

## On the effects of spatial heterogeneity on the persistence of interacting species

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**Abstract.** The dynamics of two interacting theoretical populations inhabiting a heterogeneous environment are modelled by a system of two weakly coupled reaction–diffusion equations having spatially dependent reaction terms. Longterm persistence of both populations is guaranteed by an invasibility condition, which is itself expressed via the signs of certain eigenvalues of related linear elliptic operators with spatially dependent lowest order coefficients. The effects of change in these coefficients upon the eigenvalues are here exploited to study the effects of spatial heterogeneity on the persistence of interacting species through two particular ecological topics of interest. The first concerns when the location of favorable hunting grounds within the overall environment does or does not affect the success of a predator in predator–prey models, while the second concerns cases of competition models in which the outcome of competition in a spatially varying environment differs from that which would be expected in a spatially homogeneous environment.

**Key words:** Population dynamics – Spatial heterogeneity – Reaction–diffusion equations – Permanence – Eigenvalue problems – Compressivity – Predator–prey – Competition–Lotka–Volterra – Invasibility

### 1 Introduction

In this article we are interested in the effects that a spatially heterogeneous environment may have on the persistence of the species which inhabit it. To study this problem, we focus on the interaction of two species and seek to determine whether the interaction results in their longterm coexistence. Our mathematical framework is given by diffusion models whose coefficients vary spatially in order to capture spatial heterogeneity. In this context there is an

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interacting species in all cases where both species are present initially. In those models that describe two competitors we could use either uniform persistence or compressivity as our criterion for coexistence since the conditions leading to those two sorts of coexistence are identical. This point is observed in [9]. To be slightly more precise, we should note that all the models we consider have the property that all nonnegative initial data evolve eventually into a fixed bounded region and remain there thereafter (i.e. the models are *point dissipative*). The term *permanence* is used to describe systems that are both uniformly persistent and point dissipative, so in practice our definition of coexistence is actually based on permanence rather than uniform persistence. For those competition models where we could use compressivity to define coexistence we will also have dissipativity and the conditions leading to permanence and to compressivity will be identical, so we shall generally use the term permanence to describe our notion of coexistence. A general account of the theory of permanence is given in [22]. Some applications to reaction-diffusion systems are discussed in [10-12]. Compressivity in reaction-diffusion models for two competitors is discussed in [21]. The relative merits and ranges of applicability of permanence, compressivity, and other formulations of longterm coexistence are discussed in [15].

In [11] we demonstrated that permanence for diffusion models can be characterized in terms of the instabilities of states where only one population is present. The same was done for compressivity in competition models in [21]. Roughly speaking, the biological interpretation of these instabilities is that one population can invade the environment when the other population is already established there. Put another way, the results of [10-12, 21] provide mathematical rigor to the idea that invasibility implies coexistence. The study of the stability or instability of a state (in this case an ordered pair of population density profiles) leads to the examination of linear eigenvalue problems (in this case, for linear elliptic differential operators). As a consequence, the results of [10-12, 21] guarantee permanence (i.e. longterm coexistence) when the eigenvalues of certain linear elliptic differential operators are positive. In this article, we explore how the signs of these eigenvalues may change as the coefficients in the original models vary spatially in order to examine the effects on the persistence of interacting species. In particular, we consider two biological situations. First, we examine cases of competition models in which the outcome of the competition in a spatially varying environment differs from that which would be expected in a spatially homogeneous environment. Second, we address the question of when the location of favorable hunting grounds within the overall environment does or does not affect the success of the predator in predator-prey models. We give analytic justification and explanation for some such phenomena that have been observed in the numerical simulations of [32].

The models we employ are reaction-diffusion systems of the form

$$\begin{aligned} \frac{\partial u_i}{\partial t} &= \mu_i \Delta u_i + f_i(x, u_1, u_2) u_i & \text{in } \Omega \times (0, \infty) \\ B_i u_i &= 0 & \text{on } \partial\Omega \times (0, \infty), \end{aligned} \quad (1.1)$$

immediate question which arises. Namely, what should be meant by the longterm coexistence of two interacting species and what mathematical techniques can be employed to guarantee it? The conventional wisdom is that "invasibility implies coexistence". What that means is that if each species can increase its population if introduced at a low density into an environment where the other species is already present at its carrying capacity (or an analogous equilibrium or steady state in heterogeneous situations) then the two species can coexist. We shall describe some mathematical formulations of what is meant by coexistence and invasibility so that the idea that invasibility implies coexistence can be rigorously justified. We shall then examine how certain types of spatial heterogeneity affect invasibility and hence coexistence. There are a number of reasons why a careful consideration of what is meant by coexistence is necessary. Diffusion models are nontrivial to analyze. The states in these models represent the population densities of the species in question and the asymptotic behavior of the states frequently is more complicated than just convergence to equilibrium densities. Hence, while converging to a componentwise positive equilibrium is a clear indicator of longterm coexistence, it by no means exhausts the possible forms of coexistence and therefore is not suitable as the definition of longterm coexistence. Instead, we take longterm coexistence to mean the existence of fixed positive population density profiles  $v_1$  and  $v_2$  so that any initial population density profiles which are nontrivial in both components will at some point in time (and then for all future time) exceed  $v_1$  and  $v_2$  throughout the habitat in question. (The time required to exceed  $v_1$  and  $v_2$  of course will depend on the initial state.)

There are two abstract formulations which lead to coexistence according to the above definition for the models we consider. The first approach is based on interpreting the model in a setting that permits the use of order methods, typically an ordered Banach space. If the model has appropriate monotone and order preserving properties (as in the case of models for two competitors or arbitrarily many mutualists) it may turn out to be *compressive* in the sense of Hess [21]; i.e. it may have a globally attracting order interval to which certain solutions converge monotonically and thus trap all other positive solutions via the order preserving properties of the system. (This sort of idea and related methods based on sub- and supersolutions and comparison or maximum principles have been in use for some time; see for example [16, 24] and the references therein.) In situations where the system does not have good monotone properties (as in the case of predator-prey systems) an alternative approach is to use dynamical systems ideas to show the existence of a positive attractor which is uniformly bounded away from zero in all components. This second notion of longterm coexistence is called *uniform persistence* and is usually considered in terms of convergence to the attractor with respect to a metric in contrast to the convergence with respect to an ordering used to define compressivity. In all of our examples we can choose our spaces, metrics, and orderings so that either compressivity or uniform persistence implies the existence of density profiles  $v_1$  and  $v_2$  for the two components in the model which are asymptotic lower bounds for the density profiles of the two

interacting species in all cases where both species are present initially. In those models that describe two competitors we could use either uniform persistence or compressivity as our criterion for coexistence since the conditions leading to those two sorts of coexistence are identical. This point is observed in [9]. To be slightly more precise, we should note that all the models we consider have the property that all nonnegative initial data evolve eventually into a fixed bounded region and remain there thereafter (i.e. the models are *point dissipative*). The term *permanence* is used to describe systems that are both uniformly persistent and point dissipative, so in practice our definition of coexistence is actually based on permanence rather than uniform persistence. For those competition models where we could use compressivity to define coexistence we will also have dissipativity and the conditions leading to permanence and to compressivity will be identical, so we shall generally use the term permanence to describe our notion of coexistence. A general account of the theory of permanence is given in [22]. Some applications to reaction-diffusion systems are discussed in [10-12]. Compressivity in reaction-diffusion models for two competitors is discussed in [21]. The relative merits and ranges of applicability of permanence, compressivity, and other formulations of longterm coexistence are discussed in [15].

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$$\begin{aligned} \frac{\partial u_i}{\partial t} &= \mu_i \Delta u_i + f_i(x, u_1, u_2) u_i & \text{in } \Omega \times (0, \infty) \\ B_i u_i &= 0 & \text{on } \partial\Omega \times (0, \infty), \end{aligned} \quad (1.1)$$

$i = 1, 2$ , where  $u_1$  and  $u_2$  denote the densities of the species inhabiting the connected region  $\Omega$ . The boundary of  $\Omega$ ,  $\partial\Omega$ , may be lethal to a species ( $Bu = u$ ) or may act as a barrier ( $Bu = \partial u/\partial\eta$ , where  $\partial/\partial\eta$  is an outer normal derivative). In the case where the boundary is lethal and the functions  $f_i$  do not depend on  $x$ , such models are sometimes called KISS models after Kierstead and Slobodkin [23] and Skellam [35]. KISS models have been used fairly extensively to study area effects, but since we want to study spatial heterogeneity and allow boundaries which act as barriers we must use the more general formulation (1.1).

The results and methods of [10–12, 21] allow either the boundary condition  $u_i = 0$  or  $\partial u_i/\partial\eta = 0$  on each component in (1.1). The spatial heterogeneity in the model as well as the intra- and interspecies interactions are expressed through the local per capita growth laws  $f_i(x, u_1, u_2)$  for each species. The constraints we place on the  $f_i$ 's are modest and biologically reasonable, and they fall into two general categories. The first group of constraints serve to guarantee that (1.1) is point dissipative. These are discussed in detail in Sect. 4 of [11]. We shall not discuss them further here, beyond noting that all the examples we consider in this article are point dissipative. The second group of constraints serve to restrict the dynamics of one population in the absence of the other. In particular, they guarantee that if  $i \neq j$ ,  $u_i$  tends to an equilibrium  $\bar{u}_i$  (possibly zero) when  $u_j \equiv 0$ . We discuss this group of constraints in more detail in Sect. 2, where we outline our procedure for determining permanence, or compressivity in the competitive case. The analysis leads up to the eigenvalue problems

$$\begin{aligned} \mu_1 \Delta w_1 + f_1(x, 0, \bar{u}_2)w_1 &= \sigma_1 w_1 & \text{in } \Omega \\ B_1 w_1 &= 0 & \text{on } \partial\Omega \end{aligned} \quad (1.2)$$

and

$$\begin{aligned} \mu_2 \Delta w_2 + f_2(x, \bar{u}_1, 0)w_2 &= \sigma_2 w_2 & \text{in } \Omega \\ B_2 w_2 &= 0 & \text{on } \partial\Omega \end{aligned} \quad (1.3)$$

The result is that (1.1) is permanent provided that the unique principal eigenvalues  $\sigma_1$  and  $\sigma_2$  for which (1.2) and (1.3) admit positive solutions are both positive. The positivity of  $\sigma_1$  and  $\sigma_2$  implies the local instability of the equilibria  $(\bar{u}_1, 0)$  and  $(0, \bar{u}_2)$ . This can be interpreted as an invasibility condition. The reader should note that if for instance  $\sigma_1 \leq 0$ , the extinction state  $(0, \bar{u}_2)$  is in a sense stable, so that coexistence cannot be expected.

In Sect. 3, we explore how the outcome of competition in heterogeneous environments may differ from that in homogeneous environments. This issue is one we have addressed before in the context of refuge design ([9]). Our results here are of a different flavor. In particular, we use results derived in [10] to examine cases in which the diffusion rates  $\mu_i$  are either very large or very small. We demonstrate that the competitors may coexist even when competition is very strong throughout  $\Omega$  (which would not be possible on

a homogeneous environment), provided that the populations segregate spatially, with the mechanism for segregation being spatial variation in growth rates and carrying capacities, rather than the geometry of  $\Omega$  *per se*. Likewise, we observe that coexistence is possible with no such spatial segregation, provided strong competition is restricted to small spatial regions. Finally, we examine situations treated by Pacala and Roughgarden [32]. We elaborate on their numerical observations that invasion in competition models is possible globally when it would fail in a homogeneous environment corresponding to any local region of the global environment and that, conversely, invasion may fail globally when it would be possible in a homogeneous environment corresponding to any local region of the global environment. We show that the underlying reason for these phenomena lies in the way that such mathematical models average environmental quality, different averages being appropriate in different contexts.

In Sect. 4, we consider a predator–prey interaction where the predator's functional response to the prey has the spatially varying form  $e(x)f(u_1)$ , with  $e(x) \geq 0$  on  $\Omega$ ,  $f(0) = 0$ ,  $f(u_1) > 0$  for  $u_1 > 0$  and  $f(u_1)$  nondecreasing in  $u_1$  for  $u_1 \geq 0$ . The term  $e(x)$  indicates the efficiency of the predation at location  $x$ . A large value of  $e(x)$  indicates that  $x$  is a favorable locale for predation, a smaller value of  $e(x)$  indicates a less favorable locale, and  $e(x) = 0$  indicates that the prey is inaccessible to the predator at  $x$ . Our interest in this problem is in how the size and spatial arrangement of favorable hunting grounds affects the model's predictions on the longterm viability of the predator. We establish that if there is a sufficient amount of habitat where the predator is highly efficient or where the predator is rather inefficient, then the location and configuration (so long as it remains contiguous) of this habitat within  $\Omega$  does not affect the model's prediction on the success of the predator. The predator persists in the first case and goes extinct in the second. Moreover, we also demonstrate that for a hunting ground of intermediate size and favorability for predation, location and spatial arrangement with  $\Omega$  of the hunting ground become crucial factors in determining whether the model predicts persistence or extinction for the predator. In our results we derive quantitative criteria for the survival or extinction of the predator. These criteria can be explored further on the basis of our previous work ([4–6]) on eigenvalue problems with indefinite weights. The situations we consider have some relation to those examined in studies of the effects of prey refuges on predator–prey interactions, e.g. [30, 34], but we address different questions. In particular we do not attempt to analyze the effects of heterogeneity on the size or stability of a coexistence equilibrium but only on the prediction of coexistence or extinction.

