligned}$$

where  $\partial/\partial\nu$  denotes differentiation in the direction normal to  $\partial\Omega$ . Neumann boundary conditions are assumed throughout although much of the analysis easily extends to more general boundary conditions. The domain  $\Omega$  is taken to be open and bounded with smooth boundary, and  $a \in C^{2+\alpha}(\bar{\Omega})$ . The following conditions are imposed throughout.

(H1)  $0 < d_1 < d_2 < \dots < d_n$ .

(H2) The  $n \times n$  matrix  $M$  is constant. Also,  $M_{ii} < 0$  ( $1 \leq i \leq n$ ) and  $M_{ij} \geq 0$  ( $1 \leq i, j \leq n, i \neq j$ ).

It may be remarked that, because of the special form of the basic equations (2.2), there is no loss in generality in assuming the strict inequality  $d_j < d_{j+1}$  in (H1). For if  $d_j = d_{j+1}$ , the  $j$ th and  $(j+1)$ th equations may be added to yield a new equation for  $u_j + u_{j+1}$  of exactly the same form as the other equations.

As the setting for the study of the equilibria of (2.2) we shall use the space  $[C^{2+\alpha}(\bar{\Omega})]^n$ . The norms in  $C^{2+\alpha}(\bar{\Omega})$  and  $C^\alpha(\bar{\Omega})$  are denoted by  $\|\cdot\|_{2,\alpha}$  and  $\|\cdot\|_\alpha$  respectively. Let  $K^+$  denote the cone of non-negative functions in the particular space under consideration. We take  $\mathcal{D} = \{u \in C^{2+\alpha} : \partial u / \partial \nu = 0 \text{ on } \partial\Omega\}$  and consider operators  $\mathcal{D}^n \rightarrow [C^\alpha]^n$ .

Consider first the situation on the 'axes' of (2.2), that is, the sequence of scalar problems obtained by setting all the  $u_i$  zero except for one component. The following well known result

(see [20] for example) will be central in the sequel. Consider the eigenvalue problem

$$(2.3) \quad \mu \Delta \phi + h \phi = \lambda \phi \quad ,$$

where  $\mu > 0$ ,  $h \in C^{2+\alpha}(\bar{\Omega})$  and as always zero Neumann conditions are assumed. It is well known that there is a unique eigenvalue  $\lambda(h, \mu)$ , say, called the principal eigenvalue, such that the associated ‘principal eigenfunction’ (unique up to a multiplicative constant) is strictly positive.

LEMMA 2.1. *The principal eigenvalue  $\lambda(h, \mu)$  of (2.3) is a continuous non-increasing function of  $\mu$ , and is strictly decreasing if  $h$  is not a constant. Furthermore, the following hold.*

- (i)  $\lambda(h, \mu) \uparrow \max_{\bar{\Omega}} h$  as  $\mu \rightarrow 0$ .
- (ii)  $\lambda(h, \mu) \downarrow \hat{h}$  as  $\mu \rightarrow \infty$ , where  $\hat{h}$  denotes the average of  $h$  over  $\bar{\Omega}$ .
- (iii) If  $h_1(x) \geq h_2(x)$  for  $x$  in  $\Omega$ , then  $\lambda(h_1, \mu) \geq \lambda(h_2, \mu)$  with strict inequality if  $h_1 \not\equiv h_2$ .

LEMMA 2.2. [20] *Consider the initial value problem for the scalar equation*

$$\frac{\partial u}{\partial t} = \mu \Delta u + u(h - u).$$

*If  $\lambda(h, \mu) \leq 0$ , then 0 is the global attractor for positive solutions. If  $\lambda(h, \mu) > 0$ , then there is a unique, strictly positive steady-state solution which is a global attractor for non-trivial positive solutions, the convergence in both cases being in  $\|\cdot\|_{\infty}$ .*

In addition to (H1)-(H2) we shall assume the following throughout.

(H3) The function  $a$  is non-constant and  $\lambda(a, d_i) > 0$  for all  $i$ .

Note that by Lemma 2.1, for this condition to hold it is necessary that  $a(x) > 0$  for some  $x \in \Omega$ . Also, in view of Lemma 2.2, the condition (H3) ensures that there is a semi-trivial equilibrium  $U_i = (0, \dots, 0, \bar{u}_i, 0, \dots, 0)$  on the  $i^{\text{th}}$  axis for each  $i$ . It is clearly essential that  $\lambda(a, d_1) > 0$  as otherwise all orbits of the system will tend to  $\mathcal{O} = (0, \dots, 0)$ . The assumption used is not indeed essential and the analysis may be carried through without it, but it represents the most general situation and simplifies the flow of the account. We note that if  $a$  is positive for some  $x \in \Omega$ , from Lemma 2.1 (i), (H3) holds if every  $d_i$  is small enough. Alternatively  $\hat{a} > 0$ , by Lemma 2.1 (ii), is also sufficient.

We next turn to the dynamics of the full system (2.2). This type of system has been much studied, see the extensive discussion in [23] for example, or the outlines in [16, 6] of the basis for several of the following observations. We first note that local existence together with  $L^{\infty}$  *a priori* bounds ensure the global existence of classical solutions. The *a priori* bounds and indeed dissipativity follow from the next result.

Set  $a^* = \max_{x \in \bar{\Omega}} a(x)$  and take any  $A > a^*$ . Let  $\bar{w}$  be the solution of the ordinary differential equation

$$\frac{d\bar{w}}{dt} = \bar{w}(a^* - \bar{w}),$$

with  $\bar{w}(0) = A$ ; clearly  $\bar{w}$  is strictly decreasing and  $\lim_{t \rightarrow \infty} \bar{w}(t) = a^*$ .

LEMMA 2.3. *Assume that  $\epsilon M_{ij} \leq a^*$  for all  $i, j$  with  $i \neq j$ . For some  $T > 0$ , let  $u$  be a classical solution of the system (2.2) on  $(0, T]$  and be continuous on  $[0, T]$ . Suppose that  $0 \leq u_i(x, 0) \leq A$  for  $x \in \bar{\Omega}$  and all  $i$ . Then for all  $i$ , on  $\bar{\Omega} \times (0, T]$ ,*

$$0 \leq u_i(x, t) \leq \bar{w}(t),$$

*and if  $u_i(x, 0) \not\equiv 0$ , then  $u_i(x, t) > 0$ .*

*Proof.* This is a direct application of [23, Theorem 1.2-6]. In the notation of that theorem  $L_i = \Delta - \partial/\partial t$  and the reaction terms of the system (2.2) are  $f_i(x, u)$ . Let  $(v_1, \dots, v_n)$ ,  $(w_1, \dots, w_n)$  satisfy the same differentiability conditions as  $u$ , and define the region

$$Q = \{(x, t, u) : v_i(x, t) \leq u_i \leq w_i(x, t), \forall i, x, t \in \Omega \times (0, T]\}.$$

Choose  $v_i(x, t) = 0, w_i(x, t) = \bar{w}(t)$  for all  $i$ . We need to show that for each  $i$ ,

$$(2.4) \quad L_i v_i + f_i(x, \bar{u}) \geq 0$$

for all  $(x, t, \bar{u}) \in Q$  with  $\bar{u}_i = v_i$ , and

$$(2.5) \quad L_i w_i + f_i(x, \bar{u}) \leq 0$$

for all  $(x, t, \bar{u}) \in Q$  with  $\bar{u}_i = w_i$ . The relation (2.4) is easy to check and (2.5) is verified as follows using the definition of  $\bar{w}$ .

$$\begin{aligned} L_i w_i + f_i(x, \bar{u}) &= -\frac{\partial w_i}{\partial t} + d_i \Delta w_i + w_i[a - w_i - \sum_{j \neq i} \bar{u}_j] + \epsilon M_{ii} w_i + \epsilon \sum_{j \neq i} M_{ij} \bar{u}_j \\ &= -\bar{w}[a^* - a - \epsilon M_{ii}] - \sum_{j \neq i} \bar{u}_j(\bar{w} - \epsilon M_{ij}) \\ &\leq 0, \end{aligned}$$

since  $a < a^*(x \in \bar{\Omega}), M_{ii} < 0$  by (H2), and  $\epsilon M_{ij} < a^* < \bar{w}(t)$  for  $t \geq 0$ .  $\square$

Our final remark is that the system generates a semi-flow on  $[C(\bar{\Omega})]^n$ . This follows from results of [34], see also [26] for a convenient review. The detailed verification is rather straightforward and is given for example in [32] or [6]. The existence of a global attractor is standard [12].

