

TWO-SPECIES COMPETITION WITH HIGH DISPERSAL: THE WINNING STRATEGY

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ABSTRACT. This paper is motivated by the following simple question: how does diffusion affect the competition outcomes of two competing species that are identical in all respects other than their strategies on how they spatially distribute their birth rates. This may provide us with insights into how species learn to compete in a relatively stable setting, which in turn may point out species evolution directions. To this end, we formulate some extremely simple two- species competition models that have either continuous or discrete diffusion mechanisms. Our analytical work on these models collectively and strongly suggests the following in a fast diffusion environment: where different species have the same birth rates *on average*, those that do well are those that have greater spatial variation in their birth rates. We hypothesize that this may be a possible explanation for the evolution of grouping behavior in many species. Our findings are confirmed by extensive numerical simulation work on the models.

1. Introduction. Recently, Hutson et al. [9] proposed and analyzed the reaction diffusion system

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

on a bounded domain Ω , with homogeneous Neumann boundary conditions. Equations (1.1) were taken as a simple model of two species that are identical in all respects, except for their birth rates. It is supposed that species u is a mutation of species v , and thus the difference between $\alpha(x)$ and $\beta(x)$ is viewed as small. The limiting resource subject to competition is implicitly assumed to be constant (such as habitable space) or has a dynamics much faster than that of the competition mechanism [12]. In these cases, conventional competition models such as (1.1) are plausible and can be employed to study issues related to how diffusion affect the competition outcomes of competing species that are identical in all respects other than their strategies on how they spatially distribute their birth rates. This may provide us with insights into how species learn to compete in a relatively stable setting, which in turn may point out species evolution directions.

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Two specific key ecological questions motivated the study of system (1.1) in [9]; (1) under what circumstances does the mutant u invade; and (2) if it does invade, does it drive the original phenotype v to extinction, or will there be coexistence? Some of the results proved in [9] about system (1.1) are rather striking. For example, when $\alpha(x) = \beta(x) + \tau g(x)$, it was shown that for a large class of functions $g(x)$ and small τ , the stability of the two species varies in a complex manner; in particular, stability can change back and forth many times as d is increased over $(0, \infty)$. In fact, for any positive integer n , the function $g(x)$ can be chosen (from an open set of possibilities) such that the stability of the semitrivial equilibria (i.e., equilibria with one component zero and the other positive, sometimes known as boundary equilibria) changes at least n times as d is increased from zero to infinity. Competition between the species and the mutant thus depends in a particularly delicate way on the balance between the diffusivity d and resource utilization as described by the form of the reproduction rate $\beta(x)$.

Another important result proved in [9] about system (1.1) is that there is no optimal form of resource utilization if there is no upper bound on birth rate functions. In other words, there is no birth rate $\beta(x)$ for species v that is optimal in the sense that an invading mutant u with birth rate $\beta(x) + \tau g(x)$, subject to a fairness assumption $\int_{\Omega} g(x) dx = 0$, will necessarily die out. Said another way, given a particular value for the diffusivity and a particular spatially dependent birth function $\beta(x)$, there will always exist a birth rate $\alpha(x)$ for the mutant u that differs pointwise from $\beta(x)$ but is the same on average, such that u will invade.

The aim of the present paper is twofold. First, we continue the study in [9] by proving some further results about system (1.1). One result we establish concerns the case when $\beta(x) = \beta$, a constant. We prove that if $\alpha(x)$ is nonconstant but has mean value β , and *if the diffusivity d is sufficiently large*, then automatically the mutant u wins, driving v to extinction. This suggests that, for large diffusivities, if v has a constant birth rate then the mutant u has only to vary its birth rate at different points in space while preserving the same mean to win the competition. This is perhaps one possible explanation for the evolution of the *aggregation* (grouping together) tendency of many animals. Second, we consider a two-patch model analogous to (1.1) and investigate its properties, elucidating in particular how exactly the mutant must vary its birth rate to win the competition and drive the other to extinction. The advantages of using a patch model are that the analysis can be much more explicit than is possible for a nonautonomous reaction-diffusion system, and also that patch-type models are particularly amenable to computation. The dynamics of this two-patch model seems to agree with that of (1.1). Our analytical work on these models collectively and strongly suggests the following in a fast diffusion environment: where different species have the same birth rates *on average*, those that do well are those that have greater spatial variation in their birth rates. We hypothesize that this may be a possible explanation for the evolution of grouping behavior in many species. Our findings are confirmed by extensive numerical simulation work on the models.

The paper is organized as follows. We formulate and perform some pointed analysis of an extremely simple two-patch model for two similar competing species. In section 3, we continue the study in [9] by proving some new results about system (1.1). We conclude with a discussion section containing implications of our findings, simulation results, and statements of open questions.

2. A two-patch model. We propose the following simple two-patch system as a model for two similar competing species:

$$\begin{aligned}\frac{du_1}{dt} &= u_1(\alpha_1 - u_1 - v_1) + d(u_2 - u_1), \\ \frac{du_2}{dt} &= u_2(\alpha_2 - u_2 - v_2) + d(u_1 - u_2), \\ \frac{dv_1}{dt} &= v_1(\beta_1 - u_1 - v_1) + d(v_2 - v_1), \\ \frac{dv_2}{dt} &= v_2(\beta_2 - u_2 - v_2) + d(v_1 - v_2),\end{aligned}\tag{2.1}$$

in which all parameters are positive, v_i is the number of species v in patch i , u_i is the same for the mutant u , and there is diffusion between the two patches with diffusivity d . Naturally, we assume that $v_i(0) \geq 0$ and $u_i(0) \geq 0$, $i = 1, 2$. It is easy to show that all such solutions exist globally and have nonnegative component values. In fact, if $u_1(0) + u_2(0) > 0$, then one can easily show $u_i(t) > 0$ for $t > 0$, $i = 1, 2$. The same is true for v_i , $i = 1, 2$. Notice that

$$\frac{du_1}{dt} + \frac{du_2}{dt} \leq (u_1 + u_2)\{\max\{\alpha_1, \alpha_2\} - \frac{1}{2}(u_1 + u_2)\}.$$

A similar inequality holds for $v_1 + v_2$. Hence, we have the following uniform boundedness result.

LEMMA 2.1. *Solutions of (2.1) with positive initial values are uniformly bounded. In fact*

$$\limsup_{t \rightarrow \infty} (u_1(t) + u_2(t)) \leq 2 \max\{\alpha_1, \alpha_2\}, \quad \limsup_{t \rightarrow \infty} (v_1(t) + v_2(t)) \leq 2 \max\{\beta_1, \beta_2\}.$$

Notice also that

$$\frac{du_1}{dt} + \frac{dv_1}{dt} \geq (u_1 + v_1)\{\min\{\alpha_1, \beta_1\} - d - (u_1 + v_1)\}.$$

A similar inequality holds for $u_2 + v_2$. Hence, we have the following patch population persistence result.

LEMMA 2.2. *Assume $d < \min\{\min\{\alpha_1, \beta_1\}, \min\{\alpha_2, \beta_2\}\}$ in (2.1). Then populations in both patches persist. In fact, we have*

$$\liminf_{t \rightarrow \infty} (u_1(t) + v_1(t)) \geq \min\{\alpha_1, \beta_1\} - d, \quad \liminf_{t \rightarrow \infty} (u_2(t) + v_2(t)) \geq \min\{\alpha_2, \beta_2\} - d.$$

Except at the end of this section, we assume, without loss of generality, that

$$\beta_2 > \beta_1.$$

The following global stability result for $d = 0$ (which reduces (2.1) to a decoupled system) is elementary. This result is useful for understanding Figure 1 in the discussion section that depicts a bifurcation diagram of (2.1).