In Sect. 5 we describe the biological conclusions of our work in a relatively nonmathematical way, give a brief discussion of how our work is (or is not) related to other theoretical studies, and try to suggest some possible ways in which our theoretical results could be connected with empirical studies.

The mathematical results of Sect. 2 are all proved in one or more of our references or follow directly from the results or methods discussed in those

references. Essentially all of the new mathematical results are stated in Sects. 3 and 4 and proved in the Appendix. All the results whose proofs are given in the Appendix are to our knowledge new.

## 2. Mathematical background

The models we consider all have the form

$$\begin{aligned} u_{it} &= \mu_i \Delta u_i + f_i(x, u_1, u_2) u_i && \text{in } \Omega \times (0, \infty) \\ B_i u_i &= 0 && \text{on } \partial\Omega \times (0, \infty) \\ u_i(x, 0) &= u_i^0(x) \geq 0 && \text{in } \Omega \end{aligned} \quad (2.1)$$

for  $i = 1, 2$ , where  $u_i$  denotes the *population density* of the  $i$ th interacting species,  $\Omega \subseteq \mathbb{R}^n$  (usually  $n = 1, 2$  or  $3$ ) is the habitat in question, and the homogeneous boundary condition,  $B_i$  represents either a barrier ( $B_i u_i = \partial u_i / \partial \nu$ , the outer normal derivative) or a completely hostile exterior (i.e.  $B_i u_i = u_i$ ). Here  $u_{it}$  denotes  $\partial u_i / \partial t$  and as usual  $\Delta = \partial^2 / \partial x_1^2 + \cdots + \partial^2 / \partial x_n^2$  is the Laplace operator,  $\mu_i > 0$  is the diffusion rate for the  $i$ th species, and  $f_i(x, u_1, u_2)$  is the local per capita growth law for the  $i$ th species (accounting for possible spatial heterogeneity in the habitat and for the effects of interspecies interactions). We shall assume  $\partial\Omega$  is smooth.

If the functions  $f_i$  are jointly  $C^2$  in  $x, u_1$ , and  $u_2$  then the system (2.1) generates a semiflow in  $C(\bar{\Omega})^2$ ; see [10–12, 22]. Even if the functions are merely Lipschitz in  $u_1$  and  $u_2$  and piecewise continuous in  $x$  then the system generates semiflows on function spaces generated by fractional powers of the Laplace operator acting on an appropriate domain in  $L^p(\Omega)^2$ . A competition model with coefficients that are only piecewise continuous is treated in [9].

The notions of permanence and (in the competitive case) compressivity require a definition of positivity. In the case of Neumann boundary conditions we can work in  $C(\bar{\Omega})^2$  and define  $(u, v) > 0$  to mean simply that  $u > 0, v > 0$  on  $\bar{\Omega}$ . In the Dirichlet case we can never have solutions of (2.1) which are positive on  $\bar{\Omega}$  because of the boundary condition. However, we still want to arrange for a positive cone with nonempty interior. To do that we define  $(u, v) > 0$  if  $u > 0, v > 0$  in  $\Omega$  and  $\partial u / \partial \eta < 0, \partial v / \partial \eta < 0$  on  $\partial\Omega$ . The positive cone corresponding to this definition will have nonempty interior in  $C^1(\bar{\Omega})^2$ , so in the Dirichlet case we will work in  $C^1(\bar{\Omega})^2$ . (To use monotonicity and establish compressivity in the competitive case we would also need to use the ordering  $(u_1, u_2) > (v_1, v_2)$  if  $u_1 > v_1$  and  $u_2 < v_2$ ; however, we would still work in  $C(\bar{\Omega})^2$  in the Neumann case and  $C^1(\bar{\Omega})^2$  in the Dirichlet case, and the componentwise definitions of positivity would still be as above.)

A system is said to be permanent if it is point dissipative, preserves the positive cone and its boundary, and has a positive set  $A$  lying some distance  $\varepsilon > 0$  away from the boundary of the positive cone such that  $A$  is globally attracting for solutions with positive initial data. In the Dirichlet case the conclusion is that there are functions  $v_1(x), v_2(x)$  with  $v_i > 0$  on  $\Omega, \partial v_i / \partial \eta < 0$

on  $\partial\Omega$  for  $i = 1, 2$  such that every positive solution eventually satisfies  $u_i \geq v_i$  on  $\Omega$  and  $\partial u_i / \partial \eta \leq \partial v_i / \partial \eta$  on  $\partial\Omega$  for  $i = 1, 2$ . In the competitive case the alternative approach of compressivity uses monotonicity and asserts the existence of a positive globally attracting order interval, but the implications about asymptotic lower bounds for  $u_1$  and  $u_2$  are identical to those of permanence and are valid under precisely the same hypotheses.

We now outline of the procedure established in [11] for a determination of permanence for (2.1). We then follow with a discussion of the biological interpretation of the result and the underlying prerequisites on the diffusion rates  $\mu_i > 0$  and the local *per capita* growth laws  $f_i(x, u_1, u_2)$ . Further discussion of these prerequisites may be found in [4] and [10]. In the competitive case the same procedure and prerequisites establish compressivity as in [15, 21].

### 2.1 The procedure for establishing coexistence

In all cases we shall need some sort of upper bounds on the solutions of (2.1) as  $t \rightarrow \infty$ , and for all of the models we consider such bounds are available. Specifically, all of our systems will be point dissipative, that is, they will have the property that any initial data will eventually be drawn into a fixed bounded set. Establishing dissipativity may be difficult, but once it is established conditions for coexistence may be obtained via three steps.

**Step 1.** We require  $\mu_1 > 0$  with the property that

$$\begin{aligned} u_{1t} &= \mu_1 \Delta u_1 + f_1(x, u_1, 0) u_1 && \text{in } \Omega \times (0, \infty) \\ B_1 u_1 &= 0 && \text{on } \partial\Omega \times (0, \infty) \\ u_1(x, 0) &= u_1^0(x) \geq 0 && \text{in } \Omega \end{aligned} \quad (2.2)$$

admits a globally attracting equilibrium solution which is positive on  $\Omega$ . Denote this solution by  $\bar{u}_1(x)$ .

**Step 2.** We consider the companion problem

$$\begin{aligned} u_{2t} &= \mu_2 \Delta u_2 + f_2(x, 0, u_2) u_2 && \text{in } \Omega \times (0, \infty) \\ B_2 u_2 &= 0 && \text{on } \partial\Omega \times (0, \infty) \\ u_2(x, 0) &= u_2^0(x) \geq 0 && \text{in } \Omega. \end{aligned} \quad (2.3)$$

There are two alternatives:

- There is a  $\mu_2 > 0$  so that (2.3) admits a globally attracting equilibrium solution which is positive on  $\Omega$ . In this case, for such a  $\mu_2$ , denote the solution by  $\bar{u}_2(x)$ .
- There is no such  $\mu_2$ . In this case, we let  $\mu_2 > 0$  be arbitrary and take  $\bar{u}_2(x) \equiv 0$ .

**Step 3.** Given  $\mu_1$  and  $\bar{u}_1$  from Step 1 and  $\mu_2$  and  $\bar{u}_2$  from Step 2, we assume  $f_1(x, 0, 0) \geq f_1(x, 0, \bar{u}_2(x))$  for all  $x$  in  $\Omega$ . We then formulate the eigenvalue problems

$$\mu_1 \Delta w_1 + f_1(x, 0, \bar{u}_2(x)) w_1 = \sigma_1 w_1 \quad \text{in } \Omega \quad (2.4)$$

$$B_1 w_1 = 0 \quad \text{on } \partial\Omega$$

and

$$\mu_2 \Delta w_2 + f_2(x, \bar{u}_1(x), 0) w_2 = \sigma_2 w_2 \quad \text{in } \Omega \quad (2.5)$$

$$B_2 w_2 = 0 \quad \text{on } \partial\Omega.$$

The theory of partial differential equations guarantees the existence of unique real numbers  $\sigma_1$  and  $\sigma_2$  so that (2.4) and (2.5) admit solutions  $w_1$  and  $w_2$ , respectively, with  $w_i > 0$  on  $\Omega$ . The main result of [11] is that (2.1) is permanent provided  $\sigma_1 > 0$  and  $\sigma_2 > 0$ . In the special case of competition systems the condition  $\sigma_1 > 0$  and  $\sigma_2 > 0$  also implies compressivity; see [15, 21].

### 2.2 Biological interpretation of Steps 1–3

The point of Step 1 is that in our models the species represented by  $u_1$  will be either the prey in a predator–prey system or one of the competitors in a competition system. For coexistence to be possible it is necessary that the first species can persist by itself in the absence of the damaging effects of the other species. The formulation of persistence in terms of the existence of a globally attracting positive equilibrium  $\bar{u}_1$  is rather strong, but it will be satisfied in many models provided the growth rate  $f_1(x, u_1, 0)$  is decreasing with respect to  $u_1$  and is sufficiently large over a large enough region of  $\Omega$  when  $u_1 = 0$ , e.g. if  $f_1(x, u_1, 0) = r(1 - u_1/K)$  with  $r$  large. In some situations the additional restriction that  $\mu_1$  is sufficiently small may be required. This will be the case when the boundary of  $\Omega$  is lethal so that  $u_1 = 0$  on the boundary.

In Step 2 we must distinguish between cases a) and b). In case a) the condition on the species described by  $u_2$  is the same as that on  $u_1$ , i.e. it is assumed that  $u_2$  tends toward a stable positive equilibrium density if  $u_1 = 0$  and  $u_2 > 0$  initially. This is the only case which can lead to coexistence if  $u_1$  and  $u_2$  are competitors. If  $u_2$  represents a predator which preys upon  $u_1$  the case a) corresponds to a situation where  $u_2$  has sources of food other than  $u_1$  and satisfies something like a logistic equation when  $u_1$  is absent. Case b) reflects a situation where the predator starves in the absence of the prey.

The condition  $\sigma_1 > 0$  in Step 3 is an instability criterion at the equilibrium  $(0, \bar{u}_2(x))$  of (2.1). It guarantees that if for a solution  $(u_1(x, t), u_2(x, t))$  of (2.1) there is  $t_0 > 0$  so that  $(u_1(x, t_0), u_2(x, t_0))$  is a close enough approximation to  $(0, \bar{u}_2(x))$ , then  $\partial u_1 / \partial t(x, t) > 0$  for  $t$  in some time interval  $(t_0, t_0 + \delta)$ . Consequently introducing the species with density  $u_1$  into the system (2.1) at a low density when  $u_2(x, \cdot)$  is near  $\bar{u}_2(x)$  on  $\bar{\Omega}$  prompts  $u_1(x, t)$  to increase with  $t$ .

Likewise introducing  $u_2$  at a low density into the system when  $u_1$  is close to the equilibrium density it approaches in the absence of  $u_2$  prompts growth of  $u_2$  as a function of time. Such a system is sometimes called *invasible* in the literature. Consequently, the main result of [11] can be cast as claiming that “invasibility implies permanence”.

### 2.3 Mathematical requirements and justifications

All of the mathematical results in this section follow directly from results and methods already in the literature. Our first result synthesizes a number of theorems from [11] about permanence:

**Theorem 2.1.** *Suppose that the functions  $f_i$  in (2.1) are smooth and that (2.1) is dissipative in the sense that there exist constants  $U_1, U_2$  such that for any nonnegative initial data  $u_1^0, u_2^0$  there exists a finite time  $T$  (which may depend on  $u_1^0, u_2^0$ ) such that the solution of (2.1) satisfies  $0 \leq u_1(x, t) \leq U_1$  and  $0 \leq u_2(x, t) \leq U_2$  for  $t > T$ . Suppose that the equilibria  $\bar{u}_1, \bar{u}_2$  have the properties described in Steps 1 and 2 (in case (b) of Step 2 we have  $\bar{u}_2 = 0$ ). Suppose finally that the principal eigenvalues  $\sigma_1$  and  $\sigma_2$  in (2.4) and (2.5) respectively are both positive. Under these hypotheses the system (2.1) is permanent in  $[C^1(\bar{\Omega})]^2$ . It follows (by the appropriate definition of positivity in  $[C^1(\bar{\Omega})]^2$  and the strong maximum principle) that there exist density profiles  $v_1(x)$  and  $v_2(x)$  which are positive in  $\Omega$  such that solutions to (2.1) with each of the initial densities  $u_1^0, u_2^0$  nonnegative on  $\Omega$  and strictly positive on some open subsets of  $\Omega$  have the property that  $u_1(x, t) \geq v_1(x)$  and  $u_2(x, t) \geq v_2(x)$  on  $\Omega$  for  $t$  sufficiently large.*

*Remark.* The smoothness conditions on  $f_i$  can be reduced somewhat by working in Sobolev spaces or in interpolation spaces constructed via fractional powers of the Laplace operator; see for example [20].