**3. Equilibria and Their Stability.** We start by considering the situation when there is no mutation, that is  $\epsilon = 0$ . Recall from Section 2 that it is assumed that the diffusion rates  $d_i$  are such that there is a (semi-trivial) equilibrium on each axis:  $U_1, U_2, \dots, U_n$ . The first result, Theorem 3.2, is central. It states that for the full system (2.2),  $U_1$  is asymptotically stable, but all  $U_i$  ( $i \geq 2$ ) are unstable; furthermore there are no other equilibria in the positive cone. This might be thought to be a rather surprising result from a mathematical point of view as it holds without restriction on the spatial environment described by the function  $a$ . From a biological point of view it suggests but does not prove that evolution is always towards a lower diffusion rate. We leave until the next section a detailed discussion of the extent to which we are able to justify this statement without and with mutation.

Next, the behavior of equilibrium when mutation is ‘switched on’ is examined with the aim of seeing whether the broad conclusions for  $\epsilon = 0$  go over. We show that under minimal conditions (H2) on the mutation matrix,  $U_1$  remains in the positive cone and retains its stability, and that under stronger but natural conditions, it moves into the interior of the positive cone. On the other hand, the other equilibria  $U_i$  ( $i \geq 2$ ) do not perturb into the interior.

A preparatory result is needed. Let  $u \in C^{2+\alpha}$  be fixed and define linear operators  $L_1, L_2 : \mathcal{D} \rightarrow C^\alpha$  by setting

$$L_1[u; d]v = d\Delta v + (a - u)v,$$

$$L_2[u; d]v = d\Delta v + (a - 2u)v.$$

Denote the principal eigenvalue of  $L_1$  by  $\lambda(u, d)$ ; the principal eigenvalue of  $L_2$  will then be  $\lambda(2u, d)$ .

LEMMA 3.1. *The following hold*

$$(3.6) \quad \lambda(\tilde{u}_i, d_j) \begin{cases} > 0 & (j < i), \\ < 0 & (j > i), \end{cases}$$

$$(3.7) \quad \lambda(2\tilde{u}_i, d_i) < 0.$$

$L_1, L_2$  have bounded inverses whenever the corresponding principal eigenvalue is less than zero. Furthermore, then  $(-L_1)^{-1}$  and  $(-L_2)^{-1}$  are positive in the sense that  $v \geq 0$  implies that  $-L_1^{-1}v \geq 0$  and  $-L_2^{-1}v \geq 0$ , and if  $v \not\equiv 0$  the inequalities are strict.

*Proof.* By definition  $\tilde{u}_i$ , which is of course a positive function, satisfies the equation

$$d_i \Delta \tilde{u}_i + \tilde{u}_i [a - \tilde{u}_i] = 0.$$

That is,  $\tilde{u}_i$  is the principal eigenfunction of  $L_1[\tilde{u}_i; d_i]$  with principal eigenvalue zero. Hence (3.6) follows immediately from (H1) and the fact that the principal eigenvalue is a strictly decreasing function of  $d$  (Lemma 2.1). Since  $\tilde{u}_i > 0$ , it follows from Lemma 2.1 (iii) that  $\lambda(2\tilde{u}_i, d_i) < \lambda(\tilde{u}_i, d_i) = 0$ . We next want to prove that  $L_1$  is invertible under the given condition, the proof for  $L_2$  being similar. From standard *a priori* estimates ([26] or [29, page 15]), there is a  $c > 0$  such that

$$\|u\|_{2,\alpha} \leq c(\|L_1\|_{0,\alpha} + \|u\|_{0,\alpha}).$$

From this estimate and standard embedding results [11], it follows from Theorem 12.12 [37] that  $L_1$  is a Fredholm operator. Since  $0 \notin \sigma(L_1)$ , where  $\sigma$  denotes the spectrum, the operator is invertible. The positivity is a consequence of the maximum principle, see [15, Theorem 16.6].  $\square$

The main issue in the following theorem is the question of stability of the semi-trivial equilibria  $U_i$ ; the result is in essence close to that of Hastings [13]. The proof depends on knowledge of the sign of the principal eigenvalue of the linearised system at each  $U_i$ . At first sight this seems to present a difficult problem because the  $\tilde{u}_i$  are not known explicitly - each is a solution of a nonlinear elliptic problem. However, one observes that, as  $a$  is not constant, the principal eigenvalues of the linear operators  $L_1(\tilde{u}_i; d_k)$  decrease as  $k$  increases (by (H1) and Lemma 2.1). The signs follow on noting that  $\lambda(\tilde{u}_i, d_i) = 0$ . The details of the proof are given in Lemma 3.1.

THEOREM 3.2. *Assume that  $\epsilon = 0$ . Then  $U_1$  is hyperbolic and asymptotically stable, whereas  $U_i$  is unstable for  $i \geq 2$  (although not necessarily hyperbolic). Except for  $\mathcal{O}$  there are no other equilibrium in  $K^+$ .*

*Proof.* For fixed  $i$  ( $1 \leq i \leq n$ ) put  $u_i = \tilde{u}_i + v_i$ ,  $u_k = v_k$  ( $k \neq i$ ). Then linearization leads to the system

$$(3.8) \quad \begin{aligned} \frac{\partial v_i}{\partial t} &= L_2[\tilde{u}_i; d_i]v_i - \tilde{u}_i \sum_{j \neq i} v_j, \\ \frac{\partial v_k}{\partial t} &= L_1[\tilde{u}_i; d_k]v_k \quad (k \neq i). \end{aligned}$$

It is sufficient to check the spectrum of the linearization, see [26, Theorem 6.2], and from compactness we need only consider the sign of the largest eigenvalue of the above system. From the special form of (3.8) it is clear that the largest eigenvalue is the largest of the eigenvalues of  $L_1[\tilde{u}_i; d_k]$  and  $L_2[\tilde{u}_i; d_i]$ . If  $i = 1$ , from Lemma 3.1 all these eigenvalues are negative. If  $i \geq 2$ , then  $\lambda(\tilde{u}_i, d_k) > 0$  for  $k = 1, \dots, (i - 1)$ .

To prove the final assertion of the theorem we argue by contradiction. By a rearrangement of indices we may assume that the equilibrium is of the form  $(\bar{u}_1, \bar{u}_2, \dots, \bar{u}_i, 0, \dots, 0)$  where  $2 \leq i \leq n$  and each  $\bar{u}_j \geq 0$  but  $\bar{u}_j \neq 0$ . Then for  $1 \leq j \leq i$ ,  $\bar{u}_j$  satisfies the equation  $L_1[\bar{u}; d_j]\bar{u}_j = 0$  where  $\bar{u} = \sum \bar{u}_j$ . However, from Lemma 2.1 this is impossible.  $\square$

We now examine the equilibria of (2.2) when there is a small mutation rate, that is  $\epsilon > 0$  is small. Define the operator  $F : \mathcal{D}^n \times \mathbf{R} \rightarrow [C^\alpha(\bar{\Omega})]^n$  by setting

$$F(u, \epsilon) = D\Delta u + [a - \langle \mathbf{1}, u \rangle]u + \epsilon Mu.$$

Equilibria of the system (2.2) are thus solutions of  $F(u, \epsilon) = 0$ , and the plan is first to use the implicit function theorem to describe the perturbation of  $U_1 = (\bar{u}_1, 0, \dots, 0)$ .