LEMMA 2.3. *Assume $\alpha_1 < \beta_1 < \beta_2 < \alpha_2$ and $d = 0$ in (2.1). Then*

$$\lim_{t \rightarrow \infty} (u_1(t), u_2(t), v_1(t), v_2(t)) = (0, \alpha_2, \beta_1, 0).$$

We study the dynamics of system (2.1) largely through the predictions of linearized analysis of the boundary equilibria (equilibria in which one of u or v is zero), together with numerical simulations to confirm these predictions. Linearized analysis about the boundary equilibria is tractable because the Jacobian matrix at a boundary equilibrium has a block diagonal structure. Unfortunately, it is very difficult to analytically study the linear stability of a coexistence equilibrium.

Let us first consider the boundary equilibrium with $u_1 = u_2 = 0$ (i.e., the mutant is absent). Intuitively, one expects that the v_1 and v_2 components of such an equilibrium would both be between β_1 and β_2 , and indeed it can be shown that the equilibrium equations $v_1(\beta_1 - v_1) + d(v_2 - v_1) = 0$, $v_2(\beta_2 - v_2) + d(v_1 - v_2) = 0$ admit precisely one such solution. After some algebra, one finds that the unique boundary equilibrium $(u_1, u_2, v_1, v_2) = (0, 0, v_1^*, v_2^*)$ is determined by

$$v_1^* = \frac{v_2^*(v_2^* - \beta_2)}{d} + v_2^*, \tag{2.2}$$

where v_2^* is the largest real root of $f(v_2) = 0$ with

$$f(v_2) := -\frac{v_2^3}{d^2} + \frac{2}{d} \left(\frac{\beta_2}{d} - 1 \right) v_2^2 + \left(\frac{\beta_1}{d} - 1 - \left(\frac{\beta_2}{d} - 1 \right)^2 \right) v_2 + \beta_1 + \beta_2 - \frac{\beta_1 \beta_2}{d} \tag{2.3}$$

(small values for d actually yield two roots of $f(v_2) = 0$ between β_1 and β_2 , but only the larger one produces an admissible value for v_1). For the subsequent analysis, we need some information on the size of v_2^* . Now

$$f(\beta_2) = \beta_1 - \beta_2 < 0,$$

while

$$\begin{aligned} f\left(\frac{1}{2}(\beta_2 - d + \sqrt{(\beta_2 - d)^2 + 4\beta_1 d})\right) &= \frac{1}{2}(\beta_2 + d) - \frac{1}{2}\sqrt{\beta_2^2 - 2\beta_2 d + d^2 + 4\beta_1 d} \\ &> 0, \quad \text{since } \beta_1 < \beta_2. \end{aligned}$$

Hence,

$$v_2^* \in \left(\frac{1}{2}(\beta_2 - d + \sqrt{(\beta_2 - d)^2 + 4\beta_1 d}), \beta_2 \right). \tag{2.4}$$

Linearizing about the equilibrium $(0, 0, v_1^*, v_2^*)$ in the usual way, one finds that the eigenvalue equation corresponding to trial solutions proportional to $\exp(\lambda t)$ is

$$\begin{aligned} &(\lambda^2 - (\alpha_1 + \alpha_2 - 2d - v_1^* - v_2^*)\lambda + (\alpha_1 - v_1^* - d)(\alpha_2 - v_2^* - d) - d^2) \\ &\times (\lambda^2 - (\beta_1 + \beta_2 - 2d - 2v_1^* - 2v_2^*)\lambda + (\beta_1 - 2v_1^* - d)(\beta_2 - 2v_2^* - d) - d^2) = 0. \end{aligned} \tag{2.5}$$

From the structure of the linearization matrix (Jacobian matrix) that led to equation (2.5), it is easy to appreciate that the second quadratic factor is associated with perturbations from $(0, 0, v_1^*, v_2^*)$ in which the u_i remain zero. We show that the eigenvalues attributable to this second quadratic factor have negative real parts. To do so, it suffices to show that the coefficient of λ and the constant term are both positive. The coefficient of λ will be positive if $v_1^* + v_2^* > \frac{1}{2}(\beta_1 + \beta_2) - d$, which is obviously true if $\frac{1}{2}(\beta_1 + \beta_2) < d$, and so it remains to consider the case when $\frac{1}{2}(\beta_1 + \beta_2) > d$. In this case, graphical considerations in the (v_1, v_2) plane reveal that it is sufficient to check that the intersection of the line $v_1 + v_2 = \frac{1}{2}(\beta_1 + \beta_2) - d$ with the curve $v_1 = \frac{v_2^2}{d} + v_2(1 - \frac{\beta_2}{d})$ is at a value of v_2 less than v_2^* . In other words, we need to check that the positive root v_2 of

$$g(v_2) := \frac{v_2^2}{d} + v_2 \left(2 - \frac{\beta_2}{d} \right) + d - \left(\frac{\beta_1 + \beta_2}{2} \right) = 0$$

is less than v_2^* . Since we assume $\beta_2 > \beta_1$, we know that (2.4) holds. Therefore, to show that the positive root of $g(v_2) = 0$ is less than v_2^* , it is sufficient to show

that the root is less than $\frac{1}{2}(\beta_2 - d + \sqrt{(\beta_2 - d)^2 + 4\beta_1 d})$, and this will follow if g is positive at the latter value. But

$$g(\frac{1}{2}(\beta_2 - d + \sqrt{(\beta_2 - d)^2 + 4\beta_1 d})) = \frac{1}{2}(d + \beta_1) + \frac{1}{2}\sqrt{\beta_2^2 - 2\beta_2 d + d^2 + 4\beta_1 d} > 0$$

as desired. Thus $v_1^* + v_2^* > \frac{1}{2}(\beta_1 + \beta_2) - d$. Checking that $(\beta_1 - 2v_1^* - d)(\beta_2 - 2v_2^* - d) - d^2 > 0$ can be done similarly. Our conclusion at this stage is that the boundary equilibrium $(0, 0, v_1^*, v_2^*)$ is locally stable to perturbations in which the u_i remain zero. It may of course be unstable to perturbations involving the introduction of the mutant u , and this will depend on the relative sizes of the birth rates α_i , β_i and the diffusivity d as we now show.

Considerations similar to those already described lead us to the existence of another boundary equilibrium, $(u_1^*, u_2^*, 0, 0)$, in which u_1^* and u_2^* are both between α_1 and α_2 . This equilibrium is linearly stable to perturbations in which the v_i remain zero. Next, we prove the following result, which predicts for large diffusivities that if the birth rates for the species v in the two patches are unequal, and if the mutant u increases the disparity between the birth rates (but preserving the same mean), then the mutant will win and drive the original species v to extinction.

PROPOSITION 2.1. *If $\beta_2 > \beta_1$ and $\alpha_1 = \beta_1 - \varepsilon$, $\alpha_2 = \beta_2 + \varepsilon$ with $0 < \varepsilon < \beta_1$, and d is sufficiently large, then $(0, 0, v_1^*, v_2^*)$ is unstable and $(u_1^*, u_2^*, 0, 0)$ is linearly stable.*

Proof. To show that $(0, 0, v_1^*, v_2^*)$ is unstable, it is sufficient to show that the first quadratic factor in the eigenvalue equation (2.5) yields an unstable eigenvalue (one such that $\text{Re } \lambda > 0$). We shall in fact show that a real positive eigenvalue exists, by proving that for d sufficiently large, the constant term in the first quadratic factor is negative, i.e., that

$$(\alpha_1 - v_1^*)(\alpha_2 - v_2^*) - d(\alpha_1 + \alpha_2 - v_1^* - v_2^*) < 0 \tag{2.6}$$

(with $\alpha_1 = \beta_1 - \varepsilon$ and $\alpha_2 = \beta_2 + \varepsilon$). This is not immediately clear since, as $d \rightarrow \infty$, v_1^* and v_2^* both approach $\frac{1}{2}(\beta_1 + \beta_2)$ so that the bracketed coefficient of d in (2.6) approaches zero. However, a little asymptotic analysis yields that

$$\begin{aligned} v_1^* &= \frac{\beta_1 + \beta_2}{2} - \frac{1}{4d}\beta_1(\beta_2 - \beta_1) + O\left(\frac{1}{d^2}\right), \\ v_2^* &= \frac{\beta_1 + \beta_2}{2} + \frac{1}{4d}\beta_2(\beta_2 - \beta_1) + O\left(\frac{1}{d^2}\right); \end{aligned}$$

so that after some algebra, the left hand side of (2.6) becomes

$$-\left(\frac{\beta_2 - \beta_1}{2} + \varepsilon\right)^2 + \left(\frac{\beta_2 - \beta_1}{2}\right)^2 + O\left(\frac{1}{d}\right),$$

which is negative for sufficiently large d , since $\beta_2 > \beta_1$ and $\varepsilon > 0$.