In the competitive case it is possible to replace permanence with compressivity, i.e. the existence of an attracting order interval, by using the methods developed in [21] and described in [15]. (The basic ideas go back much further; see [16, 24].) A consequence of those methods and results is:

**Theorem 2.2.** *Suppose that the hypotheses of Theorem 2.1 are satisfied with case a) holding in Step 2 and suppose further that the system is competitive, i.e.  $\partial f_i / \partial u_j \leq 0$  for  $i \neq j$  when  $u_1, u_2 \geq 0$ . Then the system is compressive, i.e. it has an attracting order interval, and there are solutions starting arbitrarily close to  $(\bar{u}_1, 0)$  and  $(0, \bar{u}_2)$  which converge monotonically to the equilibria bounding the order interval. (The ordering is the usual one for two species competition models, i.e.  $(p_1, p_2) \leq (q_1, q_2)$  if  $p_1 \leq q_1$  and  $p_2 \geq q_2$ .)*

*Remark.* Because the permanence results of [11] are refined by combining them with order arguments, the abstract conclusion of compressivity is stronger than that of permanence in the present context but only to the extent that there are solutions which converge monotonically to the attracting set

and which (by the order preserving properties of the system) bound the dynamics of other solutions. In specific cases it is sometimes possible to obtain estimates on the location of the attracting order interval via sub- and super-solutions, and if there is a unique coexistence equilibrium then order methods can be used to show stability. These ideas were introduced in [24] for Lotka–Volterra models and are further developed in [15, 16, 21], and some of the references in those articles. Related results are used to study two species subsystems of three species models in [12]. Note that the conditions for permanence and for compressivity in terms of invasibility are identical. There is, however another sort of result which can be obtained by using order methods:

**Lemma 2.3.** *Suppose that (2.1) is competitive and that case a) holds in Step 2. Suppose that the principal eigenvalue  $\sigma_1$  in (2.4) satisfies  $\sigma_1 > 0$  and that (2.1) does not admit an equilibrium  $(u_1^*, u_2^*)$  with  $u_i^* > 0$  on  $\Omega$  for  $i = 1, 2$ . In that case  $u_1$  excludes  $u_2$ , i.e.  $u_1 \rightarrow \bar{u}_1$  and  $u_2 \rightarrow 0$  as  $t \rightarrow \infty$  (If  $\sigma_2 > 0$  in (2.5) and there is no positive equilibrium for (2.1) then  $u_2$  excludes  $u_1$ .)*

*Remark.* This result follows from the proof of Lemma 3.3 of [12].

We now describe conditions under which the hypotheses of Theorems 2.1 and 2.2 are satisfied. Results of [11] imply:

**Lemma 2.4.** *The system (2.1) is dissipative in the sense required in Theorem 2.1 provided  $f_1(x, u_1, u_2)$  is decreasing in  $u_2$  for  $u_1, u_2 \geq 0$ , there exists a constant  $K > 0$  such that  $f_1(x, u_1, 0) < 0$  for all  $x \in \bar{\Omega}$  if  $u_1 > K$ , and that either there is a constant  $L > 0$  such that  $f_2(x, u_1, u_2) < 0$  for  $0 \leq u_1 < K + 1$  and  $u_2 > L$ , or there exist constants  $\alpha, \beta, \gamma$  with  $\alpha, \beta > 0$  such that  $\alpha f_1(x, u_1, u_2)u_1 + f_2(x, u_1, u_2)u_2 \leq \gamma - \beta(\alpha u_1 + u_2)$  for  $0 \leq u_1 \leq K + 1$  and  $u_2 \geq 0$ . (Stronger forms of dissipativity then follow via parabolic regularity.)*

To achieve Steps 1 and 2 we use results on single reaction-diffusion equations and related linear eigenvalue problems which are derived or discussed in [2–6, 14, 21, 29, 33].

**Lemma 2.5.** *Suppose that  $f_1(x, 0, 0) > 0$  on an open subset of  $\Omega$ . The linear eigenvalue problem*

$$\begin{aligned} -\Delta z &= \lambda f_1(x, 0, 0)z & \text{in } \Omega \\ B_1 z &= 0 & \text{on } \partial\Omega \end{aligned} \quad (2.6)$$

*has a nonnegative principal eigenvalue  $\lambda_1(f_1(x, 0, 0))$  which is characterized by the existence of an eigenfunction  $z > 0$  in  $\Omega$ . In the case that  $B_1 z = z$  or  $\int_{\Omega} f_1(x, 0, 0)dx < 0$ , we have  $\lambda_1(f_1(x, 0, 0)) > 0$ . If  $\int_{\Omega} f_1(x, 0, 0)dx \leq 0$  and  $B_1 z = \partial z / \partial \nu$  then  $\lambda_1(f_1(x, 0, 0)) = 0$ .*

*Discussion.* Versions of this result are obtained in [3, 21, 29, 33]; for a survey of related results see [14].

The existence and uniqueness of the equilibrium  $\bar{u}_1$  in Step 1 follows from results of [4, 21, 33]:

**Lemma 2.6.** *Suppose that*

- (i) *the intrinsic rate of growth at low densities  $f_1(x, 0, 0)$  is positive on an open subset of  $\Omega$ ;*
- (ii)  *$f_1(x, u_1, 0)$  decreases in  $u_1$  for all  $x \in \Omega$ ;*
- (iii) *there is a value  $K > 0$  so that  $f_1(x, u_1, 0) \leq 0$  for all  $x \in \Omega$  provided that  $u_1 \geq K$ .*

*Additionally, if  $\lambda_1(f_1(x, 0, 0)) > 0$  in (2.6) we restrict the diffusion rate  $\mu_1$  by requiring*

$$\mu_1 < \frac{1}{\lambda_1(f_1(x, 0, 0))}. \quad (2.7)$$

*Under these hypotheses (2.2) has a unique positive equilibrium  $\bar{u}_1$  which is globally attracting among nontrivial nonnegative solutions. If inequality (2.7) is replaced by*

$$\mu_1 \geq \frac{1}{\lambda_1(f_1(x, 0, 0))}. \quad (2.8)$$

*then (2.2) has no positive equilibrium and all nonnegative solutions approach zero as  $t \rightarrow \infty$ .*

*Remark.* Inequality (2.8) holds if and only if the principal eigenvalue  $\sigma_0$  for

$$\begin{aligned} \mu_1 \Delta \psi + f_1(x, 0, 0)\psi &= \sigma_0 \psi & \text{in } \Omega \\ B_1 \psi &= 0 & \text{on } \partial\Omega \end{aligned}$$

satisfies  $\sigma_0 \leq 0$ . This is noted in [5, 33]. (In fact if  $\sigma_0 \leq 0$  then all positive solutions of (2.2) approach zero as  $t \rightarrow \infty$ , even when  $f_1(x, 0, 0) \geq 0$  on  $\Omega$ .)

The analysis for Step 2 is similar to that for Step 1. In Step 2, alternative (a), we place conditions on  $f_2(x, 0, u_2)$  and  $\mu_2$  analogous to those on  $f_1(x, u_1, 0)$  and  $\mu_1$  in Step 1. Alternative (b) in Step 2 is included so that we may treat predation in cases when the local per capita growth law for the predator fails to exhibit self regulation (as postulated in condition (iii) for  $f_2(x, 0, u_2)$ ), for example,  $f_2(x, u_1, u_2) = -d(x) + \alpha(x)u_1/(u_1 + \beta(x))$ , where  $d, \alpha, \beta$  are positive functions on  $\Omega$ . In such cases, we require that  $f_2(x, 0, u_2) \leq 0$  for all  $u_2 \geq 0$  and all  $x \in \Omega$ , so that  $\bar{u}_2 \equiv 0$  is the globally attracting equilibrium for (2.3) for all  $\mu_2 > 0$ . To these initial restrictions we add in Step 3 the requirement that  $f_1(x, 0, 0) \geq f_1(x, 0, \bar{u}_2(x))$ , so that the  $u_2$  species has a deleterious effect on the  $u_1$  species.

All the prerequisites we have noted concern situations in which one or the other of  $u_1$  and  $u_2$  is identically zero. Consequently, our results say that “invasibility implies permanence” under a broad range of assumptions about the interactions  $f_i(x, u_1, u_2)$ . Moreover, since invasibility depends on the instability of states where only one of the species is present relative to the introduction of the other species, it is natural that our conditions for permanence occur in terms of eigenvalues for linear elliptic operators. The use of eigenvalues allows us to treat situations with spatial heterogeneity in the

models themselves or with complicated geometry in a unified way. It also permits us to treat a range of different boundary conditions. Thus we can analyze systems far more complicated than those derived from standard KISS models. (Recall that KISS models are the special cases of (2.1) where there is no explicit spatial dependence, i.e.  $f_1$  and  $f_2$  depend only on  $u_1, u_2$ , and where  $B_1 u = B_2 u = u$ .) All of our new applied results in this paper are based on making estimates that relate how  $\sigma_1$  and  $\sigma_2$  in Step 3 (equations (2.4) and (2.5)) depend on  $f_1, f_2, \bar{u}_1, \bar{u}_2, \mu_1, \mu_2, B_1, B_2$  and/or  $\Omega$ .

### 3 Competition and spatial heterogeneity

In this section we examine the implications of the results of [10] for a competition model with spatial heterogeneity. We base the model on a Lotka-Volterra system describing the dynamics of the populations  $U_1$  and  $U_2$  of two competitors in a favorable homogeneous environment:

$$\frac{dU_i}{dt} = r_i \left( 1 - \frac{U_i}{k_i} - \frac{\alpha_{ij} U_j}{k_i} \right) U_i, \quad (3.1)$$

for  $i, j = 1, 2, j \neq i$ . In (3.1),  $r_i$  is the intrinsic growth rate of the  $i$ th population at low densities,  $k_i$  is the carrying capacity of the  $i$ th population, and  $\alpha_{ij}$  describes the impact of competition from the  $j$ th population on the  $i$ th population. The coefficient  $\alpha_{ij}$  can be broken down into a term arising from direct competition for resources and another term arising from interference competition. The coefficients  $r_i$  and  $k_i$  and the part of  $\alpha_{ij}$  arising from resource competition can be derived from a consumer/resource model under suitable scaling assumptions; see [28, 36]. The part of  $\alpha_{ij}$  arising from interference competition can be derived from the average costs and benefits of acts of interspecific interference; see [13]. We shall use a different notation because in our spatially heterogeneous models, we will want to consider situations where  $r_i$  is negative on parts of the environment. If  $r_i < 0$  then the term  $(-r_i/k_i)$  multiplying  $U_i^2$  on the right side of (3.1) becomes a growth term rather than a logistic self-limitation term, and could lead to a prediction of unbounded population growth for a sufficiently large initial populations. That is not reasonable, since changing the intrinsic growth rate into a death rate should not cause unbounded growth, even for a large initial population. Thus, for our models with diffusion we take  $u_1, u_2$  to be population densities on a bounded region  $\Omega$  and write our system as in [10]:

$$\begin{aligned} \frac{\partial u_i}{\partial t} &= \mu_i \Delta u_i + [m_i(x) - b_{ii}(x)u_i - b_{ij}(x)u_j]u_i \\ &\text{in } \Omega \times (0, \infty), j \neq i, i, j = 1, 2. \end{aligned} \quad (3.2)$$

We assume that  $b_{ii}$  is bounded below by a positive constant and that for  $j \neq i$   $b_{ij}$  is nonnegative. In regions where the intrinsic growth rate is positive

we have the interpretation  $r_i = m_i, k_i = m_i/b_{ii}, \alpha_{ij} = b_{ij}/b_{ii}$  in terms of the coefficients of (3.1).