The Frechét derivative of  $F$  at  $(U_1, 0)$  is the linear operator  $\mathcal{L} : \mathcal{D}^n \rightarrow [C^\alpha(\bar{\Omega})]^n$  given by

$$\mathcal{L}\Phi = D\Delta\Phi + [a - \langle \mathbf{1}, U_1 \rangle]\Phi - \langle \mathbf{1}, \Phi \rangle U_1,$$

and from the form of this in components,

$$(3.9) \quad \begin{aligned} (\mathcal{L}\Phi)_1 &= L_2[\bar{u}_1; d_1]\Phi_1 - \sum_{j=2}^n \bar{u}_1 \Phi_j, \\ (\mathcal{L}\Phi)_i &= L_1[\bar{u}_1; d_i]\Phi_i \quad (i \geq 2), \end{aligned}$$

it is clear that

$$\sigma(\mathcal{L}) \subset \sigma(L_2[\bar{u}_1; d_1]) \bigcup_{i=2}^n \sigma(L_1[\bar{u}_1; d_i]).$$

It follows from Lemma 3.1 that  $\sigma(\mathcal{L})$  lies in the open left half plane, and from an argument similar to that used in the proof of Lemma 3.1,  $\mathcal{L}$  has bounded inverse. Because of the simple form of (3.9), the structure of  $\mathcal{L}^{-1}$  may be obtained explicitly:

$$-\mathcal{L}^{-1} = \begin{bmatrix} P_1 & Q_2 & \dots & \dots & Q_n \\ 0 & P_2 & 0 & \dots & 0 \\ \vdots & & & & \vdots \\ 0 & 0 & \dots & P_{n-1} & 0 \\ 0 & 0 & \dots & 0 & P_n \end{bmatrix},$$

where  $P_1 = -L_2^{-1}[\bar{u}_1; d_1]$ ,  $P_i = -L_1^{-1}[\bar{u}_1; d_i]$  for  $i \geq 2$ . Thus from Lemma 3.1, each  $P_i$  is a positive operator, and the  $Q_i$  are of course bounded. We have thus proved the following.

**LEMMA 3.3.**  *$\mathcal{L}$  has a bounded inverse and  $-\mathcal{L}^{-1}$  has diagonal elements which are positive operators.*

**THEOREM 3.4.** *There is an  $\epsilon_0 > 0$  such that the system (2.2) has an equilibrium  $U_1(\epsilon) \in [C_{2+\alpha}(\bar{\Omega})]^n$  for  $|\epsilon| < \epsilon_0$  with  $U_1(0) = U_1$ , and  $U_1(\cdot)$  is real analytic. Further, this solution is hyperbolically stable.*

*Proof.* An analytic version of the implicit function theorem is used, see [14, p. 15]. From standard results on products of Hölder continuous functions (see [38, p. 268]) it is easy to show that  $F$  is continuous. Indeed since  $F$  is quadratic in  $U$  and linear in  $\epsilon$ , it is clear that it is analytic. Since  $\mathcal{L}$  has a bounded inverse, the existence and analyticity follow. The hyperbolicity and stability are consequences of the corresponding property for  $U(0)$  [14].  $\square$

This theorem shows that  $U_1$  perturbs smoothly under  $\epsilon$ . However, we want to prove that  $U(\epsilon)$  is a biologically relevant solution, that is it lies in the closed positive cone. The following results show that a great deal of information concerning  $U(\epsilon)$  may be obtained under minimal assumptions on  $M$ , which are biologically natural. A preliminary result concerning the powers of  $M$  is needed; its proof follows from Lemma 8.1 in the Appendix.

LEMMA 3.5. *For each  $i$  with  $2 \leq i \leq n$  there are precisely two possibilities:*

(i) *There is a  $p = p(i)$  with  $1 \leq p \leq n - 1$  such that*

$$(M^k)_{i1} \begin{cases} = 0 & (1 \leq k < p), \\ > 0 & (k = p). \end{cases}$$

*The irreducibility of  $M$  [1] is sufficient (but not necessary) for this to hold for all  $2 \leq i \leq n$ .*

(ii)  $(M^k)_{i1} = 0 \quad (k \geq 1)$ .

COROLLARY 3.6. *Suppose mutation is ‘step-wise’ [3], that is in addition to (H2) the entries of  $M$  above and below the principal diagonal are strictly positive and all other off-diagonal elements are zero. Then  $p(i) = i - 1$ .*

THEOREM 3.7. *Put  $\hat{U}(\epsilon) = U_1(\epsilon) - U_1$ . Fix  $i$  with  $2 \leq i \leq n$  and suppose that for this choice of  $i$  case (i) in Lemma 3.5 holds. Then for  $0 < \epsilon < \epsilon_0$ ,*

$$(3.10) \quad \hat{U}(\epsilon)_i = \epsilon^{p(i)} v_i + O(\epsilon^{p(i)+1})$$

*where  $v_i$  is independent of  $\epsilon$  and  $v_i(x) > 0$  ( $x \in \bar{\Omega}$ ). If case (ii) holds, then  $\hat{U}(\epsilon)_i \equiv 0$  on  $\bar{\Omega}$ .*

*Proof.* From Theorem 3.4,  $\hat{U}(\epsilon)$  is a real analytic function of  $\epsilon$ , so the aim is to show that the first non-zero term in the Taylor series expansion of the  $i^{\text{th}}$  component is of the form (3.10). Define  $\partial_\epsilon^k \hat{U}(0) = [\partial^k \hat{U}(\epsilon) / \partial \epsilon^k]_{\epsilon=0}$ , and note that  $\hat{U}(\epsilon)$  satisfies the equation

$$\mathcal{L}\hat{U}(\epsilon) = -\epsilon M(U_1 + \hat{U}(\epsilon)) + \langle \mathbf{1}, \hat{U}(\epsilon) \rangle \hat{U}(\epsilon).$$

Since  $\hat{U}(0) = 0$ , differentiation of this equation yields on setting  $\epsilon = 0$ ,

$$(3.11) \quad \mathcal{L}\partial_\epsilon \hat{U}(0) = -MU_1,$$

$$(3.12) \quad \mathcal{L}\partial_\epsilon^k \hat{U}(0) = \sum_{j=1}^{k-1} \binom{k}{k-j} \langle \mathbf{1}, \partial_\epsilon^{k-j} \hat{U}(0) \rangle \partial_\epsilon^j \hat{U}(0) - kM\partial_\epsilon^{k-1} \hat{U}(0) \quad (k \geq 2).$$

By Lemma 3.3,  $\mathcal{L}$  is invertible, Thus (3.11) and (3.12) may be solved by multiplying (3.11) by  $\mathcal{L}^{-1}$ , substituting for  $\partial_\epsilon \hat{U}(0)$  in (3.12) with  $k = 2$ , and continuing inductively to back substitute in (3.12) with  $k = 3, 4, \dots$ . Recalling that  $U_1 = (\bar{u}_1, 0, \dots, 0)$  and  $i \geq 2$ , one readily sees that if  $[\partial_\epsilon^j \hat{U}(0)]_i = 0$  for  $j = 1, \dots, k - 1$ , then the  $i^{\text{th}}$  component of the first term on the right hand side of (3.12) is zero. It follows from the form of  $\mathcal{L}^{-1}$  that  $[\partial_\epsilon^k \hat{U}(0)]_i$  is non-zero if and only if  $[M\partial_\epsilon^{k-1} \hat{U}(0)]_i \neq 0$ . That is a non-zero term appears only through the second term in (3.12), and using Lemma 8.1 (and the remark following the proof), we obtain for each  $i$

$$[\partial_\epsilon^k \hat{U}(0)]_i = 0 \quad (k < p(i)),$$

$$[\partial_\epsilon^{p(i)} \hat{U}(0)]_i = p(i)! [(-\mathcal{L}^{-1}M)^{p(i)} U_1]_i.$$