The characteristic equation of the linearization about $(u_1^*, u_2^*, 0, 0)$ is

$$\begin{aligned} &(\lambda^2 - (\beta_1 + \beta_2 - 2d - u_1^* - u_2^*)\lambda + (\beta_1 - u_1^* - d)(\beta_2 - u_2^* - d) - d^2) \\ &\times (\lambda^2 - (\alpha_1 + \alpha_2 - 2d - 2u_1^* - 2u_2^*)\lambda + (\alpha_1 - 2u_1^* - d)(\alpha_2 - 2u_2^* - d) - d^2) = 0 \end{aligned} \tag{2.7}$$

with $\alpha_1 = \beta_1 - \varepsilon$ and $\alpha_2 = \beta_2 + \varepsilon$, and this time we need to show for d sufficiently large that both quadratic factors produce only eigenvalues λ with $\text{Re } \lambda < 0$. The coefficients of λ in both factors are clearly positive for d sufficiently large (u_1^* and

u_2^* depend on d but are always between α_1 and α_2). Thus, we need to show that the constant terms are positive, i.e., that

$$(\beta_1 - u_1^*)(\beta_2 - u_2^*) - d(\beta_1 + \beta_2 - u_1^* - u_2^*) > 0 \quad (2.8)$$

and that

$$(\beta_1 - \varepsilon - 2u_1^*)(\beta_2 + \varepsilon - 2u_2^*) - d(\beta_1 + \beta_2 - 2u_1^* - 2u_2^*) > 0. \quad (2.9)$$

But for d large,

$$\begin{aligned} u_1^* &= \frac{\alpha_1 + \alpha_2}{2} - \frac{1}{4d}\alpha_1(\alpha_2 - \alpha_1) + O\left(\frac{1}{d^2}\right), \\ u_2^* &= \frac{\alpha_1 + \alpha_2}{2} + \frac{1}{4d}\alpha_2(\alpha_2 - \alpha_1) + O\left(\frac{1}{d^2}\right). \end{aligned}$$

Since $\alpha_1 = \beta_1 - \varepsilon$ and $\alpha_2 = \beta_2 + \varepsilon$ the left-hand side of (2.8) becomes

$$\frac{1}{4}((\beta_2 - \beta_1 + 2\varepsilon)^2 - (\beta_2 - \beta_1)^2) + O\left(\frac{1}{d}\right),$$

which is positive for d sufficiently large. Similarly, the left-hand side of (2.9) is given asymptotically in d by $(\beta_1 + \beta_2)d + O(1) > 0$. The proof of Proposition 2.1 is complete.

In an entirely similar way, we obtain the following proposition:

PROPOSITION 2.2. *If $\beta_2 > \beta_1$ and $\alpha_1 = \beta_1 + \varepsilon$, $\alpha_2 = \beta_2 - \varepsilon$ with $\varepsilon > 0$ but not too large and d is sufficiently large, then $(0, 0, v_1^*, v_2^*)$ is linearly stable and $(u_1^*, u_2^*, 0, 0)$ is unstable.*

For the case when the diffusivity d is large, our predictions thus far for model (2.1) mirror the results described in [9] regarding the absence of an optimal form of resource utilisation. It follows from Propositions 2.1 and 2.2 that, in system (2.1), there is no optimal way for the species v to choose its birth parameters β_1 and β_2 (optimal meaning that the mutant would die out whatever the values of its birth parameters α_1 and α_2 , subject to a ‘‘fairness condition’’ $\alpha_1 + \alpha_2 = \beta_1 + \beta_2$). However, Propositions 2.1 and 2.2 do throw more light on what the mutant’s strategy must be for it to win. Essentially, if β_1 and β_2 are unequal and if the mutant widens the disparity between these birth rates (i.e., adopts a higher birth rate in the patch where the birth rate for v is already high, and a lower birth rate than v in the other patch), then the mutant will win (if d is large enough). On the other hand, if the species v has unequal birth rates and the mutant ‘‘closes the gap,’’ subject to $\alpha_1 + \alpha_2 = \beta_1 + \beta_2$, then the mutant will become extinct if d is large.

It is natural to wonder what happens if $\beta_1 = \beta_2$. The following proposition predicts that in this case if the diffusivity is large then the mutant can win, driving v to extinction, simply by introducing some disparity in its birth rate between the two patches.

PROPOSITION 2.3. *Let $\beta_1 = \beta_2 = \beta > 0$ and $\alpha_1 = \beta - \varepsilon$, $\alpha_2 = \beta + \varepsilon$ with ε of either sign and $|\varepsilon| < \beta$. Then, if d is sufficiently large, $(0, 0, v_1^*, v_2^*)$ is unstable and $(u_1^*, u_2^*, 0, 0)$ is linearly stable.*

Proof. The proof is similar to that of Proposition 2.1. Note that when $\beta_1 = \beta_2$, $v_1^* = v_2^* = \beta$.

3. The reaction-diffusion model. Motivated by the predictions in the analysis for the two-patch model in the previous section, the purpose of this section is to establish some results for the reaction-diffusion system (1.1), which complement the results proved in [9].

Proposition 2.3 in particular leads us to wonder whether some analogous result might hold for (1.1). Let us consider the system

$$\begin{aligned} u_t &= d\Delta u + u[\beta + \varepsilon g(x) - u - v], \\ v_t &= d\Delta v + v[\beta - u - v] \end{aligned} \quad (3.1)$$

subject to $\partial u/\partial n = \partial v/\partial n = 0$ on $\partial\Omega$, where n is the outward-pointing unit normal on $\partial\Omega$. In this section we will assume that

$$\beta > 0, \quad \varepsilon \neq 0, \quad g(x) \text{ is nonconstant and } \int_{\Omega} g(x) dx = 0. \quad (3.2)$$

Clearly, system (3.1) has a boundary equilibrium $(u, v) = (0, \beta)$ corresponding to the mutant being absent, and another boundary equilibrium $(\tilde{u}(x), 0)$ (original species v is absent), in which $\tilde{u}(x)$ is the solution of

$$d\Delta \tilde{u} + \tilde{u}[\beta + \varepsilon g(x) - \tilde{u}] = 0, \quad \partial \tilde{u}/\partial n = 0 \quad \text{on } \partial\Omega. \quad (3.3)$$

Assumptions (3.2) assure us of the existence of a unique positive solution \tilde{u} of (3.3).

We will prove the following result:

PROPOSITION 3.1. *Let (3.2) hold. Then, if d is sufficiently large, the equilibrium $(u, v) = (0, \beta)$ is unstable as a solution of (3.1), and the equilibrium $(\tilde{u}(x), 0)$ is linearly stable.*

Proof. Linearizing (3.1) about $(0, \beta)$ furnishes an eigenvalue problem from which one equation decouples. To show that $(0, \beta)$ is unstable, it is sufficient to show the existence of a positive eigenvalue λ to the eigenvalue problem

$$\lambda\phi = d\Delta\phi + \varepsilon g(x)\phi, \quad \partial\phi/\partial n = 0 \quad \text{on } \partial\Omega \quad (3.4)$$

that results from trial solutions with temporal dependence of the form $\exp(\lambda t)$. Let λ_1 be the principal eigenvalue of (3.4) (the eigenvalue of greatest real part), and $\phi_1 > 0$ be the corresponding eigenfunction ($\phi_1 > 0$ follows from Theorem 11.10 in [15]). Division by ϕ_1 and integration over Ω yields

$$\begin{aligned} \lambda_1|\Omega| &= d \int_{\Omega} \frac{1}{\phi_1} \Delta\phi_1 dx + \varepsilon \underbrace{\int_{\Omega} g(x) dx}_{=0} \\ &= d \int_{\Omega} \frac{1}{\phi_1^2} |\nabla\phi_1|^2 dx > 0, \end{aligned}$$

since ϕ_1 is nonconstant (if ϕ_1 were constant then $g(x)$ would have to be constant). Thus, $\lambda_1 > 0$ and so $(0, \beta)$ is unstable.