#### 3.1 Technical preliminaries

In the context of the model (3.2) the condition for permanence is that  $\sigma_i > 0$  in

$$\begin{aligned} \mu_i \Delta \psi_i + (m_i(x) - b_{ij}(x)\bar{u}_j)\psi_i &= \sigma_i \psi_i \quad \text{in } \Omega \\ B_i \psi_i &= 0 \quad \text{on } \partial\Omega \end{aligned} \quad (3.3)$$

for  $i = 1, 2, j \neq i$ , where  $\bar{u}_i$  is the equilibrium for (3.2) when  $u_j \equiv 0$ . The remainder of this section will be devoted to studying the connection between permanence and the coefficients of (3.2) to gain insight into the biological circumstances in which coexistence is expected. An important tool in our analysis is the following result which is proved in [10]:

**Lemma 3.1.** *In (3.3),  $\sigma_i > 0$  if*

$$\int_{\Omega} (b_{ii}\bar{u}_i - b_{ij}\bar{u}_j)\bar{u}_i^2 dx > 0 \quad (j \neq i). \quad (3.4)$$

We shall proceed by examining how  $\bar{u}_i$  behaves as  $\mu_i \rightarrow 0$  or  $\mu_i \rightarrow \infty$  and then using Lemma 3.1 and other results to draw conclusions about coexistence or exclusion. Recall that Lemmas 2.5 and 2.6 imply that the problem

$$\begin{aligned} \frac{\partial u}{\partial t} &= \mu \Delta u + m(x)u - b(x)u^2 \quad \text{in } \Omega \times (0, \infty), \\ Bu &= 0 \quad \text{on } \partial\Omega \times (0, \infty) \end{aligned} \quad (3.5)$$

(where  $Bu = u$  or  $Bu = \partial u / \partial \eta$  and  $b(x) \geq 0$ ) will have a positive equilibrium  $\bar{u}$  which is globally attracting among nonnegative solutions provided that either

$$B = \frac{\partial u}{\partial \eta} \quad \text{and} \quad \int_{\Omega} m(x) dx \geq 0$$

or

$$\mu < \frac{1}{\lambda_1(m(x))}.$$

**Lemma 3.2.** *Suppose  $m(x)$  and  $b(x)$  are piecewise smooth and  $b(x) \geq b_0 > 0$ . In (3.5) we have*

$$\begin{aligned} \bar{u} &\rightarrow m(x)/b(x) \quad \text{as } \mu \rightarrow 0 \quad \text{if } m(x) > 0 \\ \bar{u} &\rightarrow 0 \quad \text{as } \mu \rightarrow 0 \quad \text{if } m(x) < 0 \end{aligned} \quad (3.6)$$

where the convergence is uniform on closed subsets of  $\Omega$  where  $m(x)$  and  $b(x)$  are smooth and  $m(x)$  is strictly of one sign.



If  $Bu = \partial u / \partial \eta$  and  $\int_{\Omega} m(x) dx > 0$  then

$$\bar{u} \rightarrow \frac{\int m(x) dx}{\int b dx} \quad \text{as } \mu \rightarrow \infty \quad (3.7)$$

uniformly on  $\Omega$ .

*Discussion.* The first part of this lemma i.e. (3.6), is proved in [10] in this case  $b \equiv 1$ , but the same methods work for general  $b > 0$ . Notice that the convergence in (3.6) need not be uniform because of possible boundary layer effects. However, the sort of convergence in (3.6) implies convergence in  $L^p(\Omega)$  for any  $p \geq 1$  since by the maximum principle  $\bar{u} \leq \sup(\frac{m(x)}{b(x)})$  uniformly in  $\mu$ . The fact that we do not generally have uniform convergence in (3.6) necessitates the following technical lemma.

**Lemma 3.3.** Suppose that  $m(x) \in C^\alpha(\bar{\Omega})$  and there exists a positive equilibrium  $\bar{u}$  for (3.5). For  $p$  sufficiently large but finite the equilibrium  $\bar{u}$  depends continuously as an element of  $C^{1+\alpha}(\bar{\Omega})$  on  $m(x)$  as an element of  $L^p(\Omega)$ ; i.e. for any  $\varepsilon > 0$  there exists a  $\delta > 0$  such that if  $\tilde{m} \in L^p(\Omega)$  with  $\|m - \tilde{m}\|_p < \delta$  then there is an equilibrium  $\tilde{u}$  for

$$\begin{aligned} \frac{\partial u}{\partial t} &= \mu \Delta u + \tilde{m}(x)u - b(x)u^2 & \text{in } \Omega \times (0, \infty) \\ Bu &= 0 & \text{on } \partial\Omega \times (0, \infty) \end{aligned} \quad (3.8)$$

satisfying  $\|\bar{u} - \tilde{u}\|_{C^{1+\alpha}(\bar{\Omega})} < \varepsilon$ .

*Proof.* See Appendix.

*Remark.* In general,  $\bar{u}$  will belong to the Sobolev space  $W^{2,p}(\Omega)$ , and the precise condition on  $p$  is that  $p$  be large enough that  $W^{2,p}(\Omega) \subseteq C^{1+\alpha}(\bar{\Omega})$ . If  $\tilde{m} \in L^p(\Omega)$  then  $\tilde{u}$  is unique. (See [4].)

We now have the technical results needed for an analysis of (3.2).

### 3.2 Competition in heterogeneous environments when dispersal rates are small or large

The first two results in this subsection deal with the case where both species disperse slowly.

**Proposition 3.4.** Suppose that  $m_i(x)$  is piecewise smooth and  $m_i(x) > 0$  on an open subset of  $\Omega$  for  $i = 1, 2$  and that for either  $i = 1$  and  $j = 2$  or  $i = 2$  and  $j = 1$ ,

$$m_i - \frac{b_{ij}(m_j)_+}{b_{jj}} > 0 \quad (3.9)$$

on an open subset of  $\Omega$ . If  $\mu_1$  and  $\mu_2$  are sufficiently small then  $\sigma_i > 0$  for  $i = 1, 2$  and hence (3.2) is permanent and compressive by Theorems 2.1 and 2.2.

*Proof.* See Appendix.

*Remark.* This result sharpens a result in [10] based on Lemma 3.1.

**Proposition 3.5.** Suppose that for either  $i = 1$  or  $i = 2$  (3.9) holds but that for  $j \neq i$

$$m_j - b_{ji} \frac{\left[ m_i - \frac{b_{ij}(m_j)_+}{b_{jj}} \right]_+}{b_{ii}} < 0 \quad \text{on } \bar{\Omega}. \quad (3.10)$$

If  $\mu_1$  and  $\mu_2$  are sufficiently small then species  $i$  excludes species  $j$ , i.e. if  $u_i(x, 0) > 0$  then  $u_j \rightarrow 0$  as  $t \rightarrow \infty$ .

*Proof.* See Appendix.

### 3.3 Remarks and biological interpretation

In the case of constant coefficients, having the condition (3.9) hold for  $i, j = 1, 2$  is exactly the standard condition for the coexistence in the classical spatially uniform Lotka–Volterra competition model. Proposition 3.4 says that if each species has some region where it can locally coexist with or exclude the other, then for sufficiently low dispersal rates the population will coexist. On the other hand, Proposition 3.5 implies exclusion of one species by the other provided that (3.10) holds everywhere, so that one species always has an advantage over the other. In the case of positive coefficients, (3.10) may be rewritten as  $m_j(1 + \frac{b_{ij}b_{ii}}{b_{ii}b_{jj}}) - \frac{b_{ij}m_i}{b_{ii}} < 0$ . This is stronger than simply the reverse inequality in (3.9), which would be  $m_j - \frac{b_{ij}m_i}{b_{ii}} < 0$ . How much stronger (3.10) is than the reverse of (3.9) depends on the relative sizes of the coefficients describing competition and self-limitation. It is not surprising that in the diffusive case there is some gap between the condition for coexistence and that for exclusion. The parameter dependence of the set of positive equilibria for (3.2) can be quite complicated, and there are no simple necessary and sufficient conditions for the existence of a positive equilibrium except in special cases. (See [2, 7, 8, 16–19, 24, 26, 27, 31].) Another complication is that in the diffusive case permanence (and compressivity) and exclusions are not the only practical possibilities. Even in the spatially uniform situation there is the case of contingent competition, where both states  $(\bar{u}, 0)$  and  $(0, \bar{u}_2)$  are locally stable but there is an unstable coexistence equilibrium. In the spatially uniform situation almost any small deviation from the coexistence equilibrium results in the extinction of one or the other species, so the practical prediction is that coexistence will not be observed. However, in the diffusive case there can be situations where both  $(\bar{u}_1, 0)$  and  $(0, \bar{u}_2)$  are locally stable but there also exist stable equilibria with both species present. This can occur if the domain  $\Omega$  consists of two large regions separated by a narrow corridor: the coexistence equilibria then have one species dominant on one of the other large region. (Results of this type are obtained in [31]; E. N. Dancer also has obtained

related results.) The significance here is that although invasibility implies coexistence, failure of invasibility ( $\sigma_i < 0$  for one or both of  $i = 1$  and  $2$ ) does not imply exclusion.

There are a number of scenarios under which (3.9) can be satisfied for  $i = 1, 2, j \neq i$  so that coexistence is predicted. The standard one is the case where  $b_{ij}$  is small for  $i \neq j$ ; i.e. competition is relatively weak. However, it is also possible that  $b_{ij}$  is large everywhere for  $i \neq j$  but that  $m_i$  is large where  $m_2$  is small and vice-versa. Such a scenario could arise if the two populations had growth rates that were strongly affected by some spatially variable quantity other than the availability of those resources for which the species compete. (Some factors of that type might be the presence or absence of refugees from predators or of some additional resource needed by one population but not the other.) In that case competition might be very strong but occur only rarely because the populations would segregate themselves for reasons not related to their competition. Another possibility might be competition (as measured by  $b_{ij}$ ) which is strong in some regions and weak in others, or where each species has an advantage ( $b_{ij} \gg b_{ji}$ ) in some type of habitat.

In the case where the growth rates  $m_i$  are positive throughout  $\Omega$  we may use the notation of (3.1), so that  $m_i = r_i$ ,  $b_{ii} = r_i/k_i$ , and  $b_{ji} = \alpha_{ij}r_i/k_i$ . In that notation (3.9) becomes

$$k_i - \alpha_{ij}k_j > 0 \quad \text{on an open subset of } \Omega \quad (3.11)$$

and (3.10) becomes

$$k_j - \frac{\alpha_{ij}k_i}{(1 + \alpha_{ij}\alpha_{ji})} < 0 \quad \text{on } \bar{\Omega}. \quad (3.12)$$

The next two results treat the case where one species disperses rapidly but the other disperses slowly. The only case where a population can persist with very rapid dispersal (i.e.  $\mu \rightarrow \infty$ ) is when the boundary condition is  $B_i u = \partial u / \partial \eta$  and where  $\int m_i dx > 0$ ; thus we shall always assume that those conditions hold for the rapidly dispersing population.

We shall use the notation

$$\bar{m}_i = \int m_i dx, \quad \bar{b}_{ii} = \int b_{ii} dx, \quad \bar{b}_{ij} = \int b_{ij} dx. \quad (3.13)$$

**Proposition 3.6.** Suppose that  $\bar{m}_i > 0$ ,  $B_i u = \partial u / \partial \eta$ , and  $m_j(x) > 0$  on an open subset of  $\Omega$ . If

$$\bar{m}_i - \int \left[ \frac{b_{ij}(m_j)_+}{b_{jj}} \right] dx > 0 \quad (3.14)$$

and

$$m_j - \frac{b_{ji}\bar{m}_i}{\bar{b}_{ii}} > 0 \quad (3.15)$$

on an open subset of  $\Omega$  then for  $\mu_i$  sufficiently large and  $\mu_j$  sufficiently small  $\sigma_i > 0$  and  $\sigma_j > 0$  so that the species coexist.

*Discussion.* The proof is similar to that of Proposition 3.4. A sketch is given in the Appendix. If (3.14) above holds then  $\sigma_i > 0$  for  $\mu_i$  sufficiently large and  $\mu_j$  sufficiently small; similarly (3.15) alone implies  $\sigma_j > 0$  in that case.

**Proposition 3.7.** Suppose that (3.14) holds but

$$m_j - \frac{\bar{b}_{ji} \left[ \bar{m}_i - \int \left( \frac{b_{ij}(m_j)_+}{b_{ij}} \right) dx \right]}{\bar{b}_{ii}} < 0 \quad \text{on } \bar{\Omega} \quad (3.16)$$

Then  $u_i$  excludes  $u_j$  if  $\mu_i$  is sufficiently large and  $\mu_j$  sufficiently small. Suppose that (3.15) holds but

$$\bar{m}_i - \int \left[ \frac{\bar{b}_{ij} \left( m_j - \frac{b_{ji}\bar{m}_i}{\bar{b}_{ii}} \right)_+}{b_{jj}} \right] dx < 0 \quad (3.17)$$

Then for  $\mu_j$  small and  $\mu_i$  large,  $u_j$  excludes  $u_i$ .

*Discussion.* The proof is similar to that of Proposition 3.5. A sketch is given in the Appendix.