The lemma also shows that this term is positive. □



COROLLARY 3.8. *For the step-wise mutation of Corollary 3.6,*

$$[\hat{U}(\epsilon)]_i = \epsilon^{i-1}v_i + O(\epsilon^i) \quad (2 \leq i \leq n) \quad .$$

The biological implications of Theorem 3.7 and Corollary 3.8 may be briefly summarized as follows. Under minimal conditions on the mutation matrix  $M$ , the stable equilibrium  $U_1 = (\tilde{u}_1, 0, \dots, 0)$  never leaves the positive cone (and so is always feasible) and remains stable. If the first case of Lemma 3.5 holds for each component (for which the irreducibility of  $M$  is sufficient), the equilibrium  $U_1$  enters the interior of the positive cone, that is each component is strictly positive. In a special case (step-wise mutation), but one with perhaps the most frequently encountered assumption on mutation, the size of the components decrease in powers of  $\epsilon$  as the ‘distance’ (in the sense of mutation) from the first component increases.

The section concludes with some technical results needed in the next section. Consider the situation near  $U_i (i \geq 2)$  and let  $u_i = \tilde{u}_i + v_i$ ,  $u_j = v_j (j \neq i)$ ; note that  $v_j \geq 0$  in  $K^+$  if  $j \neq i$ , but  $v_i$  is not necessarily positive, although  $u_i = \tilde{u}_i + v_i \geq 0$  obviously lies in  $K^+$ .  $B(U_i, \delta)$  will denote the closed ball in  $[C(\bar{\Omega})]^n$  with  $\|\cdot\|_\infty$ , center  $U_i$ , radius  $\delta$ .

LEMMA 3.9. *Fix any  $i$  with  $2 \leq i \leq n$ . Let  $\lambda, \phi$  be the principal eigenvalue and eigenfunction respectively of  $L_1[\tilde{u}_i; d_{i-1}]$ . Then  $\lambda > 0$ , and there is a  $\delta > 0$  such that for small enough  $\epsilon, p$ ,  $\underline{v} = \gamma \exp(pt)\phi$  is a subsolution for the  $(i-1)^{\text{th}}$  equation in  $B(U_i, \delta) \cap K^+$ .*

*Proof.* The  $(i-1)^{\text{th}}$  equation is

$$\begin{aligned} \frac{\partial v_{i-1}}{\partial t} - d_{i-1}\Delta v_{i-1} - (a - \tilde{u}_i)v_{i-1} = \\ \epsilon M_{i-1,i}\tilde{u}_i + \epsilon M_{i-1,i-1}v_{i-1} + \epsilon M_{i-1,i}v_i + \epsilon \sum_{j \neq i, i-1} M_{i-1,j}v_j - v_{i-1} \sum_{j=1}^n v_j \quad . \end{aligned}$$

Substitution of  $\underline{v}$  in the above equation shows that we need to prove that

$$\gamma \exp(pt)(p - \lambda - \epsilon M_{i-1,i-1} + \sum_i^n v_j)\phi \leq \epsilon M_{i-1,i}(\tilde{u}_i + v_i) + \epsilon \sum_{j \neq i, i-1} M_{i-1,j}v_j.$$

Both terms on the right hand side are non-negative. With  $n\delta < \lambda$ , for small enough  $\epsilon$  and  $p$ , the bracketed term on the left hand side is  $< 0$ .  $\square$

We can draw two important conclusions from this Lemma. The first is the following theorem.

THEOREM 3.10. *The equilibria  $U_i, (i \geq 2)$  do not perturb into  $\text{int}K^+$ , i.e. there are no equilibria in  $B(U_i, \delta) \cap \text{int}K^+$ . Similarly,  $\mathcal{O}$  is the only equilibrium in  $B(\mathcal{O}, \delta) \cap \text{int}K^+$ .*

The second point, which will be used in the next section, is that under the hypothesis of Lemma 3.9 the invariant set of  $(B(U_i, \delta) \cap \text{int}K^+)$  under (1.1) for small  $\epsilon > 0$  is empty, that is, any semi-orbit with initial condition in  $(B(U_i, \delta) \cap \text{int}K^+)$  eventually leaves this set.

**4. Global Dynamics under Mutation.** Having addressed the question of existence and stability of the equilibria of (1.1) in the previous section, we now turn to the problem of describing the global dynamics on  $K^+$ . When  $\epsilon = 0$ , by Theorem 3.2 there are no equilibria in  $\text{int}K^+$ . As  $\epsilon$  increases, by Theorem 3.10 none of the boundary equilibria, except perhaps  $U_i$ , can perturb into  $\text{int}K^+$ . Furthermore, by Theorems 3.4 and 3.7,  $U_1(\epsilon)$  lies in  $K^+$  and is hyperbolically stable; if the mutation is step-wise (Corollary 3.6), by Corollary 3.8,  $U_1(\epsilon)$  lies in  $\text{int}K^+$ . It is, therefore, plausible that  $U_1(\epsilon)$  is a global attractor for  $\text{int}K^+$  and it is the purpose of the present section to see how far we can go in proving this.

In outline the argument is based on assuming that the global dynamics are known when  $\epsilon = 0$ . This enables us to find a Morse decomposition of the flow. The importance of this is

that Morse decompositions in general are stable under small perturbations, and this enables us to deduce the dynamics for small  $\epsilon$ . The principal difficulty is in obtaining the unperturbed dynamics; we shall see that this may be done when  $n = 2$  for the system is competitive and may be made cooperative by a change of variable, see [17] for background. The results of [19, 18, 33] may be used to yield Lemma 4.1 below, since by Theorem 3.2 there are no equilibria in  $\text{int}K^+$ . For  $n > 2$  this trick can no longer be applied, but we conjecture that the dynamics has similar structure. This does not seem to be easy to prove. In a fairly special case for three species [7] the result holds, and numerical evidence supports the conjecture. The fact that for a simple system of equations such as (1.1) there do not appear to be any general techniques for determining when the set of critical points form a Morse decomposition seems to indicate how poorly understood the interaction between diffusion and heterogeneity of domain is for the dynamics generated by reaction-diffusion systems.

The analysis is set in  $[C(\bar{\Omega})]^n$ . From the remarks at the end of section 2 it is known that the system generates a semi-flow on this space and that there is a global attractor. Let  $\text{Inv}K^+$  denote the set of bounded solutions in  $K^+$ . The  $\omega$  and  $\alpha$ -limit sets of a point  $u$  are denoted by  $\omega(u)$  and  $\alpha(u)$ , respectively. A finite collection of disjoint compact invariant subsets of  $\text{Inv}K^+$ ,

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

is a *Morse decomposition* if for every  $u \in \text{Inv}K^+ \setminus \cup_{p=1}^P M(p)$ , there exists  $p$  with  $1 \leq p \leq P$  such that  $\omega(u) \subset M(p)$ , and for each full trajectory in backward time through  $u$  there exists  $q$  such that  $p < q \leq P$  and  $\alpha(u) \subset M(q)$ .

Using this language, the above mentioned results for (1.1) when  $n = 2$  can be stated as follows.