Next, we demonstrate that $(\tilde{u}(x), 0)$ is linearly stable for sufficiently large values of d . Linear stability of this equilibrium is determined by the eigenvalue problem

$$\begin{aligned} \lambda\phi &= d\Delta\phi + (\beta + \varepsilon g(x) - 2\tilde{u}(x))\phi - \tilde{u}(x)\psi, \\ \lambda\psi &= d\Delta\psi + (\beta - \tilde{u}(x))\psi, \\ \partial\phi/\partial n &= \partial\psi/\partial n = 0 \quad \text{on } \partial\Omega. \end{aligned} \quad (3.5)$$

Certain facts concerning this eigenvalue problem follow from remarks on p464 of [9]. The eigenvalues can be examined using a suitable positive operator (see [6]), and it can be established that (3.5) has a principal eigenvalue (a simple real eigenvalue that

is larger than the real part of any other eigenvalue). Also, and very importantly, the principal eigenvalue for (3.5) coincides with the principal eigenvalue of the scalar problem

$$\lambda\psi = d\Delta\psi + (\beta - \tilde{u}(x))\psi, \quad \partial\psi/\partial n = 0 \quad \text{on } \partial\Omega \quad (3.6)$$

(see [8]). To emphasize dependence on the large parameter d , let λ_d and $\psi_d > 0$ be the principal eigenvalue and corresponding eigenfunction of (3.6), with ψ_d normalized such that

$$\int_{\Omega} \psi_d^2 dx = 1.$$

We aim to show that $\lambda_d < 0$. Multiplying $\lambda_d\psi_d = d\Delta\psi_d + (\beta - \tilde{u}(x))\psi_d$ by ψ_d and integrating over Ω yields

$$\begin{aligned} \lambda_d &= d \int_{\Omega} \psi_d \Delta\psi_d dx + \int_{\Omega} (\beta - \tilde{u}(x))\psi_d^2 dx \\ &= -d \int_{\Omega} |\nabla\psi_d|^2 dx + \int_{\Omega} (\beta - \tilde{u}(x))\psi_d^2 dx. \end{aligned} \quad (3.7)$$

But $\tilde{u}(x)$ satisfies (3.3) and it is known from [7] that, as $d \rightarrow \infty$,

$$\tilde{u}(x) \rightarrow \frac{1}{|\Omega|} \int_{\Omega} (\beta + \varepsilon g(x)) dx = \beta \quad \text{uniformly for } x \in \bar{\Omega}. \quad (3.8)$$

Also, there is a well-known comparison theorem for eigenvalue problems of the form $\lambda u = d\Delta u + a(x)u$ on homogeneous Neumann or Dirichlet boundary conditions, which states that if $a(x) \geq \tilde{a}(x)$ for all $x \in \Omega$, then the principal eigenvalue of the problem with $a(x)$ exceeds that of the corresponding problem in which $a(x)$ is replaced by $\tilde{a}(x)$ ([15], Thm 11.6). And if $a(x)$ equals a constant a , then the principal eigenvalue for the homogeneous Neumann problem is simply a itself. From these facts, it follows that the principal eigenvalue λ_d of (3.6) is between $-\sup_{x \in \bar{\Omega}} |\beta - \tilde{u}(x)|$ and $\sup_{x \in \bar{\Omega}} |\beta - \tilde{u}(x)|$, and so, by (3.8),

$$\lambda_d \rightarrow 0 \quad \text{as } d \rightarrow \infty.$$

It is therefore easily seen from (3.7) that

$$\int_{\Omega} |\nabla\psi_d|^2 dx \rightarrow 0 \quad \text{as } d \rightarrow \infty.$$

So, for large d , ψ_d approximates to a constant, $\psi_d \approx |\Omega|^{-1/2}$ (by the normalization condition), and it remains to show that $\lambda_d < 0$. But, from (3.7),

$$\lambda_d \leq \int_{\Omega} (\beta - \tilde{u}(x))\psi_d^2 dx \approx \frac{1}{|\Omega|} \int_{\Omega} (\beta - \tilde{u}(x)) dx.$$

Finally, dividing (3.3) by \tilde{u} and integrating yields

$$\int_{\Omega} (\beta - \tilde{u}(x)) dx = -d \int_{\Omega} \frac{\Delta\tilde{u}}{\tilde{u}} dx = -d \int_{\Omega} \frac{|\nabla\tilde{u}|^2}{\tilde{u}^2} dx < 0,$$

since $\tilde{u}(x)$ is nonconstant. Hence $\lambda_d < 0$.

Our next result, concerning the reaction-diffusion system (1.1), mirrors Proposition 2.1 on the two-patch model. The result predicts that if the birth rate for v is nonconstant and the mutant has a birth rate with higher variability *but the*

same mean, then the mutant will win and drive v to extinction. For the purposes of establishing this result, it will be convenient to write (1.1) as

$$\begin{aligned} u_t &= d\Delta u + u[\beta + \delta_2 g(x) - u - v], \\ v_t &= d\Delta v + v[\beta + \delta_1 g(x) - u - v], \\ u(x, 0) &= u_0(x) \geq 0, \quad v(x, 0) = v_0(x) \geq 0, \\ \partial u / \partial n &= \partial v / \partial n = 0 \quad \text{on } \partial\Omega \end{aligned} \quad (3.9)$$

in which

$$\beta, \delta_1, \delta_2 > 0, \quad g(x) \text{ is nonconstant, and } \int_{\Omega} g(x) dx = 0. \quad (3.10)$$

Cantrell and Cosner [2] established some results that have a similar flavor to those of this section in that they involve hypotheses on the means of spatially varying coefficients (see, in particular, Proposition 3.9 in [2], which deals with large diffusivities). However, their theorems do not include system (3.9), because the birth rates in (3.9) have exactly the same mean.

System (3.9) has a unique boundary equilibrium of the form $(\tilde{u}(x), 0)$, where $\tilde{u}(x) > 0$ satisfies

$$d\Delta\tilde{u} + \tilde{u}[\beta + \delta_2 g(x) - \tilde{u}] = 0, \quad \partial\tilde{u}/\partial n = 0 \quad \text{on } \partial\Omega \quad (3.11)$$

and a unique equilibrium of the form $(0, \tilde{v}(x))$, with $\tilde{v}(x) > 0$ satisfying

$$d\Delta\tilde{v} + \tilde{v}[\beta + \delta_1 g(x) - \tilde{v}] = 0, \quad \partial\tilde{v}/\partial n = 0 \quad \text{on } \partial\Omega. \quad (3.12)$$

We prove Proposition 3.2 below. Before doing so, we point out that Proposition 3.1, which effectively addresses the case $\delta_1 = 0$, is *not* a particular case of Proposition 3.2. The proof of the latter leans heavily on the assumption $\delta_1 > 0$; it is this fact that assures us that $\tilde{v}(x)$ is nonconstant, which is essential for the proof.