### 3.4 Remarks and biological interpretation

As in the case where both populations have low dispersal rates, the conditions (3.14) and (3.15) for invasibility and hence coexistence reduce to the standard conditions for a spatially homogeneous Lotka-Volterra model (i.e. (3.11) in the notation of (3.1)) provided the coefficients are all constant. The conditions (3.16) and (3.17) for exclusion are analogous to (3.10) and in the case of constant coefficients reduce (in the notation of (3.1)) to (3.12). However, (3.14) and (3.17) are integral conditions and (3.16) involves integrated terms. This is natural since one competitor is assumed to disperse quite rapidly. However, the way in which coefficients are averaged in terms such as  $\int [b_{ij}(m_j)_+ / b_{jj}] dx$  (which occurs in (3.14) and (3.16)) is more complex than simply replacing each coefficient with its (arithmetic) mean value. This can produce counterintuitive results, some of which were observed in numerical experiments by Pacala and Roughgarden [32]. We shall discuss this point in detail in the next subsection.

Another similarity with the case of low dispersal rates is that the conditions for each competitor to persist may fail to hold locally on parts of  $\Omega$  but the populations may still persist. In the case of the slow disperser the essential point of condition (3.15) is that there must be some region where that competitor has an advantage relative to a certain average of the competitive strength of the rapid disperser. The mechanism is simply that the slow dispersers tend to remain in the region where their population has an advantage and is thus able to recruit effectively. The rapid disperser can also persist with only a local advantage if the advantage is sufficiently great, but the mechanism is different. Condition (3.14) is an averaged condition, so that if  $m_i - (b_{ij}(m_j)_+ / b_{jj})$  is sufficiently large in some places the condition may hold

even though  $m_i - (b_{ij}(m_j)_+/b_{jj}) < 0$  elsewhere. A scenario leading to (3.14) might occur if the fast dispersers had a sufficiently great advantage in some region and visited that region enough (because of their rapid dispersal) so that the local advantage was still adequate for persistence after averaging over the environment.

The last two results in this section treat the case where both populations disperse rapidly ( $\mu_1$  and  $\mu_2$  large). In this case we must have  $B_i = \partial u/\partial \eta$  and  $\int m_i dx > 0$  for  $i = 1, 2$  for the species to be able to persist without competition at arbitrarily high dispersal rates.

**Proposition 3.8.** *Suppose that for  $i = 1, 2$ ,  $B_i = \partial u/\partial \eta$ . If*

$$\bar{m}_i - \frac{\bar{b}_{ij}\bar{m}_j}{\bar{b}_{jj}} > 0 \quad (i \neq j) \quad (3.18)$$

(where the bars denote integration over  $\Omega$ ) then for  $\mu_1$  and  $\mu_2$  sufficiently large we have  $\sigma_i > 0$ .

Thus, if (3.18) holds for  $i = 1, 2$ , then (3.2) is permanent and compressive for  $\mu_1, \mu_2$  sufficiently large.

*Discussion.* This result follows from Lemmas 3.1 and 3.2 in the same way as the part of Proposition 3.6 involving inequality (3.14), so the proof is omitted.

**Proposition 3.9.** *Suppose that  $B_i = \partial u/\partial \eta$  for  $i = 1, 2$  and that (3.18) holds but*

$$\bar{m}_j - \frac{\bar{b}_{ij}\left(\bar{m}_j - \frac{\bar{b}_{ji}\bar{m}_i}{\bar{b}_{ii}}\right)}{\bar{b}_{jj}} < 0. \quad (3.19)$$

Then  $u_i$  excludes  $u_j$  if  $\mu_1$  and  $\mu_2$  are sufficiently large.

*Discussion.* The result is analogous to Proposition 3.5 and (3.7) and is proved in the same way. The details of the proof are omitted.

*Remarks.* Again, the conditions for persistence reduce to the usual conditions in the spatially uniform model provided the coefficients are constant. The conditions for exclusion are also the same as those imposed in Propositions 3.5 and (3.7) provided that coefficients are constant. (These conditions are shown in terms of the coefficients of (3.1) in (3.11) and (3.12).) As in the previous cases, it turns out that a species can persist if it has a suitable advantage somewhere. What is interesting in this case is that some of the averages occurring in (3.18) and (3.19) are *not* simple averages over the environment  $\Omega$  of biologically interpretable quantities such as carrying capacities  $k_i$  in (3.1) or competition coefficients  $\alpha_{ij}$  in (3.1) but instead are averages of combinations or functions of those quantities. This can have some significant consequences, which we describe next.

We have seen that in general the conditions for invasibility (e.g. (3.9), (3.14), (3.15), (3.18)) need only hold in some regions or in some average sense rather

than throughout the entire environment  $\Omega$ . This can have some counterintuitive consequences, as was observed by Pacala and Roughgarden [32] in numerical experiments. We can use the results obtained in the present article to explain and rigorously verify some of those counterintuitive observations. The system treated in [32] was written as a diffusive version of (3.1) in one space dimension, with growth rates  $r_i$  and competition coefficients  $\alpha_{ij}$  constant but carrying capacities  $k_i = k_i(x)$  depending on location. The boundary conditions were of Neumann type (i.e. no flux or closed environment). We consider the analogous system

$$\begin{aligned} \frac{\partial u_i}{\partial t} &= \mu_i \Delta u_i + r_i \left[ 1 - \frac{u_i}{k_i(x)} - \frac{\alpha_{ij} u_j}{k_i(x)} \right] u_i \quad \text{in } \Omega \times (0, \infty) \\ B_i u_i &\equiv \frac{\partial u_i}{\partial \eta} = 0 \quad \text{on } \partial \Omega \times (0, \infty). \end{aligned} \quad (3.20)$$

Recall that in the spatially homogeneous case the condition for coexistence is

$$\alpha_{ij} < \frac{k_i}{k_j}. \quad (3.21)$$

The counterintuitive observations of [32] can be paraphrased as follows:

*Observation II.* When  $\mu_i$  is relatively large and  $\mu_j$  is relatively small, it may be possible for species  $j$  to invade when species  $i$  is at equilibrium (i.e.  $\sigma_j > 0$ ) even though

$$\alpha_{ji} > \frac{k_j(x)}{k_i(x)} \quad \text{on } \Omega \quad (3.22)$$

*Observation III.* When  $\mu_j$  is large, it may be impossible for species  $j$  to invade with species  $i$  at equilibrium ( $\sigma_j < 0$ ) even though

$$\alpha_{ji} < \frac{k_j(x)}{k_i(x)} \quad \text{on } \Omega. \quad (3.23)$$

(Recall that  $\mu_1$  and  $\mu_2$  represent dispersal rates.)

We first treat Observation II. The condition for  $\sigma_j > 0$  for  $\mu_i$  large and  $\mu_j$  small is given by (3.15). We have

**Corollary 3.10.** *In the system (3.20),  $\sigma_j > 0$  if  $\mu_i$  is sufficiently large,  $\mu_j$  is sufficiently small, and*

$$\alpha_{ji} < \left( \frac{k_j(x)}{|\Omega|} \right) \int \frac{1}{k_i(x)} dx \quad \text{on some open subset of } \Omega. \quad (3.24)$$

*Proof.* This result follows from identifying  $m_j = r_j$ ,  $b_{ji} = r_j \alpha_{ji}/k_j(x)$ ,  $m_i = r_i$ , and  $b_{ii} = r_i/k_i(x)$  in (3.15), and then applying Proposition 3.6.

*Remarks.* We could write (3.24) as

$$\alpha_{ji} < \frac{k_j(x)}{\left(1/\int_{|\Omega|} \frac{1}{k_i(x)} dx\right)} = \frac{k_j(x)}{(\text{harmonic mean of } k_i(x))} \quad (3.25)$$

on some subset of  $\Omega$ . (Recall that the harmonic mean of two positive numbers  $A$  and  $B$  is

$$\text{harmonic mean } \{A, B\} = \frac{1}{\frac{1}{2}\left(\frac{1}{A} + \frac{1}{B}\right)} = \frac{2AB}{A+B}$$

and that the harmonic mean is less than or equal to the arithmetic mean. For a positive function  $f(x)$ , the harmonic mean of  $f(x) = 1/((1/|\Omega|) \int (1/f(x))) dx$ . By the Schwartz inequality,

$$|\Omega|^2 = \left(\int 1 dx\right)^2 \leq \left(\int f(x) dx\right) \left(\int \frac{1}{f(x)} dx\right)$$

so that

$$\left[\frac{1}{|\Omega|} \int \left(\frac{1}{f(x)}\right) dx\right] \leq \frac{1}{|\Omega|} \int f(x) dx. \quad (3.26)$$

This is the integral version of the arithmetic-harmonic mean inequality.)

To examine the relationship between Corollary 3.10 and Observation II of [32] more closely let us assume that the terms  $k_i(x)$ ,  $i = 1, 2$  behave as in [32]. Specifically, suppose that for  $i = 1, 2$  the function  $k_i(x)$  equals a constant  $k_{i1}$  on a subdomain  $\Omega_1 \subset \Omega$  and another constant  $k_{i2}$  on  $\Omega_2 \equiv \Omega \setminus \Omega_1$ . (This type of coefficient violates some of the smoothness hypotheses needed to establish permanence via abstract methods; however, there is no major problem in handling coefficients with jump discontinuities from either the viewpoint of eigenvalues or compressivity. See [4, 6, 9] for detailed treatments of models with possibly discontinuous coefficients.) Let  $\beta = |\Omega_1|/|\Omega|$ .

**Corollary 3.11** Suppose that  $k_1(x)$  and  $k_2(x)$  have the form described above with

$$\alpha_{21}k_{11} > k_{21} > \alpha_{21}k_{12} > k_{22} \quad (3.27)$$

and  $\beta > 0$  sufficiently small. If  $\mu_1$  is sufficiently large and  $\mu_2$  sufficiently small then  $\sigma_2 > 0$  even though  $\alpha_{21} > k_2(x)/k_1(x)$  on  $\Omega$ .

*Proof.* We need only to verify that (3.25) will be satisfied so that Corollary 3.10 applies with  $j = 2$ ,  $i = 1$ . Computing the harmonic mean of  $k_1$  yields  $k_{11}k_{12}/(\beta k_{12} + (1-\beta)k_{11})$  which approaches  $k_{12}$  as  $\beta \rightarrow 0$ . By (3.27) we have  $\alpha_{21} < k_{21}/k_{12}$  so that  $\alpha_{21} < k_{21}/(\text{harmonic mean of } k_1)$  for  $\beta$  small, and hence is satisfied on  $\Omega_1$ .

*Remarks.* The first and last inequalities in (3.27) simply restate the hypotheses that  $(k_2(x)/k_1(x)) < \alpha_{21}$  of Observation II. The inequality (3.26) and the

assumptions that  $\mu_1$  is large and  $\mu_2$  is small are precisely conditions (14) and (15) of [32]. It turns out that to satisfy (3.25) with  $k_1$  and  $k_2$  as above we must have  $k_{22} < k_{21} < k_{11}$ . The hypotheses that  $\mu_2$  is small may sometimes be refined or omitted, since what is really needed to imply  $\sigma_2 > 0$  is that either

$$\mu_2 < \frac{1}{\lambda_1 \left(1 - \frac{\alpha_{21}\bar{u}_1}{k_2}\right)} \quad \text{or} \quad \int \left(1 - \frac{\alpha_{21}\bar{u}_1}{k_2}\right) dx > 0.$$

We have that if  $\mu_1 \rightarrow \infty$  then  $u \rightarrow$  harmonic mean of  $k_1(x)$ . If we write  $h(k_1) =$  harmonic mean of  $k_1$  we have  $\sigma_2 > 0$  for all  $\mu_2$  if

$$\int \left[1 - \frac{\alpha_{21}h(k_1)}{k_2(x)}\right] dx > 0$$

as well, or if

$$\mu_2 < \frac{1}{2\lambda_1 \left(1 - \frac{\alpha_{21}h(k_1)}{k_2(x)}\right)}$$

and  $\mu_1$  is large enough that

$$\lambda_1 \left(1 - \frac{\alpha_{21}\bar{u}_1}{k_2(x)}\right) < 2\lambda_1 \left(\frac{1 - \alpha_{21}h(k_1)}{k_2(x)}\right).$$

We now turn to Observation III of [32]. The phenomenon suggested there will occur under the hypotheses of the following proposition.

**Proposition 3.12.** Suppose that  $\mu_i > 0$  is fixed and that

$$\frac{\gamma k_j(x)}{k_i(x)} < \alpha_{ji} < \frac{k_j(x)}{k_i(x)} \quad \text{on } \Omega \quad (3.28)$$

for some  $\gamma < 1$ . If  $\gamma$  is sufficiently close to 1 and  $\mu_j$  is sufficiently large then  $\sigma_j > 0$ .

*Proof.* See Appendix.

*Remarks.* Proposition 3.12 shows that the phenomenon suggested in Observation III of [32] does in fact occur in reaction-diffusion models. In [32] it is stated that the phenomenon requires both  $\mu_i$  and  $\mu_j$  to be large; however, an analytic treatment in [32] of a simpler two-patch model based on ordinary differential equations suggests that for a given value of  $\mu_j$  the phenomenon will not occur if  $\mu_i$  is either too small or too large. (For a given value of  $\mu_i$  the phenomenon does seem to occur for  $\mu_j$  sufficiently large. See [32, Fig. 6] and the associated discussion.)