LEMMA 4.1. *If  $n = 2$  and  $\epsilon = 0$ , the Morse decomposition for  $\text{Inv}K^+$  is given by  $M(1) = U_1, M(2) = U_2, M(3) = \mathcal{O}$ .*

*Proof.* From Theorem 3.2 there are no equilibria in  $\text{int}K^+$ . Furthermore,  $U_1$  is an asymptotically stable equilibrium and  $U_2$  is unstable. It follows from [[18],Theorem 5.1] and [[19],Theorem B] that the  $\omega$ -limit set of every  $u \in \text{int}K^+$  is  $U_1$ . On the boundary of  $K^+$  the flow is known from Lemma 2.2:  $U_1, U_2$  are, respectively, global attractors for the flows in the interior of the  $u_2 = 0$  and  $u_1 = 0$  axes. The existence of the stated Morse decomposition is an immediate consequence.  $\square$

We speculate that the following is true in general.

CONJECTURE 1. *The set  $\{U_i : i = 1, \dots, n\} \cup \mathcal{O}$  is a Morse decomposition of  $\text{Inv}K^+$  for  $\epsilon = 0$ .*

The rest of this section will be spent proving the following theorem.

THEOREM 4.2. *If Conjecture 1 holds, then for sufficiently small  $\epsilon > 0$ ,  $U_1(\epsilon)$  is a global attractor for all orbits in  $\text{int}K^+$ .*

Under appropriate conditions on  $M$  (essentially ensuring that if any phenotype is not identically zero, mutation leads to all phenotypes being produced), this result can be strengthened and  $\text{int}K^+$  replaced by  $K^+ \setminus \{\mathcal{O}\}$ .

PROPOSITION 4.3. *Under the hypothesis of Conjecture 1 the Morse decomposition of  $\text{Inv}K^+$  is given by*

$$M(p) = U_p, \quad p = 1, \dots, n \text{ and } M(n+1) = \mathcal{O}.$$

*Proof.* The assumption that  $\{U_i : i = 1, \dots, n\} \cup \mathcal{O}$  is a Morse decomposition implies that it is possible to order each equilibrium point according to the dynamics. Consider the dynamics on

$$K_{i,i-1}^+ := \{(u_1, u_2, \dots, u_n) \in K^+ \mid u_j = 0, j \neq i, i-1\}.$$

We are now in the setting of Lemma 4.1 in which case we know that the flow induced order is  $\mathcal{O}$  greater than  $U_i$  greater than  $U_{i-1}$ . The only order on  $\{U_i \mid i = 1, \dots, n\} \cup \mathcal{O}$  which is consistent with the orderings from each face  $K_{i,i-1}^+$  is the one of the proposition.  $\square$

The importance of the Morse decomposition is that in general it is robust with respect to perturbation. Unfortunately, in the setting we are considering here we are not interested in the perturbation of invariant sets in  $[C(\bar{\Omega})]^n$ , but only in  $K^+$ . From Theorem 3.10 it is clear that some of the Morse sets may perturb outside of  $K^+$ . Therefore, rather than being able to quote the standard perturbation results, we must reprove them in this special setting.

REMARK 1. *The existence of the above Morse decomposition of  $\text{Inv}K^+$  is equivalent to the existence of a continuous function  $V : N \rightarrow \mathbf{R}$  where  $N$  is any neighbourhood of  $\text{Inv}K^+$  relative to  $K^+$  with the following properties:*

- (1)  $M(p) \in V^{-1}(p)$ ,
- (2) given  $u \in N \setminus \bigcup_{p=1}^{n+1} M(p)$ ,

$$V(u) > V(\varphi(t, u)) \quad (t > 0).$$

The function  $V$  will be used to control the global dynamics for  $\epsilon > 0$ .

LEMMA 4.4. *Given  $\eta > 0$  there exists a neighbourhood  $W$  of  $\text{Inv}K^+$  relative to  $K^+$ ,  $\mu > 0$ , and  $T = T(\mu) > 0$  such that for all  $t > T$ , if  $u \in W$  and*

$$\varphi([0, t], u) \subset W \setminus \left( \bigcup_{p=1}^{n+1} B_\eta(M(p)) \right),$$

then

$$V(u) - V(\varphi(t, u)) > \mu.$$

*Proof.* Let  $W^s(M(p)) := \{u \in K^+ \mid \omega(u) = M(p)\}$  and let

$$u \in W^s(M(p)) \cap \partial B_\eta(M(p)) \cap \text{Inv}K^+.$$

Assuming that  $u \neq M(q)$  for some  $q \neq p$ ,  $V(u) > V(\varphi(t, u))$  for  $t > 0$ . Since  $V$  is continuous and  $\text{Inv}K^+$  is compact, there exists  $\mu_p > 0$  such that  $V(u) \geq p + \mu_p$ .

The lemma now follows from a proof by contradiction. In particular, fix  $T > 0$  and assume that there exist sequences  $\{u^n\} \subset N$  and  $\{\mu_n\} \subset (0, \infty)$  such that  $\mu_n \rightarrow 0$ ,  $\varphi([0, t], u) \subset W \setminus \left( \bigcup_{p=1}^{n+1} B_\eta(M(p)) \right)$ , and  $V(u^n) - V(\varphi(T, u^n)) < \mu_n$ . Observe that since  $\text{Inv}K^+$  is compact it can be assumed that  $u^n \rightarrow \bar{u} \in \text{Inv}K^+ \setminus \left( \bigcup_{p=1}^{n+1} B_\eta(M(p)) \right)$ . Now

$$\begin{aligned} 0 &< V(\bar{u}) - V(\varphi(T, \bar{u})) \\ &= \lim_{n \rightarrow \infty} (V(u^n) - V(\varphi(T, u^n))) \\ &< \lim_{n \rightarrow \infty} \mu_n = 0, \end{aligned}$$

a contradiction.  $\square$

From now on we assume that  $0 < \eta < \delta/2$  where  $\delta$  is chosen to satisfy Lemma 3.9 and such that given  $u \in B_\eta(M(p))$  and  $v \in B_\eta(M(q))$  with  $p \neq q$ ,  $|V(u) - V(v)| > 1/2$ . We now choose  $0 < \mu < 1/4$ .

*Proof. (of Theorem 4.2)* Let  $InvK_\epsilon^+$  denote the maximal invariant set in  $K^+$  under (1) with  $\epsilon > 0$ , and let  $\varphi_\epsilon$  denote the corresponding semiflow. By upper semicontinuity of attractors, given  $W$  as in Lemma 4.4, there exists  $\epsilon_1$  such that for all  $\epsilon \in (0, \epsilon_1)$ ,  $InvK_\epsilon^+ \subset W$ . Since  $\epsilon$  represents a continuous perturbation of (1), there exists  $\epsilon_2 \in (0, \epsilon_1)$  such that for all  $\epsilon \in (0, \epsilon_2)$ ,  $u \in W$ , and  $t \in [0, T]$ ,  $\|\varphi(t, u) - \varphi_\epsilon(t, u)\| < \mu/3$ .