PROPOSITION 3.2. *Assume (3.10) holds and that $\delta_2 > \delta_1$. Then, if d is sufficiently large, the equilibrium $(0, \tilde{v}(x))$ is unstable as a solution of (3.9), and $(\tilde{u}(x), 0)$ is linearly stable.*

Proof. We first show that $(0, \tilde{v}(x))$ is unstable. The linearization about this equilibrium leads to the following eigenvalue problem, corresponding to trial solutions with temporal dependence $\exp(\lambda t)$:

$$\begin{aligned} \lambda\phi &= d\Delta\phi + (\beta + \delta_2 g(x) - \tilde{v}(x))\phi, \\ \lambda\psi &= d\Delta\psi - \tilde{v}(x)\phi + (\beta + \delta_1 g(x) - 2\tilde{v}(x))\psi, \\ \partial\phi/\partial n &= \partial\psi/\partial n = 0 \quad \text{on } \partial\Omega. \end{aligned} \quad (3.13)$$

The principal eigenvalue of (3.13) coincides with the principal eigenvalue of the problem

$$\lambda\phi = d\Delta\phi + (\beta + \delta_2 g(x) - \tilde{v}(x))\phi, \quad \partial\phi/\partial n = 0 \quad \text{on } \partial\Omega. \quad (3.14)$$

Let λ_1 and $\phi_1 > 0$ be the principal eigenvalue and corresponding eigenfunction. We wish to show that $\lambda_1 > 0$. Let $\Theta = \phi_1/\tilde{v}$; then Θ satisfies

$$\lambda_1 \tilde{v}^2 \Theta = d\nabla \cdot (\tilde{v}^2 \nabla \Theta) + [(\delta_2 - \delta_1)g(x)\tilde{v}^2]\Theta, \quad \partial\Theta/\partial n = 0 \quad \text{on } \partial\Omega. \quad (3.15)$$

As in [9], λ_1 is given by the variational characterization

$$\lambda_1 = \sup_{\{\Theta \in W^{1,2}(\Omega): \Theta \neq 0\}} \frac{-d \int_{\Omega} \tilde{v}^2 |\nabla \Theta|^2 dx + \int_{\Omega} (\delta_2 - \delta_1)g(x)\tilde{v}^2 \Theta^2 dx}{\int_{\Omega} \tilde{v}^2 \Theta^2 dx}.$$

(Note that [9] use a different notational convention; their $-\lambda$ is our λ .) The choice $\Theta = 1$ yields

$$\lambda_1 \geq \frac{(\delta_2 - \delta_1) \int_{\Omega} \tilde{v}^2 g(x) dx}{\int_{\Omega} \tilde{v}^2 dx},$$

and therefore it suffices to show that $\int_{\Omega} \tilde{v}^2 g(x) dx > 0$. This can be shown using the equation for \tilde{v} , equation (3.12). Multiplying (3.12) by \tilde{v} and integrating yields

$$\delta_1 \int_{\Omega} \tilde{v}^2 g(x) dx = d \int_{\Omega} |\nabla \tilde{v}|^2 dx + \int_{\Omega} \tilde{v}^2 (\tilde{v} - \beta) dx.$$

We know from [7] that as $d \rightarrow \infty$,

$$\tilde{v}(x) \rightarrow \frac{1}{|\Omega|} \int_{\Omega} (\beta + \delta_1 g(x)) dx = \beta \quad \text{uniformly for } x \in \bar{\Omega}. \tag{3.16}$$

Using also that \tilde{v} is nonconstant, it follows that for d sufficiently large,

$$\begin{aligned} \delta_1 \int_{\Omega} \tilde{v}^2 g(x) dx &> \beta^2 \int_{\Omega} (\tilde{v} - \beta) dx \\ &= d\beta^2 \int_{\Omega} \frac{|\nabla \tilde{v}|^2}{\tilde{v}^2} dx \\ &> 0 \quad \text{since } \tilde{v} \text{ is nonconstant.} \end{aligned}$$

Thus $\int_{\Omega} \tilde{v}^2 g(x) dx > 0$, so $\lambda_1 > 0$.

The above argument cannot be reversed to conclude that $(0, \tilde{v}(x))$ is stable when $\delta_1 > \delta_2$ (otherwise we could have inferred the stability properties of the other boundary equilibrium $(\tilde{u}(x), 0)$ without further effort). Therefore, we must study the linear stability of $(\tilde{u}(x), 0)$ separately, and a somewhat different strategy is required to establish its linear stability under the condition $\delta_2 > \delta_1$, for sufficiently large d . The eigenvalue problem resulting from the linearization about $(\tilde{u}(x), 0)$ is

$$\begin{aligned} \lambda\phi &= d\Delta\phi + (\beta + \delta_2 g(x) - 2\tilde{u}(x))\phi - \tilde{u}(x)\psi, \\ \lambda\psi &= d\Delta\psi + (\beta + \delta_1 g(x) - \tilde{u}(x))\psi, \\ \partial\phi/\partial n &= \partial\psi/\partial n = 0 \quad \text{on } \partial\Omega, \end{aligned} \tag{3.17}$$

and as before, it suffices to consider the principal eigenvalue of the scalar problem

$$\lambda\psi = d\Delta\psi + (\beta + \delta_1 g(x) - \tilde{u}(x))\psi, \quad \partial\psi/\partial n = 0 \quad \text{on } \partial\Omega. \tag{3.18}$$

Let λ_2 and $\psi_2 > 0$ be the principal eigenvalue and eigenfunction of (3.18). We want to show that $\lambda_2 < 0$. Let $\Phi = \psi_2/\tilde{u}$; then Φ satisfies

$$\lambda_2 \tilde{u}^2 \Phi = d \nabla \cdot (\tilde{u}^2 \nabla \Phi) + [(\delta_1 - \delta_2)g(x)\tilde{u}^2]\Phi, \quad \partial\Phi/\partial n = 0 \quad \text{on } \partial\Omega. \tag{3.19}$$

Define

$$C(d) = \sup_{\{\phi \in W^{1,2}(\Omega): \int_{\Omega} g\tilde{u}^2\phi^2 < 0\}} \frac{\int_{\Omega} \tilde{u}^2 |\nabla \phi|^2 dx}{\int_{\Omega} g(x)\tilde{u}^2 \phi^2 dx}. \tag{3.20}$$

It can be shown that, for d sufficiently large, $\int_{\Omega} \tilde{u}^2 g(x) dx > 0$. This means that $\phi = \text{const.}$ is *not* an admissible function in (3.20), so, for all sufficiently large d ,

$$C(d) < 0.$$

Letting ϕ^* be the actual extremizing function in (3.20), a standard argument of variational calculus yields that ϕ^* must satisfy

$$d \nabla \cdot (\tilde{u}^2 \nabla \phi^*) + dC(d)g\tilde{u}^2\phi^* = 0. \tag{3.21}$$

With the notation being used in this paper, λ_2 , as a function of δ_1 , is convex [10]. When $\delta_1 = \delta_2$, it follows from (3.19) that $\lambda_2 = 0$ (with $\Phi = \text{constant}$) and when $\delta_1 = \delta_2 + dC(d) (< \delta_2)$, λ_2 is again zero by (3.21). By convexity, λ_2 must be negative (so that $(\tilde{u}(x), 0)$ is linearly stable) for values of δ_1 such that

$$\delta_2 + dC(d) < \delta_1 < \delta_2. \tag{3.22}$$

The right-hand inequality in (3.22) holds by hypothesis. We show that the left hand one holds for sufficiently large d , by demonstrating that

$$dC(d) \rightarrow -\infty \quad \text{as } d \rightarrow \infty. \tag{3.23}$$

But we know that $\tilde{u} \rightarrow \beta$ as $d \rightarrow \infty$, uniformly in x . Therefore, as $d \rightarrow \infty$,

$$C(d) \rightarrow \sup_{\{\phi \in W^{1,2}(\Omega) : \int_{\Omega} g\phi^2 < 0\}} \frac{\int_{\Omega} |\nabla \phi|^2 dx}{\int_{\Omega} g(x)\phi^2 dx}, \tag{3.24}$$

which is strictly negative ($\phi = \text{const.}$ is not admissible since $\int_{\Omega} g(x) dx = 0$). Thus (3.23) holds. The proof of Proposition 3.2 is complete.