*Biological interpretation.* The implication of Proposition 3.12 is that even though species  $j$  satisfies the condition for invasibility in a spatially uniform environment at each point of a spatially heterogeneous environment, invasibility may fail if the dispersal rate (measured by  $\mu_j$ ) is too large. The

mechanism is that if the  $j$ th species has high dispersal rate it must satisfy an invasibility condition which is averaged over the environment. If the  $i$ th species disperses but not too rapidly, its dispersal from highly favorable to less favorable regions can give it a spatially varying equilibrium so that the averaged invasibility condition for the  $j$ th species fails. Note that the hypothesis (3.28) requires  $\gamma [\max(\frac{k_j}{k_i})] < \min(\frac{k_j}{k_i})$  so that  $\gamma$  can be taken arbitrarily close to 1 only if  $k_j = \delta k_i$  for some  $\delta > 0$ . This does not rule out the phenomenon of Observation III in other cases, but suggests that for the phenomenon to occur it might be necessary that the regions which are more favorable for the species  $j$  are also more favorable for the species  $i$ . (Something of that sort was true in those numerical simulations in [32] where Observation III occurred. The scenario treated in [32] took  $k_i(x) = k_{is}$  on  $\Omega_s$  for  $i, s = 1, 2$  with the assumption that  $k_{21} > \alpha_{21}k_{11} > k_{22} > \alpha_{21}k_{12}$ .) In [32] it is suggested that Observation III could be expected to hold when both  $\mu_i$  and  $\mu_j$  are large. This may not be correct, because if both  $\mu_i$  and  $\mu_j$  are large and  $\alpha_{ji} < k_j(x)/k_i(x)$  then  $\alpha_{ji}k_i(x) < k_j(x)$  so that  $\alpha_{ji}$  (harmonic mean of  $k_i(x)$ )  $<$  (harmonic mean of  $k_j(x)$ ) which implies (3.18) (with  $i$  and  $j$  reversed) by the same type of calculation used to derive (3.25). When (3.18) holds with  $i$  and  $j$  reversed it follows that  $\sigma_j > 0$  for  $\mu_i$  and  $\mu_j$  large by Proposition 3.8. What seems to be needed for Observation III is that  $\mu_j$  be large and  $\mu_i$  neither be too large nor too small.

#### 4 Spatial variation in the effectiveness of a predator's response to prey

In this section, we consider a class of predator-prey models of the form

$$\begin{aligned} \frac{\partial u_1}{\partial t} &= \mu_1 \Delta u_1 + u_1(a - bu_1 - c(x, u_2)) && \text{in } \Omega \times (0, \infty) \\ \frac{\partial u_2}{\partial t} &= \Delta u_2 + u_2(-d + e(x)f(u_1)) && \\ \frac{\partial u_1}{\partial \eta} &= 0 && \text{on } \partial\Omega \times (0, \infty) \\ Bu_2 &= 0 && \text{on } \partial\Omega \times (0, \infty) \end{aligned} \quad (4.1)$$

Such models are of the form (2.1), with  $f_1(x, u_1, u_2) = a - bu_1 - c(x, u_2)$  and  $f_2(x, u_1, u_2) = -d + e(x)f(u_1)$ . Our primary interest here is in examining how spatial variation in the effectiveness of a predator's functional response to prey affects the model's predictions on the long term survivability of the predator. To this end, we assume that the predator's functional response to the prey is given by  $e(x)f(u_1)$ , where  $f(u_1) \geq 0$  is nondecreasing for all  $u_1 \geq 0$  with  $f(u_1) = 0$  only when  $u_1 = 0$  and  $e(x) \geq 0$  on  $\bar{\Omega}$  with  $e(x) > \delta > 0$  on a subset of  $\Omega$  of positive Lebesgue measure. The permanence results in [11] as described in Sect. 2 strictly speaking require  $e$  and  $f$  to be twice continuously differentiable functions, which is reasonable for  $f$  but potentially somewhat limiting for  $e$ . For instance, the situation  $e(x) = e_1$ , on  $\Omega_1$ , and  $e(x) = e_2$  on

$\Omega - \Omega_1$ , where  $e_1 \neq e_2$  and  $\Omega_1$  is a subset of  $\Omega$ , which reflects sharp changes in the prey's accessibility to the predator, is not covered if  $e$  needs to be twice continuously differentiable. However, we may relax the assumption on  $e$  substantially (say to  $e$  being bounded and measurable) and maintain the validity of the results of Sect. 2. Since this issue is essentially only mathematical, we shall not pursue it in this article. Instead, we refer the interested reader to [4] and [9], where similar issues are addressed. The term  $c(x, u_2)$ , reflecting the effects of predation on the local per capita growth law for the prey, is nonnegative, with  $c(x, u_2) > 0$  unless  $e(x) = 0$  or  $u_2 = 0$ . The remaining coefficients  $\mu_1, a, b$  and  $d$ , we take to be positive constants, so that we may focus upon the effect of spatial variation in the predator's functional response to the prey on the longterm survival of the predator.

Since  $a$  and  $d$  are both positive, it is easy to observe that the conditions for Step 1 and Step 2(b) are met for any  $\mu_1 > 0$  and that  $\bar{u}_1(x) \equiv a/b$  and  $\bar{u}_2(x) \equiv 0$ . In this case, (2.4) becomes

$$\begin{aligned} \mu_1 \Delta w_1 + aw_1 &= \sigma w_1 && \text{in } \Omega \\ \frac{\partial w_1}{\partial \nu} &= 0 && \text{on } \partial\Omega, \end{aligned}$$

so that  $w_1$  is a positive constant on  $\Omega$  and  $\sigma = a > 0$ . Consequently, (4.1) is permanent provided that the value of  $\sigma$  so that

$$\begin{aligned} \Delta w_2 + \left(-d + e(x)f\left(\frac{a}{b}\right)\right)w_2 &= \sigma w_2 && \text{in } \Omega \\ Bw_2 &= 0 && \text{on } \partial\Omega \end{aligned} \quad (4.2)$$

admits a solution  $w_2 > 0$  in  $\Omega$ , is positive.

If  $-d + e(x)f(a/b) \leq 0$  on  $\Omega$ , the maximum principle implies that the relevant value of  $\sigma$  in (4.2) is negative. Consequently, we require that  $-d + e(x)f(a/b)$  be positive on a subset of  $\Omega$  of positive measure. It can be deduced from Sect. 2 that when  $B = \partial/\partial\nu$  (i.e.  $B$  represents a barrier) and  $\int_{\Omega} (-d + e(x)f(a/b)) dx \geq 0$ , there is  $y > 0$  on  $\bar{\Omega}$  so that

$$\begin{aligned} \Delta y + \left(-d + e(x)f\left(\frac{a}{b}\right)\right)y &= y^2 && \text{in } \Omega \\ \frac{\partial y}{\partial \eta} &= 0 && \text{on } \partial\Omega. \end{aligned} \quad (4.3)$$

If we multiply (4.2) by  $y$  and (4.3) by  $w_2$ , integrate both equations and employ the divergence theorem to integrate by parts, we obtain that

$$\int_{\Omega} w_2 y^2 dx = \sigma \int_{\Omega} w_2 y dx$$

which implies that  $\sigma > 0$  if  $w_2 > 0$ . We conclude that if  $B$  represents a barrier and the average value of  $e$  (i.e.  $\int_{\Omega} e(x) dx / |\Omega|$ ) is larger than  $d/f(a/b)$ , spatial

variation in  $e$  plays no role in the longterm viability of the predator. In all the other circumstances we consider,  $\sigma > 0$  in (4.2) is equivalent to

$$\lambda_1\left(-d + e(x)f\left(\frac{a}{b}\right)\right) < 1 \quad (4.4)$$

where  $\lambda_1(-d + e(x)f(a/b)) > 0$  is as in (2.7) with  $f_1(x, 0, 0)$  replaced by  $-d + e(x)f(a/b)$ . (See [10], for example.) Hence, in all other circumstances we consider, spatial variation in  $e$  can be expected to influence the longterm viability of the predator in (4.1).

Let us now consider a particular example. Take  $\Omega = (0, 1)$ ,  $Bu_2 = u_2$ , and  $f(u_1) = u_1/1 + u_1$  (a Holling Type 2 predator functional response to the prey). Let  $\alpha \in [0, 1/2]$ ,  $\Omega_\alpha = (\alpha, 1 - \alpha)$ , and define

$$e_\alpha(x) = \begin{cases} m_1 & \text{on } \Omega_\alpha \\ m_2 & \text{on } \Omega \setminus \Omega_\alpha \end{cases}$$

where  $m_1 > m_2 > 0$ . Then

$$-d + e_\alpha(x)f\left(\frac{a}{b}\right) = \begin{cases} \frac{(-d + m_1)a - db}{a + b} & \text{on } \Omega_\alpha \\ \frac{(-d + m_2)a - db}{a + b} & \text{on } \Omega \setminus \Omega_\alpha \end{cases}$$

We now have in this example that (4.1) is permanent for a value of  $\alpha \in [0, 1/2]$  precisely when  $\lambda_1(m_\alpha) < 1$ , where  $m_\alpha = -d + e_\alpha(x)f(a/b)$ . Let us suppose that

$$-d + m_1\left(\frac{a}{a+b}\right) > \pi^2 > -d + m_2\left(\frac{a}{a+b}\right) > 0.$$

When  $\alpha = 0$ , the equation for  $\lambda_1(m_\alpha)$  reduces to

$$-w'' = \lambda\left(\frac{(-d + m_1)a - db}{a + b}\right)w \quad \text{on } (0, 1)$$

$$w = 0 \quad \text{at 0 and at 1.}$$

Hence

$$\lambda_1(m_0)\left(\frac{(-d + m_1)a - db}{a + b}\right) = \pi^2,$$

which implies that  $\lambda_1(m_0) < 1$  and consequently (4.1) is permanent when  $\alpha = 0$ . However, when  $\alpha = 1/2$ , an analogous argument shows that  $\lambda_1(m_{1/2}) > 1$  and that (4.1) fails to be permanent when  $\alpha = 1/2$ . Moreover,  $m_\alpha$  is monotonically decreasing in  $\alpha$  and thus  $\lambda_1(m_\alpha)$  is monotonically increasing in  $\alpha$ . (See [4, Sect. 3], for example.) We may conclude that there is  $\alpha^* \in (0, 1/2)$  so that (4.1) is permanent (and hence the predator is theoretically expected to survive longterm) for  $\alpha < \alpha^*$ , while permanence fails in (4.1) for  $\alpha \geq \alpha^*$ .

#### 4.1 Biological interpretation

The example shows that if we think of the region upon which the predator has better access to the prey as being a single subinterval (patch) centered around the midpoint of the interval, then there is the critical length  $1 - 2\alpha^*$  for this subinterval so that permanence fails if the length of the better access patch is no more than  $1 - 2\alpha^*$ . At the corresponding  $\alpha$  value  $\alpha^*$ ,  $\lambda_1(m_{\alpha^*}) = 1$ . Our motivation for such a "mathematical experiment" comes from [6]. Proceeding along the lines of Sect. 1 of [6], we can show for any  $\alpha \in [\alpha^*, 1/2)$ , if we replace  $e_\alpha$  with

$$\tilde{e}_{\alpha, \varepsilon}(x) = \begin{cases} m_1 & \text{on } (\alpha + \varepsilon, 1 - \alpha + \varepsilon) \\ m_2 & \text{on } [0, \alpha + \varepsilon] \cup [1 - \alpha + \varepsilon, 1] \end{cases}$$

where  $\varepsilon \in [-\alpha, 0) \cup (0, \alpha]$ , then  $\lambda_1(-\alpha + \tilde{e}_{\alpha, \varepsilon}(x)f(a/b)) > 1$  and (4.1) is not permanent. We may conclude that if there is a single patch of territory where the predator has better access to the prey, it must be longer than  $1 - 2\alpha^*$  for there to be a chance for (4.1) to be permanent. If there is a single patch of territory where the predator has better access to the prey and this patch is only slightly larger than  $1 - 2\alpha^*$ , its location in the interval becomes crucial. To see that such is the case, let us consider  $\tilde{e}_{\alpha^*, \alpha^*/2}$ , which is given by

$$\tilde{e}_{\alpha^*, \alpha^*/2}(x) = \begin{cases} m_1 & \text{on } \left(\frac{3\alpha^*}{2}, 1 - \frac{\alpha^*}{2}\right) \\ m_2 & \text{on } \left[0, \frac{3\alpha^*}{2}\right] \cup \left[1 - \frac{\alpha^*}{2}, 1\right]. \end{cases}$$

For  $n$  sufficiently large,

$$\frac{3\alpha^*}{2} - \frac{1}{n} > 0 \quad \text{and} \quad 1 - \frac{\alpha^*}{2} + \frac{1}{n} < 1.$$

For such  $n$ , define

$$\bar{e}_n(x) = \begin{cases} m_1 & \text{on } \left(\frac{3\alpha^*}{2} - \frac{1}{n}, 1 - \frac{\alpha^*}{2} + \frac{1}{n}\right) \\ m_2 & \text{on } \left[0, \frac{3\alpha^*}{2} - \frac{1}{n}\right] \cup \left[1 - \frac{\alpha^*}{2} + \frac{1}{n}, 1\right]. \end{cases}$$

Notice that if  $\bar{e}_n$  is taken as  $e$  in (4.1), then the length of the subinterval of better access to the prey is now  $1 - 2\alpha^* + 2/n$ . If we were to center this subinterval about  $x = 1/2$ , the corresponding  $e$  is  $e_\alpha$  with  $\alpha = \alpha^* - 1/n$ , so that (4.1) would be permanent. On the other hand  $-d + \bar{e}_n(x)f(a/b)$  converges to  $-d + e_{\alpha^*, \alpha^*/2}(x)f(a/b)$  in  $L^p[0, 1]$  for any  $p \in [1, \infty)$ . Consequently,  $\lambda_1(-d + \bar{e}_n(x)f(a/b))$  converges to  $\lambda_1(-d + e_{\alpha^*, \alpha^*/2}(x)f(a/b)) > 1$  as  $n \rightarrow \infty$ .