To complete the proof we shall show that for  $\epsilon > 0$ , but sufficiently small, if  $u \in intK^+$ , then  $\omega(u, \varphi_\epsilon) = U_1(\epsilon)$ . Since  $V$  decreases uniformly with time on  $InvK^+ \setminus (\cup_{p=1}^{n+1} B_\eta(M(p)))$ , there exists  $T'_\epsilon > 0$  such that  $\varphi(T'_\epsilon, u) \in B_\eta(M(p))$  for some  $p > 1$ . Given our choice of  $\eta$  and  $\mu$ , it now follows that  $\varphi_\epsilon(t, u) \notin B_\eta(M(q))$  for any  $q > p$  and  $t > T'_\epsilon$ . By induction we may now assume that  $p$  and  $T'_\epsilon$  have been chosen such that  $\varphi_\epsilon(T'_\epsilon, u) \in B_\eta(M(p))$  and for all  $t > T'_\epsilon$ ,  $\varphi_\epsilon(t, u) \notin B_\eta(M(q))$  for  $q \neq p$ . Let  $v_\epsilon = \varphi_\epsilon(T'_\epsilon, u)$ . By Lemma 4.4, for any positive integer  $k$ ,  $\varphi_\epsilon([kT, (k+1)T], v_\epsilon) \cap B_\eta(M(p)) \neq \emptyset$ . Therefore,  $\omega(v_\epsilon, \varphi_\epsilon) = \omega(u, \varphi_\epsilon) \cap B_\eta(M(p)) \neq \emptyset$ . However, by Lemma 3.9 and the following remarks,  $\omega(v_\epsilon, \varphi_\epsilon) \not\subset B_\eta(M(p))$ . Let  $w_\epsilon \in \omega(v_\epsilon, \varphi_\epsilon) \setminus B_\eta(M(p))$ . By the compactness of  $InvK^+$  we can choose a sequence  $\{\epsilon_k\}$  such that  $\epsilon_k \rightarrow 0$  and  $w_{\epsilon_k} \rightarrow w$ . Then  $w \in InvK^+$  and  $p - 3/4 < V(\varphi(\mathbf{R}, w)) < p + 3/4$ . Since  $\{M(p)\}$  is a Morse decomposition of  $InvK^+$ ,  $w = M(p)$ , a contradiction since  $w \notin B_\eta(M(p))$ . Therefore, for  $\epsilon > 0$  but sufficiently small  $\omega(u, \varphi_\epsilon) = U_1(\epsilon)$  and hence  $U_1(\epsilon)$  is the global attractor for  $intK^+$ .  $\square$

**5. Convergence and Robustness - Numerical Investigations.** We consider in this section computations to elucidate the convergence to  $U_1(\epsilon)$  for small mutation rates  $\epsilon$  and the robustness of the results if the slowest diffuser suffers a ‘‘penalty’’ for a low diffusion rate. It will be assumed throughout that the function  $a$  modelling the per capita rate of increase at low densities has the form

$$(5.13) \quad a(x) = \hat{a} + \tanh\left(\frac{x - 1/2}{\delta}\right) \quad ,$$

where  $\hat{a}$ , the average of  $a$ , and  $\delta$  are parameters to be chosen. With  $\delta$  chosen small, this choice of  $a$  reflects an environment divided into regions where the per capita rate of increase is low for  $0 < x < 1/2$  and high for  $1/2 < x < 1$ .

The theoretical investigation suggests that, for small  $\epsilon$ , the solution converges to the equilibrium  $U_1(\epsilon)$  which consists principally of the slowest diffuser together with small populations of phenotypes with higher diffusion rates in the proportions given by Theorem 3.7 and Corollary 3.8. As was indicated in the previous section, a full proof of this result has only been possible when  $n = 2$ . Furthermore, the theory as developed so far gives no information as to the manner of convergence, its rate and so on. Numerical calculations have been carried out in order to throw light on this question as well as to demonstrate the ultimate convergence to  $U_1$ . To set the scene, we suppose that a region, possibly an island, has been colonized by a small number of a species, and as is surely the most likely, that it is the fastest phenotype that does the colonizing; subsequently there is no migration across the boundary region. It is assumed there are 9 phenotypes with diffusion rates  $d_k$  satisfying

$$(5.14) \quad d_k = d_1 + (k - 1) \frac{d_9 - d_1}{8} \quad (1 \leq k \leq 9) \quad .$$

Here,  $d_1 = 0.01, d_9 = 1, \epsilon = 0.01, \hat{a} = 1$ , and the spatial domain is  $(0, 1)$ . The mutation matrix is chosen to have the simplest ‘‘step-wise’’ form  $M_{ii} = -2, M_{i, i-1} = M_{i, i+1} = 1$  ( $1 < i < n$ ), and  $M_{11} = -1, M_{12} = 1, M_{98} = 1, M_{99} = -1$  with all other elements zero. The initial value of the phenotypes is taken to be  $u(x, 0) = (0, 0, \dots, 0, 0, 1)$ . The results are presented in Figure 1 where the average values  $\bar{u}_i(t)$  for each phenotype are plotted against time and phenotype  $i$ . As expected,  $u_9$  first increases rapidly towards its (unstable) equilibrium value which is approximately  $(0, 0, \dots, 0, 1)$ . Mutation slowly produces small densities  $u_8, u_7, \dots$  until

$\hat{a}$	$\delta$	$\phi = d_0/d_1$	$\bar{U}_1$	$\bar{U}_2$	$\bar{U}_3$	$\bar{U}_4$	$\bar{U}_5$	$\bar{U}_6$	$\bar{U}_7$	$\bar{U}_8$	$\bar{U}_9$
1	0.01	100	1.1060	0.0101	*	*	*	0.0001	0.0039	0.0821	1.0572
1	0.01	10	1.0942	0.0469	0.0124	0.0113	0.0190	0.0449	0.1239	0.3351	1.1713
1	0.1	100	1.0873	0.0130	0.0001	*	*	0.0001	0.0039	0.0812	1.0516
1	0.1	10	1.0643	0.0598	0.0158	0.0132	0.0208	0.0471	0.1259	0.3322	1.1550
0.25	0.01	100	0.6132	0.0027	*	*	*	*	0.0012	0.0246	0.3196
0.25	0.01	10	0.6043	0.0518	0.0196	0.0165	0.0221	0.0396	0.0821	0.1733	0.5558
0.25	0.1	100	0.5780	0.0028	*	*	*	*	0.0011	0.0238	0.3134
0.25	0.1	10	0.5686	0.0497	0.0177	0.0145	0.0195	0.0357	0.0762	0.1655	0.5353

TABLE 1

Maximal averages of  $u_i(x, t)$  for different parameter combinations and  $\epsilon = 0.001$ . Values indicated by \* are less than  $10^{-4}$ .

eventually an appreciable amount of  $u_1$  appears, which then increases rapidly towards the stable equilibrium  $U_1(\epsilon)$ . An interesting observation is that the phenotypes near the “center” on the phenotype scale, for example  $u_4, u_5$ , never reach appreciable proportions and are likely to be difficult to observe.

To test further the robustness of the phenomena observed in Fig 1, we submit a table of the maximal averages

$$\bar{U}_k = \max \int_0^1 u_k(x, t) dx$$

for different combinations of parameter values. It is evident from these results that maximal averages are high only for the very highest and lowest dispersal rates. Graphs similar to Figure 1 (not shown here) confirm that the high maximal average of  $u_9$  is due to an initial transient, whereas the high maximal average of  $u_1$  is due to the attraction to the stable equilibria  $U_1(\epsilon)$ . Furthermore, intermediate phenotypes again never reach appreciable proportions.

We next turn to the question of robustness of the results concerning the evolution towards small diffusion rates. It will certainly be the case in many realistic biological situations that the reaction terms will not be independent of the diffusion rates. For example, if the diffusion rate of a phenotype is very small, it may suffer a penalty from self-competition between parent and offspring. On the other hand, there will be a cost in supporting high dispersal. The second factor will produce an advantage for low dispersal rates, which will reinforce the general direction of our results. However, the first will act towards reducing and eventually destroying the advantage predicted for low diffusion. In order to see how difficult it is to reverse the predicted direction of evolution, we consider a simple model where there are 2 phenotypes and mutation does not act. Consider then the system