In a similar way, we have the following proposition:

PROPOSITION 3.3. *Assume (3.10) holds and that $\delta_2 < \delta_1$. Then, if d is sufficiently large, the equilibrium $(0, \tilde{v}(x))$ is linearly stable as a solution of (3.9) and $(\tilde{u}(x), 0)$ is unstable.*

Next, we demonstrate that, if d is sufficiently large, system (3.9) cannot possess a coexistence equilibrium. Doing so enables us to make statements on the global dynamics of (3.9) by employing the powerful theory of monotone dynamical systems [14].

PROPOSITION 3.4. *Let (3.10) hold, with $\delta_2 \neq \delta_1$. Then, if d is sufficiently large, system (3.9) has no coexistence equilibrium.*

Proof. For a contradiction, suppose there exist sequences $\{d_i\}$, $\{\tilde{u}_i\}$, $\{\tilde{v}_i\}$ with $d_i \rightarrow \infty$, $\tilde{u}_i(x) > 0$, $\tilde{v}_i(x) > 0$, and

$$\begin{aligned} d_i \Delta \tilde{u}_i + \tilde{u}_i[\beta + \delta_2 g(x) - \tilde{u}_i - \tilde{v}_i] &= 0, \\ d_i \Delta \tilde{v}_i + \tilde{v}_i[\beta + \delta_1 g(x) - \tilde{u}_i - \tilde{v}_i] &= 0, \\ \partial \tilde{u}_i / \partial n = \partial \tilde{v}_i / \partial n &= 0 \quad \text{on } \partial \Omega. \end{aligned} \tag{3.25}$$

By the maximum principle,

$$\|\tilde{u}_i\|_{\infty} \leq \beta + \delta_2 \|g\|_{\infty}, \quad \|\tilde{v}_i\|_{\infty} \leq \beta + \delta_1 \|g\|_{\infty}$$

so that \tilde{u}_i and \tilde{v}_i are bounded independently of i . Now set $\phi_i = \tilde{u}_i / \|\tilde{u}_i\|_{\infty}$. Then ϕ_i satisfies

$$\Delta \phi_i + \phi_i \left(\frac{\beta + \delta_2 g(x) - \tilde{u}_i - \tilde{v}_i}{d_i} \right) = 0, \quad \partial \phi_i / \partial n = 0 \quad \text{on } \partial \Omega.$$

By the regularity properties of solutions of elliptic equations in their dependence on the equation coefficients [5], it follows that as $i \rightarrow \infty$, $\phi_i \rightarrow \phi$ in $C^1(\Omega)$, where ϕ satisfies $\Delta \phi = 0$, $\partial \phi / \partial n = 0$ on $\partial \Omega$ and $\|\phi\|_{\infty} = 1$. The solution of the latter problem is simply $\phi = 1$. Thus $\phi_i \rightarrow 1$, uniformly in x .

Also, if we divide the equation for \tilde{u}_i in (3.25) by d_i and recall that \tilde{u}_i is bounded independently of i , we conclude (again by elliptic regularity) that $\tilde{u}_i(x)$ must approach, as $i \rightarrow \infty$, a limit function $\tilde{u}(x)$ satisfying $\Delta\tilde{u} = 0$, $\partial\tilde{u}/\partial n = 0$ on $\partial\Omega$. But solutions of this problems are constants. Thus, as $i \rightarrow \infty$, $\tilde{u}_i(x) \rightarrow \mu$ for some constant μ . Similarly, $\tilde{v}_i(x) \rightarrow \nu$ for some constant ν . If we now integrate the equation for \tilde{u}_i in (3.25) and then divide by $\|\tilde{u}_i\|_\infty$, we obtain

$$\int_{\Omega} \phi_i(x)(\beta + \delta_2 g(x) - \tilde{u}_i(x) - \tilde{v}_i(x)) dx = 0.$$

Taking the limit as $i \rightarrow \infty$ then yields

$$\int_{\Omega} (\beta + \delta_2 g(x) - \mu - \nu) dx = 0.$$

Since $\int_{\Omega} g(x) dx = 0$, it follows that

$$\mu + \nu = \beta.$$

Next, we derive some inequalities that will be needed later. Note that, for all i ,

$$\int_{\Omega} (\tilde{u}_i(x) + \tilde{v}_i(x) - \beta) dx = d_i \int_{\Omega} \frac{|\nabla\tilde{u}_i|^2}{\tilde{u}_i^2} dx > 0.$$

This follows by dividing the equation for \tilde{u}_i by \tilde{u}_i and then integrating. Furthermore, for large but finite i ,

$$\int_{\Omega} \tilde{u}_i(x)g(x) dx > 0 \quad \text{and} \quad \int_{\Omega} \tilde{v}_i(x)g(x) dx > 0. \tag{3.26}$$

To see the first of these inequalities (the second is derived similarly), integrate the equation for \tilde{u}_i in (3.25), and let i be large but finite (so that d_i is large but finite) to obtain

$$\begin{aligned} \delta_2 \int_{\Omega} \tilde{u}_i(x)g(x) dx &= \int_{\Omega} \tilde{u}_i(x)(\tilde{u}_i(x) + \tilde{v}_i(x) - \beta) dx \\ &\sim \mu \int_{\Omega} (\tilde{u}_i(x) + \tilde{v}_i(x) - \beta) dx \\ &> 0. \end{aligned}$$

Define $u_i = \tilde{u}_i/\tilde{v}_i$. Then u_i satisfies

$$d_i \nabla \cdot (\tilde{v}_i^2 \nabla u_i) + u_i \tilde{v}_i^2 (\delta_2 - \delta_1)g(x) = 0.$$

Multiplying this by u_i , integrating, and then replacing u_i by \tilde{u}_i/\tilde{v}_i yields

$$d_i \int_{\Omega} \tilde{v}_i^2 |\nabla(\tilde{u}_i/\tilde{v}_i)|^2 dx = \int_{\Omega} \tilde{u}_i^2 (\delta_2 - \delta_1)g(x) dx. \tag{3.27}$$

Similarly,

$$d_i \int_{\Omega} \tilde{u}_i^2 |\nabla(\tilde{v}_i/\tilde{u}_i)|^2 dx = \int_{\Omega} \tilde{v}_i^2 (\delta_1 - \delta_2)g(x) dx. \tag{3.28}$$

We arrive at a contradiction by considering (3.27) and (3.28) for large but finite i so that $\tilde{u}_i^2 \sim \mu^2$ and $\tilde{v}_i^2 \sim \nu^2$. Then $\tilde{u}_i^2 \sim (\beta - \tilde{v}_i)^2$, and so (3.27) becomes

$$\begin{aligned} d_i \int_{\Omega} \tilde{v}_i^2 |\nabla(\tilde{u}_i/\tilde{v}_i)|^2 dx &= \int_{\Omega} (\beta - \tilde{v}_i)^2 (\delta_2 - \delta_1) g(x) dx \\ &= \int_{\Omega} \tilde{v}_i^2 (\delta_2 - \delta_1) g(x) dx - 2\beta(\delta_2 - \delta_1) \int_{\Omega} \tilde{v}_i g(x) dx \\ &= -d_i \int_{\Omega} \tilde{u}_i^2 |\nabla(\tilde{v}_i/\tilde{u}_i)|^2 dx - 2\beta(\delta_2 - \delta_1) \int_{\Omega} \tilde{v}_i g(x) dx \end{aligned}$$

so that

$$d_i \int_{\Omega} \tilde{v}_i^2 |\nabla(\tilde{u}_i/\tilde{v}_i)|^2 dx + d_i \int_{\Omega} \tilde{u}_i^2 |\nabla(\tilde{v}_i/\tilde{u}_i)|^2 dx = -2\beta(\delta_2 - \delta_1) \underbrace{\int_{\Omega} \tilde{v}_i g(x) dx}_{>0},$$

which produces a contradiction if $\delta_2 > \delta_1$. It can be shown in a similar way that, for large but finite i ,

$$d_i \int_{\Omega} \tilde{v}_i^2 |\nabla(\tilde{u}_i/\tilde{v}_i)|^2 dx + d_i \int_{\Omega} \tilde{u}_i^2 |\nabla(\tilde{v}_i/\tilde{u}_i)|^2 dx = -2\beta(\delta_1 - \delta_2) \underbrace{\int_{\Omega} \tilde{u}_i g(x) dx}_{>0},$$

which produces a contradiction in the case when $\delta_1 > \delta_2$. The proof of Proposition 3.4 is complete.