(Again we refer the interested reader to [4, Sect. 3].) We may conclude that for large enough  $n$ ,  $\lambda_1(-d + \bar{e}_n(x)f(a/b)) > 1$  while  $\lambda_1(-d + e_{x^* - 1/n}(x)f(a/b)) < 1$ , so that shifting the location of the subinterval of better access to the prey results in a loss of permanence. Thus spatial heterogeneity in the effectiveness of a predator's functional response to prey can have a profound impact upon the predictions of the model.

Results similar to those just described hold for (4.1) in general. In that which follows, assume  $\Omega \subseteq \mathbb{R}^n$  is a bounded domain with sufficiently smooth boundary, and that  $e$  is a nonnegative, bounded and measurable function on  $\Omega$  so that  $\{x \in \Omega: -d + e(x)f(a/b) > 0\}$  has positive Lebesgue measure. If  $B = \partial/\partial\eta$ , assume additionally that  $\int_{\Omega} (-d + e(x)f(a/b))dx < 0$ .

Let  $\bar{e} = \text{ess sup}_{\Omega} e(x)$  and  $\underline{e} = \text{ess inf}_{\Omega} e(x)$ . We have the following result.

**Theorem 4.1.** *Suppose there is a subdomain  $\Omega_0$  of  $\Omega$  and  $e^* \in (\underline{e}, \bar{e}]$  so that  $e(x) \geq e^*$  a.e. on  $\Omega_0$  and  $\lambda_1(\Omega_0) < -d + e^*f(a/b)$ , where  $\lambda_1(\Omega_0)$  denotes the unique positive value so that*

$$\begin{aligned} -\Delta z &= \lambda z & \text{in } \Omega_0 \\ z &= 0 & \text{on } \partial\Omega_0 \end{aligned} \quad (4.5)$$

*admits a positive solution. Then  $\lambda_1(-d + e(x)f(a/b)) < 1$  and (4.1) is permanent.*

*Proof.* See Appendix.

*Interpretation.* Biologically, Theorem 4.1 says that if there is a sufficiently large amount of contiguous habitat sufficiently favorable to the predator, then no matter how favorable or not the remainder of the habitat is to predation, (4.1) will be permanent and long term survival of the predator can be expected. To see that such is the case, observe from (4.5) that for a fixed set  $\Omega_0$  and any  $t > 0$ ,  $\lambda_1(t\Omega_0) = 1/t^2\lambda_1(\Omega_0)$ , where  $t\Omega_0 = \{t\bar{x}: \bar{x} \in \Omega_0\}$  is an expansion (contraction) of  $\Omega_0$  for  $t > 1$  ( $t < 1$ ). Moreover, the location of this contiguous patch within  $\Omega$  does not matter.

**Theorem 4.2.** *Suppose that  $Bu_2 = u_2$ . Let  $C$  be a ball about the origin in  $\mathbb{R}^n$  with  $|C| = |\Omega|$ . Suppose  $C_0 \subseteq C$  is a concentric ball and that for some  $e^* \in [\underline{e}, \bar{e}]$  and*

$$m_* = \begin{cases} -d + \bar{e}f\left(\frac{a}{b}\right) & \text{on } C_0 \\ -d + e^*f\left(\frac{a}{b}\right) & \text{on } C \setminus C_0, \end{cases}$$

*$\lambda_1(m_*) \geq 1$ , where  $\lambda_1(m_*)$  denotes the unique positive value so that*

$$\begin{aligned} -\Delta z &= \lambda m_* z & \text{in } C \\ z &= 0 & \text{on } \partial C \end{aligned}$$

*admits a positive solution. Then if there is a subdomain  $\Omega_1$  of  $\Omega$  with  $|\Omega_1| = |C \setminus C_0|$  so that  $e(x) \leq e_*$  a.e. on  $\Omega_1$ ,  $\lambda_1(-d + e(x)f(a/b)) \geq 1$  and (4.1) fails to be permanent.*

*Proof.* See Appendix.

*Interpretation.* Theorem 4.2 implies that for a region with a lethal exterior, if the predator's efficiency is bounded above by  $\bar{e}$  then there is a critical number  $e^*$  and domain size  $\omega$  (depending on  $\bar{e}$ ) so that if the region  $\Omega_1$  where the predator's efficiency  $e(x)$  is no larger than  $e^*$  has size  $|\Omega_1| > \omega$  then (4.1) will not be permanent no matter how  $\Omega_1$  is arranged within  $\Omega$ . The loss of permanence will in fact imply ultimate extinction for the predator so long as the efficiency  $e(x)$  is less than the function

$$\bar{e} = \begin{cases} e_* & \text{on } \Omega_1 \\ \bar{e} & \text{on } \Omega \setminus \Omega_1. \end{cases}$$

on a set of positive measure, for then, as in [4],  $\lambda_1(-d + e(x)f(a/b)) > 1$ . That such is the case follows since the prey density  $u_1$  is a subsolution of the diffusive logistic equation

$$\frac{\partial u}{\partial t} = \mu_1 \Delta u + u(a - bu) \quad \text{in } \Omega \times (0, \infty)$$

$$\frac{\partial u}{\partial \nu} = 0 \quad \text{on } \partial\Omega \times (0, \infty),$$

so that for  $\varepsilon > 0$ , there is a  $t(\varepsilon)$  so that  $u_1 \leq (a/b) + \varepsilon$  for  $t \geq t(\varepsilon)$ . Since  $f(u_1)$  is nondecreasing, for  $t \geq t(\varepsilon)$ ,  $u_2$  is a subsolution for the linear problem

$$\frac{\partial u}{\partial t} = \Delta u + \left( -d + e(x)f\left(\left(\frac{a}{b}\right) + \varepsilon\right) \right) u \quad \text{in } \Omega \times (0, \infty)$$

$$u = 0 \quad \text{on } \partial\Omega \times (0, \infty).$$

Now if  $\lambda_1(-d + e(x)f(a/b)) > 1$ , then for  $\varepsilon > 0$  sufficiently small,  $\lambda_1(-d + e(x)f((a/b) + \varepsilon)) > 1$ , so all solutions of the linear problem must approach 0 as  $t \rightarrow \infty$ . Consequently  $u_2$  must approach zero also. Our approach so far allows us to treat any suitable predator functional response to the prey  $f(u_1)$ . In general, predator functional responses are classified as saturated or unsaturated, being saturated when  $\lim_{u_1 \rightarrow \infty} f(u_1)$  is finite. Suppose now that  $f(u_1)$  is saturated and bounded above by  $M$  and that the boundary of  $\Omega$  is lethal to the predator in (4.1). Then if  $-d + \bar{e}M \leq \lambda_1(\Omega)$ , where  $\lambda_1(\Omega)$  is as in (4.5), we cannot expect permanence regardless of the carrying capacity  $a/b$  of the prey, since if  $\phi$  is an eigenfunction corresponding

to  $\lambda_1(-d + e(x)f(a/b))$ ,

$$\begin{aligned} \lambda_1\left(-d + e(x)f\left(\frac{a}{b}\right)\right) &= \frac{\int_{\Omega} |\nabla\phi|^2}{\int_{\Omega} \left(-d + e(x)f\left(\frac{a}{b}\right)\right) \phi^2} \\ &\geq \frac{\int_{\Omega} |\nabla\phi|^2}{\int_{\Omega} (-d + \bar{e}M) \phi^2} = \frac{1}{-d + \bar{e}M} \frac{\int_{\Omega} |\nabla\phi|^2}{\int_{\Omega} \phi^2} \\ &\geq \frac{\lambda_1(\Omega)}{-d + \bar{e}M} \geq 1. \end{aligned}$$

This shows that if  $e(x)f(u_1) \leq \bar{e}M$  on  $\Omega$ , long term survival of the predator can not be expected if  $|\Omega|$  becomes too small. Suppose, on the other hand, that  $\lim_{u_1 \rightarrow \infty} f(u_1) = +\infty$ . Let  $\Omega_0 \subset \Omega$  be a subdomain of  $\Omega$  of arbitrary size (possibly very small) so that  $e(x) > \alpha$  a.e. on  $\Omega_0$ , where  $\alpha$  is an arbitrary positive constant (again possibly very small). Then if  $a/b$  is sufficiently large,  $\lambda_1(-d + e(x)f(a/b)) < 1$  and (4.1) is permanent. To see that such is the case, let  $\phi_0$  denote a positive eigenfunction corresponding to  $\lambda_1(\Omega_0)$ , where  $\lambda_1(\Omega_0)$  is as in (4.5). Let

$$\tilde{\phi}_0 = \begin{cases} \phi_0 & \text{on } \Omega_0 \\ 0 & \text{on } \Omega \setminus \Omega_0. \end{cases}$$

Choose  $a/b$  large enough so that  $-d + \alpha f(a/b) > \lambda_1(\Omega_0)$ . Then

$$\begin{aligned} \lambda_1(-d + e(x)f(a/b)) &\leq \frac{\int_{\Omega} |\nabla\tilde{\phi}_0|^2}{\int_{\Omega} \left(-d + e(x)f\left(\frac{a}{b}\right)\right) \tilde{\phi}_0^2} \\ &= \frac{\int_{\Omega_0} |\nabla\phi_0|^2}{\int_{\Omega_0} \left(-d + e(x)f\left(\frac{a}{b}\right)\right) \phi_0^2} \\ &\leq \frac{\int_{\Omega_0} |\nabla\phi_0|^2}{\int_{\Omega_0} \left(-d + \alpha f\left(\frac{a}{b}\right)\right) \phi_0^2} \\ &= \frac{\lambda_1(\Omega_0)}{\left(-d + \alpha f\left(\frac{a}{b}\right)\right)} < 1. \end{aligned}$$

To summarize, the results of this section show that if the predator is sufficiently efficient on a large enough contiguous section of the habitat, (4.1) is permanent and the predator can be expected to persist regardless of the spatial arrangement of the contiguous section. Likewise, the results show if the predator is sufficiently inefficient on a large enough contiguous section of the habitat, (4.1) fails to be permanent, whatever the spatial arrangement of the

contiguous section. However, the results also indicate for the range of efficiencies in between these extremes, the spatial arrangement of the regions of predator efficiency becomes crucial to a determination of permanence in (4.1).

## 5 Conclusions

In this section we shall describe some of the conclusions that can be drawn from the mathematical analysis in this article. The description will be as nonmathematical as possible, but some of the conclusions are about quantitative issues (e.g. how parameters should be averaged over heterogeneous environments) so we cannot avoid mathematical terminology entirely.

### 5.1 General conclusions

The broadest conclusion that we can draw is that in reaction-diffusion models for two interacting species the idea that "invasibility implies coexistence" can be formulated in a way that permits rigorous mathematical verification. Furthermore, the appropriate definition of invasibility has built into it a mathematical technique for synthesizing the effects of habitat size and geometry, the behavior of populations at the boundary of the habitat, and vital parameters such as population growth rates, dispersal rates, and carrying capacities. That technique can be applied even in cases where spatial heterogeneity causes vital parameters to vary with location. (It turns out that the same mathematical approach can be used to address similar issues in more general or different sorts of models including reaction-diffusion models with time periodicity and difference or differential/difference equation models where time, space, or both are assumed to be discrete. Some of these sorts of models are discussed in [21, 22].)