$$(5.15) \quad u_t = d_1 u_{xx} + u(\alpha(x) - u - v) \quad ,$$

$$(5.16) \quad v_t = d_2 v_{xx} + v(\beta(x) - u - v) \quad ,$$

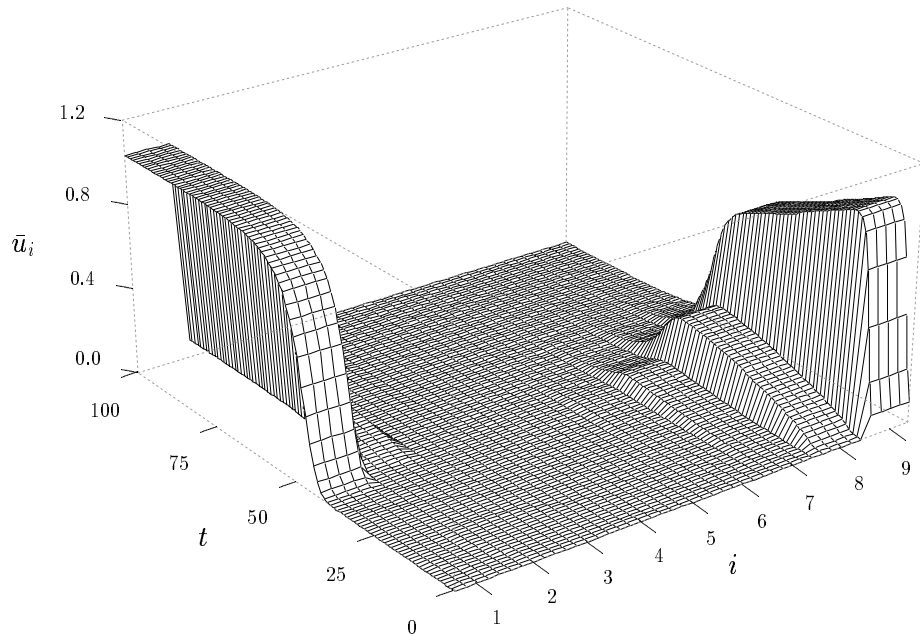


FIG. 1. *Colonization Figure: spatial averages  $\bar{u}_i(t)$  are plotted for each phenotype  $i$ . Note that the slowest diffuser dominates the dynamics for large  $t$ . Parameter values for the run were  $\epsilon = \delta = d_1 = 0.01$ ,  $d_9 = 1$ ,  $\hat{a} = 1$ .*

where

$$(5.17) \quad \alpha(x) = \hat{\alpha} + \tanh\left(\frac{x-1/2}{\delta}\right) - \lambda \quad ,$$

$$(5.18) \quad \beta(x) = \hat{\alpha} + \tanh\left(\frac{x-1/2}{\delta}\right) \quad ,$$

and  $d_1 < d_2$ . Thus  $\lambda$  is a penalty parameter for the slower diffuser.

In Figure 2, AUTO [8] was used to compute the equilibria  $\vec{u}_0$  of (5.15)-(5.16) for fixed  $d_1 = 0.05$ . Curves AC and DF represent the  $L^2$  norms of  $U_1 = (\tilde{u}_1, 0)$  and  $U_2 = (0, \tilde{u}_2)$ , respectively, as a function of  $\lambda$ . At the point B,  $U_1$  becomes unstable, throwing off a stable coexistence equilibrium into the interior, which at E is absorbed into  $U_2$  producing a stable equilibrium.

By augmenting the system (5.15)-(5.16) with its linearization about  $U_1$  and  $U_2$ , AUTO was then used to continue the branch points B and E in the  $(\lambda, d_1)$ -plane. The results of these computations are shown in Figure 3 where curves I and II correspond to branchpoints B and E, respectively. Thus, Figure 3 describes the overall effect of varying  $\lambda$  and  $d_1$  on the equilibria  $U_1$  and its stability. To the left of the curve labelled I,  $U_1$  is the sole stable equilibria. Between the curves I and II a stable (coexistence) equilibrium has bifurcated from  $U_1$  into the interior of the feasible region. As  $\lambda$  increases further, the equilibrium moves towards  $U_2 = (0, \tilde{u}_2)$  and on reaching II is absorbed into  $U_2$ .

The firm conclusion is that the model is robust, almost surprisingly strongly robust, at least if  $d_1$  is small. A considerable penalty of  $\lambda$  up to about 0.5 is allowed, which is the same order of magnitude as the variation in  $\alpha$ .

**6. Concluding Remarks.** We start by summarizing some of the implications of the results of the analysis from a biological point of view. The equations model a situation where in a spatially inhomogeneous environment the phenotypes of a species differ only in their dispersal rates. Mutation is allowed and may be of a very general nature. We show that there is a strong evolutionary force causing the phenotype with the lowest diffusion rate to be favoured. We are able to prove the main thrust of this assertion analytically, but are not able to give a full proof in the most general case. However, extensive numerical computations have been carried out to confirm the assertions.

The computations highlight an interesting feature of the evolutionary trend. Assume that an island is first colonized by the  $n$ -th phenotype, a plausible assumption because it has the highest dispersal rate. Then mutation produces phenotypes  $1, \dots, (n-1)$  and the dynamics rapidly drive the system towards an equilibrium consisting of the first phenotype together with small proportions of the others. The computations (see Figure 1 and Table 1) show strikingly that with stepwise mutation, the total populations of intermediate phenotypes always remain extremely small. Thus, perhaps rather surprisingly, it appears likely that these will not be observed.

A second important question concerns the robustness of the result. As has been observed, the dynamics are driven by the difference in the diffusion rates alone. This is a somewhat unfamiliar situation in models of this nature, but intuition may suggest that the trend noted might be rather sensitive to changes in the reaction terms. In particular, if, as is not unlikely, the slowest diffuser suffers a penalty in its birth rate, the trend might be reversed. The computations in section 5 do not confirm this view. These computations show rather strikingly that the conclusions are extremely robust and a rather substantial penalty is needed to reverse the trend.

The model raises some interesting mathematical questions. In the study of the of the dynamics of reaction-diffusion systems, it is normally expected that differences in the reaction terms will play a central role. However, in the present case the per-capita rates of increase represented by these terms are identical. Thus, the dynamics are principally driven by the differences in the

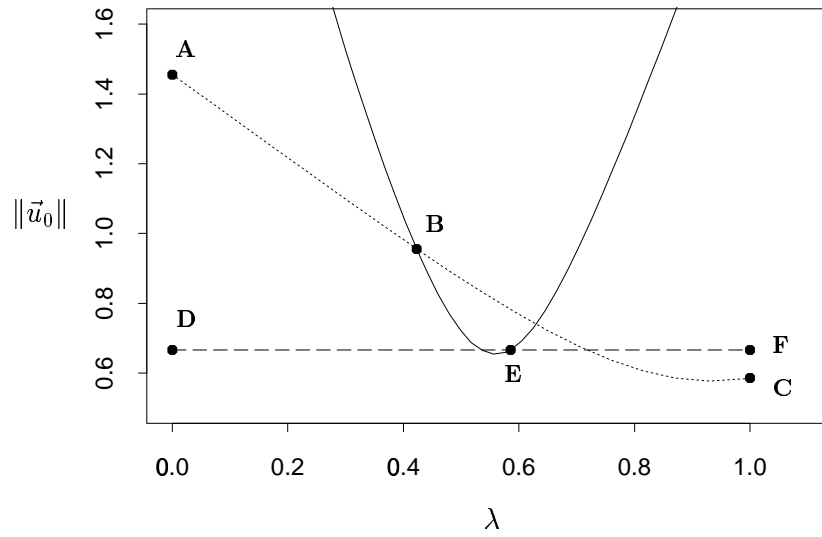


FIG. 2.  $L^2$  norm of equilibrium  $\vec{u}_0$  as a function of the penalty parameter  $\lambda$ . Three branches of the solution intersect at branch points labelled  $B$  and  $E$ .  $\hat{\alpha} = 0.25$ ,  $\delta = 0.1$ ,  $d_1 = 0.05$ ,  $d_2 = 1$ .