The nonexistence of a coexistence state for large values of the diffusivity d now enables us to make stronger statements on the outcome of the competition between u and v , by using results in [14] (Chap. 7). Before doing so, note that system (3.9) is transformed by the introduction of the new variables $u^* = u$, $v^* = -v$ into

$$\begin{aligned} u_t^* &= d\Delta u^* + u^*[\beta + \delta_2 g(x) - u^* + v^*], \\ v_t^* &= d\Delta v^* + v^*[\beta + \delta_1 g(x) - u^* + v^*], \\ u^*(x, 0) &= u_0(x) \geq 0, \quad v^*(x, 0) = -v_0(x) \leq 0, \\ \partial u^*/\partial n &= \partial v^*/\partial n = 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{3.29}$$

Solutions of (3.29) remain in the fourth quadrant, since solutions of (3.9) remain positive by the maximum principle. Accordingly, system (3.29) is a *cooperative* system, in the sense that the reaction part of the first equation is non-decreasing with respect to v^* , while that of the second equation is non-decreasing with respect to u^* (note that $v^* \leq 0$). In abstract notation, the semiflow Φ defined by

$$\Phi_t(\phi) = (u^*(t, \phi), v^*(t, \phi)),$$

where $(u^*(t, \phi), v^*(t, \phi))$ is the solution of (3.29) satisfying $(u^*(0, \phi), v^*(0, \phi)) = \phi$, is *strongly monotone* ([14], p132). It follows that Φ is *strongly order preserving* ([14], p3). The trichotomy given in ([14], p17) then applies and states that, for the original system (3.9), either a coexistence state exists, or solutions of (3.9) approach one of the boundary equilibria. The nonexistence of a coexistence state leaves us with just the latter alternative. In other words, knowledge of the equilibria and their local stability, together with the powerful results in [14], enables us to make statements about the global dynamics of (3.9). We thus have the following theorem on the outcome of the competition between u and v for large values of d .

THEOREM 3.1. *Assume (3.10) holds, and let d be sufficiently large. Then,*

1. *if $\delta_2 > \delta_1$ and $u_0(x) \not\equiv 0$, the solution of (3.9) satisfies $(u(x, t), v(x, t)) \rightarrow (\tilde{u}(x), 0)$ as $t \rightarrow \infty$;*

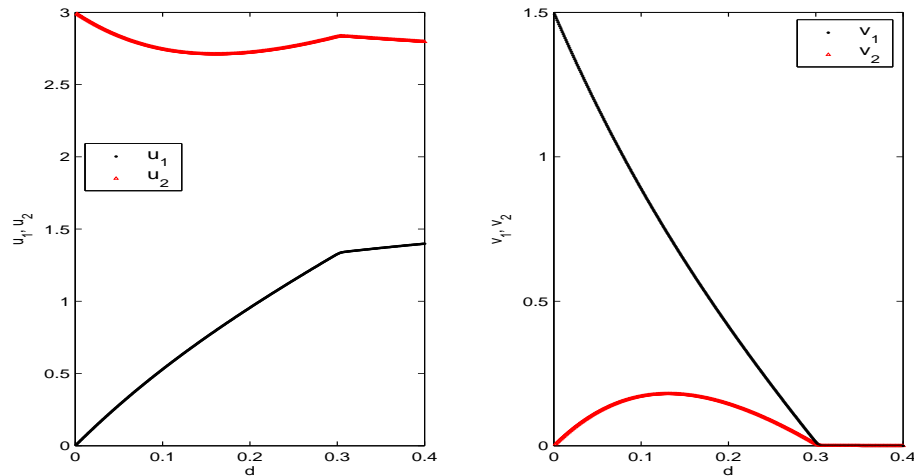


FIGURE 1. A bifurcation diagram of (2.1) with $\alpha_1 = 1$, $\alpha_2 = 3$, $\beta_1 = 1.5$, $\beta_2 = 2.5$, and initial condition $(0.5, 0.5, 0.5, 0.5)$.

2. if $\delta_2 < \delta_1$ and $v_0(x) \not\equiv 0$, the solution of (3.9) satisfies $(u(x, t), v(x, t)) \rightarrow (0, \tilde{v}(x))$ as $t \rightarrow \infty$.

4. Discussion. This paper has been inspired by the work of Hutson et al. [9] and is motivated by the simple question of how diffusion affects the competition outcomes of two competing species that are identical in all respects other than their strategies on how they spatially distribute their birth rates. This may provide us with insights into how species learn to compete in a relatively stable setting and this in turn may point out species evolution directions. To this end, we formulated some simple, though artificial, two-species competition models that incorporate either continuous or discrete diffusion mechanisms. Our analytical work on these models collectively and strongly suggests that, in a fast diffusion environment, a species will have a higher chance of success if it tries to adopt greater spatial variation in its birth rate than another competing species with a birth rate that is the same on average. This suggests that, subject to species having the same overall average birth rate over the domain, those species that adopt the greatest spatial variation in their birth rates have the greatest chance of success, which may in turn provide an explanation for the evolution of grouping behavior in animal populations in high-diffusion situations. Our findings are confirmed by extensive numerical simulation work on the models, and a main purpose of this section is to report these informative numerical findings.

Specifically, in this section, we selectively present some numerical simulation results that not only confirm but also complement the predictions of the analytical results. We also attempt to state some biological implications of our analytical and numerical findings. In addition, we mention a few open mathematical questions for future work. The numerical simulations are carried out using the routines `ode23s` and `pdepe` that are part of MATLAB.

Clearly, Figure 1 confirms the results of Lemmas 2.1– 2.2 and Proposition 2.1. It also strongly suggests the following two conjectures.

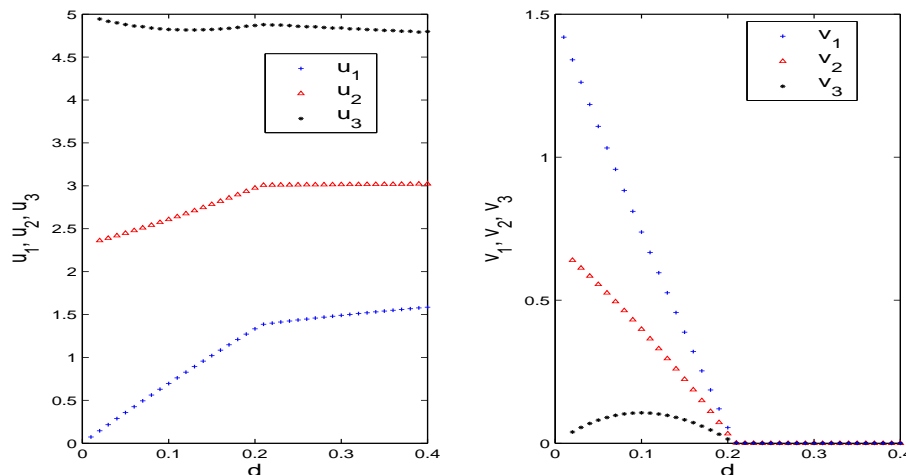


FIGURE 2. A bifurcation diagram of (4.1) with $\alpha_1 = 1, \alpha_2 = 3, \alpha_3 = 5, \beta_1 = 1.5, \beta_2 = 3, \beta_3 = 4.5$, and initial condition $(0.5, 0.5, 0.5, 0.5, 0.5, 0.5)$.