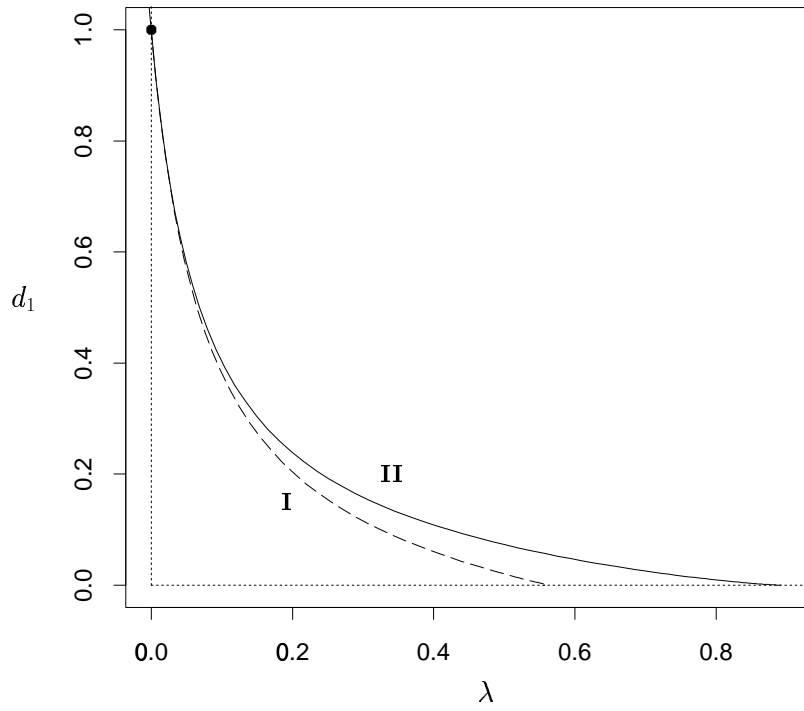


FIG. 3. Branchpoint continuation in  $(\lambda, d_1)$ -plane. Curves I and II are branchpoints corresponding to the equilibria  $(\bar{u}(x), 0)$  and  $(0, \bar{v}(x))$ , respectively. Between curves I and II, the coexistence equilibrium is stable.  $\hat{\alpha} = 0.25, \delta = 0.1, d_2 = 1$

diffusion rates. This situation seems not to be well understood, as is apparent in the discussion in Section 4. There we wished to show that the set of critical points (all of which are known, together with their local stability properties) form a Morse decomposition. This follows from standard results on monotone dynamical systems when  $n = 2$ . However, for  $n > 2$  techniques do not appear to exist for tackling this problem, and we have been forced to leave this an open question.

The analysis raises some other questions that are all of mathematical and biological interest and are worth further investigation. The first we mention is to describe at least the gross manner of convergence to  $U_1(\epsilon)$ . An attempt is being made to analyze this question by devising appropriate shadow systems, but the results are as yet too incomplete to present here. The second question is to enquire what form the results would take if the genetics were diploid. The final question is to introduce an environment that is both spatially inhomogeneous and temporally periodic. Even the local analysis raises challenging questions concerning estimates for the eigenvalues of periodic parabolic problems. However, it is a particularly interesting problem because intuition does not suggest obvious answers. Preliminary results in very special cases suggest that the effect of temporal variation, if the frequency is sufficiently large, is to cause evolution to favour the phenotype with the largest diffusion rate and so to reverse the trend discussed in this paper.

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**8. Appendix.** LEMMA 8.1. *Assume  $n > 1$ , and let  $N$  be an  $n \times n$  matrix with  $N_{ij} \geq 0$  for all  $i, j$  such that  $i \geq 2$  and  $i \neq j$ . Then for each  $i$  with  $2 \leq i \leq n$ , one of the following possibilities holds.*

(i) *There is a  $p = p(i)$  with  $1 \leq p \leq n - 1$  such that*

$$(N^k)_{i1} \begin{cases} = 0 & (1 \leq k < p) \\ > 0 & (k = p) \end{cases} .$$

(ii)  $(N^k)_{i1} = 0 \quad (k \geq 1)$ .

*Proof.* Fix  $i$  with  $2 \leq i \leq n$  throughout the proof. If  $(N^k)_{i1} = 0$  for  $1 \leq k \leq n - 1$ , by the Cayley-Hamilton theorem, case (ii) holds. If case (ii) does not hold, there is a  $p$  with  $1 \leq p \leq n - 1$  such that  $(N^k)_{i1} = 0$  for  $1 \leq k < p$  and  $(N^p)_{i1} \neq 0$ . If  $p = 1$ , by a condition of the lemma,  $N_{i1} \geq 0$  and (i) follows. Thus to prove the lemma it is enough to show that  $(N^p)_{i1} \geq 0$  for  $p \geq 2$ .

The key idea in the proof is to show that if a diagonal component  $N_{jj}$  or a component in the first row of  $N$  occurs in  $(N^p)_{i1}$ , it is multiplied by a factor which is zero. Thus only non-negative terms can occur.

Throughout the proof, terms of the form  $j_s$  are integers with  $1 \leq j_s \leq n$ . Set  $\Pi_1 = N_{i1} = 0$ , and for  $k \geq 2$  let  $\Pi_k$  be any product of the form

$$N_{ij_1} N_{j_1 j_2} \cdots N_{j_{k-1} 1} .$$

The first step is to prove that if  $1 \leq k \leq p-1$ ,  $\Pi_k = 0$  for any  $j_s$  with  $1 \leq s \leq k-1$ . The proof is by induction. The result is clearly true for  $k=1$ . It is thus enough to show that if  $k \leq p-2$  the statement  $(A_k)$ :

$$\Pi_s = 0 \quad (1 \leq j_1, \dots, j_{s-1} \leq n, 1 \leq s \leq k),$$

implies that  $(A_{k+1})$  holds. Now

$$(8.19) \quad 0 = (N^{k+1})_{i1} = \sum N_{ij_1} \dots N_{j_k 1} \quad ,$$

where the summation sums over all  $j_s$  with  $1 \leq s \leq k$ . Thus each term in the sum is of the form  $\Pi_{k+1}$ . If any  $\Pi_{k+1}$  contains a diagonal term, there are various possibilities. The first is that for some  $s$  with  $2 \leq s \leq k-1$  and some  $\Pi_k$ ,

$$\begin{aligned} \Pi_{k+1} &= N_{ij_1} \dots N_{j_{s-1} j_s} N_{j_s j_s} N_{j_s j_{s+1}} \dots N_{j_k 1} \\ &= N_{j_s j_s} \Pi_k \\ &= 0 \end{aligned}$$

by the induction hypothesis. Alternatively, the first term in  $\Pi_{k+1}$  may be of the form  $N_{ii}$  or its last term may be  $N_{i1}$ . By the same argument,  $\Pi_{k+1} = 0$  in these cases also. A very similar argument shows that any product which contains a term of the form  $N_{1m}$  is also zero. By the conditions of the Lemma, all the other terms in the sum in equation (8.19) are non-negative. Hence every term in this sum is non-negative, and it follows from (8.19) that each term is zero. This proves the assertion  $(A_{k+1})$  and the result follows by induction.

It is now easy to complete the proof. We have

$$\begin{aligned} (N^p)_{i1} &= \sum N_{ij_1} \dots N_{j_{p-1} 1} \\ &= \sum \Pi_p \end{aligned}$$

in the notation above. By exactly the same argument as applied in the previous paragraph, if  $\Pi_p$  contains a diagonal term  $N_{ss}$ , say, then

$$\Pi_p = N_{ss} \Pi_{p-1} = 0$$

by what was proved above. The same argument applies if  $\Pi_p$  contains a term of the form  $N_{1m}$ . Since by assumption of the Lemma all other terms are non-negative, it follows that  $(N^p)_{i1} \geq 0$ .

□

Of course Lemma 3.5 follows immediately from this result. It is clear that the result applies when the elements of the matrix are operators, positivity going over unchanged. We note that from (H2) and Lemma 3.3,  $(-\mathcal{L}^{-1}M)$  has the sign structure (in the sense of operators) asserted in the statement of Lemma 8.1. This is central to the proof in Theorem 3.7.

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