Conjecture 1. Assume in (2.1), $\beta_2 > \beta_1$ and $\alpha_1 = \beta_1 - \varepsilon, \alpha_2 = \beta_2 + \varepsilon$ with $0 < \varepsilon < \beta_1$, and d is sufficiently large. If $u_1(0) + u_2(0) > 0$, then $\lim(u_1, u_2, v_1, v_2) = (u_1^*, u_2^*, 0, 0)$.

Conjecture 2. Assume in (2.1), $\beta_2 > \beta_1$ and $\alpha_1 = \beta_1 - \varepsilon, \alpha_2 = \beta_2 + \varepsilon$ with $0 < \varepsilon < \beta_1$. Assume d is small enough so that (2.1) has a positive steady state E_* . If $u_1(0) + u_2(0) > 0, v_1(0) + v_2(0) > 0$, then $\lim(u_1, u_2, v_1, v_2) = E_*$.

These conjectures, if true, suggest that the species that can concentrate its birth in a single patch wins, if the diffusion rate is large enough (in Fig. 1 one needs only $d > 0.3$, far less than the maximum birth rates of either species). *In short, the winning strategy is simply to focus as much birth in a single patch as possible.* Indeed, this is also numerically confirmed by a similar bifurcation diagram (Fig. 2) for the following three-patch model of two similar species competition.

$$\begin{aligned}
 \frac{du_1}{dt} &= u_1(\alpha_1 - u_1 - v_1) + d(u_2 + u_3 - 2u_1)/2, \\
 \frac{du_2}{dt} &= u_2(\alpha_2 - u_2 - v_2) + d(u_1 + u_3 - 2u_2)/2, \\
 \frac{du_3}{dt} &= u_3(\alpha_3 - u_3 - v_3) + d(u_1 + u_2 - 2u_3)/2, \\
 \frac{dv_1}{dt} &= v_1(\beta_1 - u_1 - v_1) + d(v_2 + v_3 - 2v_1)/2, \\
 \frac{dv_2}{dt} &= v_2(\beta_2 - u_2 - v_2) + d(v_1 + v_3 - 2v_2)/2, \\
 \frac{dv_3}{dt} &= v_3(\beta_3 - u_3 - v_3) + d(v_1 + v_2 - 2v_3)/2.
 \end{aligned}
 \tag{4.1}$$

Our work in the previous section strongly suggests that a similar winning strategy holds for the continuous diffusion models (3.1) and (3.9). *Specifically, the winning strategy here is to concentrate birth in as small an area as possible.* The two simulation figures (Figs. 3 and 4) not only confirm the analytical results but also provide glimpses of how the two species evolve into the two limiting scenarios: extinction of one species and coexistence.

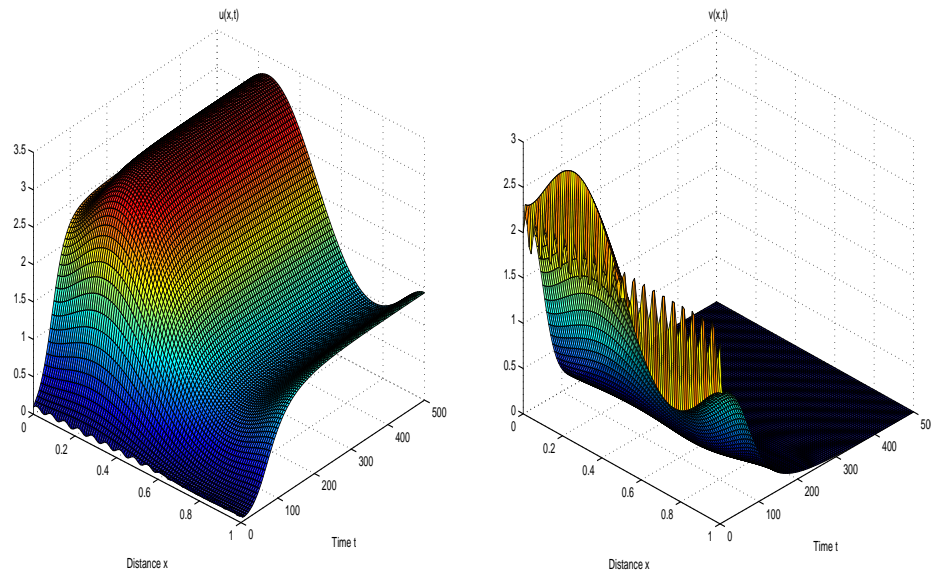


FIGURE 3. Simulation of system (3.9) on the domain $x \in [0, 1]$. Parameter values were $\beta = 2$, $\delta_1 = 1.3$, $\delta_2 = 1.4$, and $d = 0.01$, and we took $g(x) = \sin 2\pi x$. For initial data, small numbers of the mutant u were introduced throughout the domain initially inhabited mainly by v . The outcome: u wins and v goes extinct.

Figure 3 shows the result of a simulation of (3.9) in a situation in which $\delta_2 > \delta_1$. The simulation confirms the predictions of Proposition 3.2 and Theorem 3.1 in that the mutant u wins in these circumstances with v going extinct. The simulation also shows that the diffusivity d does not, in fact, have to be particularly large for the mutant to win. Other numerical simulations, results of which are not included here, support the theoretical predictions for the case when $\delta_2 < \delta_1$.

Figure 4 shows the effect of lowering the value of the diffusivity d . Parameter values this time were the same as in Figure 3, except the diffusivity was lowered to $d = 0.0001$ and the initial conditions for u and v were identical (to be certain of not biasing the outcome). The result is that u and v can coexist at this value of d , but they become spatially segregated.

In conclusion, we would like to emphasize that extensive work exists on patch population dynamics (e.g., [16], [13], [11]) and on population models involving reaction diffusion-equations (e.g., [1], [3], [4]), many of which deal with both competition and predator-prey interactions.

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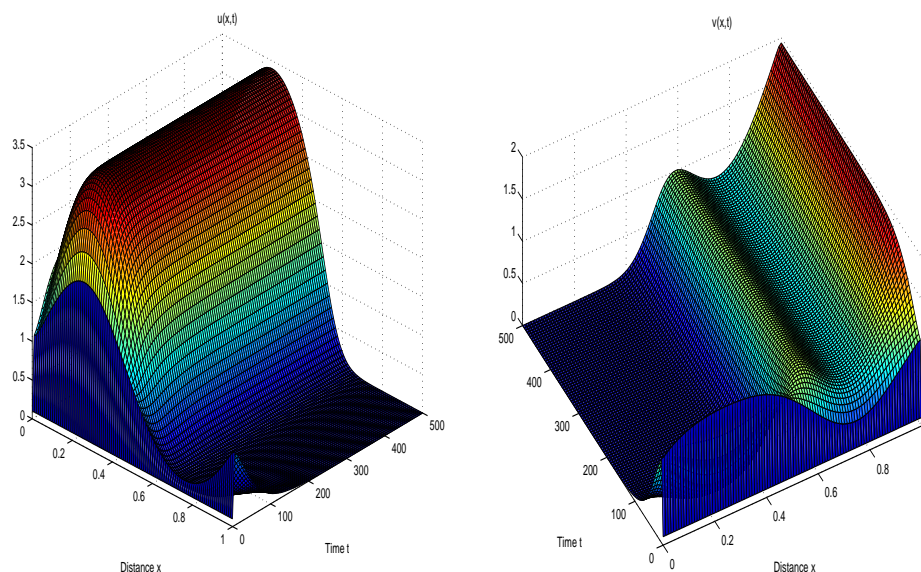


FIGURE 4. Simulation of system (3.9) on the domain $x \in [0, 1]$. Parameter values were $\beta = 2$, $\delta_1 = 1.3$, $\delta_2 = 1.4$, and $d = 0.0001$, and we took $g(x) = \sin 2\pi x$. The initial data was taken as $u(x, 0) = v(x, 0) = 0.1$ for all $x \in [0, 1]$. The outcome is that the species can coexist.

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