The formulation of coexistence used in our analysis is the existence of an attracting set of population densities wherein the density of each population is bounded above and below by some fixed (but perhaps spatially varying) density. By an attracting set we mean a set which the densities corresponding to any positive initial data must eventually approach or enter. Such a set could be a single stable equilibrium, a stable periodic steady state, or something more complicated. In the case of a system describing two competitors the attracting set (if it exists) will be bounded by two equilibria. At one equilibrium the first competitor will have an equilibrium density which is the maximum positive equilibrium density in the presence of the second competitor; at the same equilibrium the second competitor will have its minimum positive density. At the other equilibrium bounding the attracting set the roles of the two competitors will be reversed. However, these equilibria need not be the same and we are not generally able to rule out the possible existence of other equilibria or more complicated steady states. In the case of predator-prey systems or systems with three or more competitors it is not generally



possible to bound the attracting set in terms of equilibria, although it is sometimes possible to make estimates of the lower bounds on densities in the attracting set. In some cases the existence of a unique globally attracting equilibrium can be demonstrated, but that usually requires additional and stringent hypotheses. These points are addressed in [7–12, 15, 16, 21, 22, 24, 27].

The formulation we use for invasibility is the instability of those equilibria where at most one of the interacting species is present. (If we were to consider systems with  $N$  species, we would need to examine the stability of equilibria, steady states, or other attracting sets for subsystems with  $N - 1$  or fewer species present.) By instability of an equilibrium we mean the property that the linearized model predicts the growth of the populations of at least some of the species not represented at that equilibrium if those new species are introduced at low densities while the remaining species are at the equilibrium. This captures the idea of invasibility because it means that a species can increase in numbers if introduced into a system where the other species are already established. For reaction–diffusion models, instability can be characterized by the sign of the principal eigenvalue of a partial differential operator of elliptic type. Such eigenvalues will generally depend on the size and shape of the spatial region containing the environment, the behavior of the populations at the boundary of the environment, and the various parameters describing growth, dispersal, carrying capacity, and other vital rates for the populations in the model. The study of eigenvalues for such purposes was initiated by Kierstead and Slobodkin [23] and Skellam [35] in their work on the models now commonly designated by the acronym KISS of their names. The estimation and interpretation of eigenvalues is a major part of the mathematical analysis of this article. Other results on this topic and applications of eigenvalue estimates to various questions involving spatial effects are given in [3–7, 9, 10, 14–16, 21, 33]. The same sort of analysis could also be applied in models based on ordinary differential equations or discrete models. In those cases the eigenvalues would be eigenvalues of matrices. Matrix eigenvalues have been widely studied in the context of Leslie matrices where the parameters describe the life history of the organism. Our approach is similar, except that our parameters typically describe spatial and density dependent effects.

### 5.2 Conclusions on predator–prey systems

The main question we address for predator–prey systems is that of determining when the arrangement and location (as opposed to the size and quality) of prey refuges and regions favorable to the predator determines the invasibility of the system by the predator when the prey is already present. The qualitative conclusion is not surprising. If the region favorable to the predator contains a sufficiently large and sufficiently favorable subregion then the predator can invade no matter how the favorable regions and prey refuges are arranged in the remainder of the environment. On the other hand, if the favorable region is

too small and not sufficiently favorable relative to the effectiveness of the refuges, the predator cannot invade the system no matter how the favorable regions and prey refuges are arranged. For cases where the regions favoring predation are of intermediate size and favorability, their arrangement relative to the prey refuges will determine whether or not the predator can invade the system. What is new in our analysis is that we show how the ideas of “sufficiently large and favorable” and “too small and not sufficiently favorable” can be quantified. Roughly, we assume that the prey is at its carrying capacity, substitute that value into the predator equation, and analyze the behavior of the principal eigenvalue for the resulting linear (or more generally linearized) equation. The local dynamics for the predator population in our models are described by the starvation rate of the predators in the absence of prey, the mass action law or functional response describing the effects of prey density on the rate of predation, and a spatially varying factor multiplying the functional response which describes the efficiency of the predator in converting the prey it captures into new predators. This efficiency term reflects the amount of effort required by the predator to capture prey. The local dynamics are combined with a diffusion term describing the dispersal rate of the predator. To evaluate the model it would be necessary to measure four different parameters: the starvation rate of the predator; the rate at which prey are consumed by a predator when the prey population is at its carrying capacity and conditions are optimal for predation; the percentage of the optimal prey consumption rate that it is feasible for a predator to attain at each location in the environment; and the dispersal rate of the predator in terms of average distance travelled in unit time. Even if those quantities are known the mathematical or numerical analysis of the model in a given case would still require substantial effort and expertise, but such an analysis is well within the range of standard methods. Thus in principle our models could be used to treat real situations. A limitation of the work in this paper is that we consider a fairly simple class of models. In some cases additional factors might come into play or the character of density dependent effects might be more complicated. The analytic approaches we have taken could probably be applied to some more complex models but not to others.

The focus of our analysis of the effects of prey refuges and regions favoring predation is somewhat different than in other studies. We do not consider how spatial variation affects the size or stability of equilibria where neither population density is low. This is in contrast with the analysis in [30,34]. Since we address a different set of questions, our results neither support nor refute the conclusions of other studies about the effects of prey refuges on the stability of positive equilibria in predator–prey systems.

### 5.3 Conclusions about competition models

The competition models we consider are all diffusive Lotka–Volterra models, usually with spatially varying coefficients. All of our conclusions can be

interpreted as describing how the spatially varying terms should be combined and averaged over the spatial extent of the habitat to yield global predictions about invasibility and hence persistence. We explore the specific implications of the averaging procedures in a number of cases. In many of the cases we treat explicitly we assume that the dispersal rate of at least one of the competitors is either very large or very small. Some of the special cases we consider were studied via numerical simulations in [32]. Our results provide rigorous mathematical verifications and explanations of some of the observations of [32].

The quantities that would require measurement in any specific application of our results are the local values of the coefficients in a Lotka–Volterra competition model and the dispersal rates (in terms of average distance travelled per unit time) of the competitors. The Lotka–Volterra coefficients represent or depend on intrinsic population growth rates, carrying capacities, and strength of competition. The parameters describing strength of competition could be viewed as describing the extent of niche overlap for the competitors. Derivations of Lotka–Volterra coefficients in terms of resource consumption are given in [28,36]. Interference competition is treated in [13].

The general conclusion of our results is that spatial heterogeneity and diffusive dispersal can induce mutual invasibility and hence coexistence in situations where the local prediction of the model at many (or all) locations is that invasion by one or both species would fail. The reverse is also possible; that is, a situation where invasibility would be predicted locally may become noninvasible because of the interaction of dispersal and spatial heterogeneity. Such conclusions were drawn in [32] but only for a relatively restricted class of models, and in some cases their conclusions are based only on numerical experiments. Our results are quite general, but to evaluate them we need to know the equilibrium distribution for each competitor in the absence of the other. That equilibrium is always determined by a diffusive logistic equation but can be computed easily and directly only in the asymptotic limit as the diffusion rate becomes very small, or in the case of closed environments very small or very large.

In the case of a small diffusion rate the equilibrium for a spatially varying diffusive logistic equation approximately tracks the carrying capacity where the intrinsic local growth rate is positive and is approximately zero where the local intrinsic growth rate is negative. If the diffusion rates of both competitors are small the spatial variation may cause them to segregate. That can allow coexistence even if competition is uniformly severe because the spatial segregation provides each species with the what amounts to a refuge from its competitor. If the intrinsic local growth rates and carrying capacities are constant then the arithmetic means of the coefficients describing the strength of competition play a crucial role in determining invasibility and hence coexistence. Thus, competition may be very severe in some regions and still permit coexistence if the total area of those regions is small. Other more complicated interactions of spatially varying factors could also mediate coexistence.

If the boundary of the environment acts as a barrier and the intrinsic local growth rate is a positive constant, the equilibrium density for a diffusive logistic equation is approximately equal to the harmonic mean of the carrying capacity when the diffusion rate is large. In determining invasibility each competitor interacts with the logistic equilibrium of the other. It follows that if the first competitor has a large diffusion rate then it is the average carrying capacity for the first competitor in the sense of the harmonic mean rather than the local carrying capacity that influences invasibility by the second competitor. If the second competitor has a sufficiently low diffusion rate and there are regions where the local conditions favor the second competitor relative to the average carrying capacity of the first competitor, then the second competitor may be able to invade by increasing its density in those regions. (The low diffusion rate for the second competitor is needed to prevent dispersal out of the favorable regions.) Paradoxically, in the regions favoring the second competitor it may be that the carrying capacity for the first competitor is also high, even high enough that the local population dynamics would predict that the second competitor could not invade. However, it is the harmonic mean of the carrying capacity of the first competitor rather than the local value which is relevant in this scenario, so the system may be invasible by the second competitor in spite of an apparent local advantage for the first competitor at every specific location.

In the case where both competitors have large diffusion rates and the intensity of competition is spatially homogeneous, the condition for invasibility by the second competitor involves the ratio of the harmonic means of the carrying capacities of the competitors.

We can give explicit conditions for invasibility in cases where diffusion rates are either quite large or quite small. It is likely that the explicit conditions have many possible interpretations in various scenarios since they depend on the interactions of several parameters. We hope that those readers whose primary interest is in ecology will examine and perhaps suggest interpretations for some of those conditions. The derivations of the conditions are somewhat technical but are not necessary for their interpretation.

## Appendix

**Proof of Lemma 3.3.** Suppose the  $p$  is large enough that  $W^{2,p}(\Omega)$  embeds in  $C^{1+\alpha}(\bar{\Omega})$ . Let  $X = \{u \in W^{2,p}(\Omega) : Bu = 0 \text{ on } \Omega\}$ . Define  $F: L^p(\Omega) \times X \rightarrow L^p(\Omega)$  by  $F(q, u) = \mu \Delta u + (q - bu)u$ . Note that  $F(m, \bar{u}) = 0$  and that  $F$  is well defined and continuous since  $X \subset C^{1+\alpha}(\bar{\Omega})$ . Furthermore, we can compute the difference quotient

$$\begin{aligned} Q(\varepsilon) &= \frac{\{F(q + \varepsilon r, u + \varepsilon w) - F(q, u) - \varepsilon[\mu \Delta w + (q - 2bu)w + ru]\}}{\varepsilon} \\ &= \varepsilon(r - bw)w, \end{aligned}$$

so that  $Q(\varepsilon) \rightarrow 0$  in  $L^p(\Omega)$  as  $\varepsilon \rightarrow 0$ , and  $F$  is thus differentiable with

$$DF(q, u)[r, w] = \mu \Delta w + (q - 2bu)w + ru.$$

Also,

$$\|DF(q, u)[r, w]\|_p \leq \mu \|w\|_{2,p} + C \|q - 2u\|_p \|w\|_{2,p} + C \|r\|_p \|u\|_{2,p},$$

so that  $DF(q, u): L^p(\Omega) \times X \rightarrow L^p(\Omega)$  is a bounded operator. (We have used the fact that  $p$  is large enough that for some constant  $C_1$ ,  $\sup_{\Omega} |v| \leq \|v\|_{C^{1+\alpha}(\bar{\Omega})} \leq C_1 \|v\|_{2,p}$ .) Similarly,

$$\begin{aligned} & \|(DF(q_1, u_1) - DF(q_2, u_2))[r, w]\|_p \\ &= \|(q_1 - q_2 - 2bu_1 + 2bu_2)w + (u_1 - u_2)r\|_p \\ &\leq C_1(\|q_1 - q_2\|_p + 2\|b(u_1 - u_2)\|_p \|w\|_{2,p} + C_1 \|u_1 - u_2\|_{2,p} \|r\|_p) \\ &\leq C_1(\|q_1 - q_2\|_p + (1 + 2\sup b)\|u_1 - u_2\|_{2,p})(\|r\|_p + \|w\|_p) \end{aligned}$$

so that in the operator norm on  $\mathcal{L}((L^p \times X, L^p))$  we have  $\|DF(q_2, u_2) - DF(q_1, u_1)\| \leq C_1((1 + 2\sup b)(\|q_1 - q_2\|_p + \|u_1 - u_2\|_{2,p}))$  and thus  $DF(q, u)$  is continuous. It follows that we may apply the implicit function theorem to the relation  $F(q, u) = 0$  at the point  $(m, \bar{u})$  provided that the derivative with respect to  $u$ ,  $D_u F(m, \bar{u})$ , is invertible. Now,  $DF_u(m, \bar{u})[w] = \mu \Delta w + (m - 2b\bar{u})w$ . Since we have  $\mu \Delta \bar{u} + (m - b\bar{u})\bar{u} = 0$  with  $\bar{u} > 0$ , it follows that the principal eigenvalue of

$$\mu \Delta \psi + (m - b\bar{u})\psi = \sigma \psi \quad \text{in } \Omega,$$

$$Bu = 0 \quad \text{on } \partial\Omega$$

is equal to zero. Standard eigenvalue comparison theory implies that the principal eigenvalue of

$$\mu \Delta \psi + (m - 2b\bar{u})\psi = \sigma \psi \quad \text{in } \Omega,$$

$$Bu = 0 \quad \text{on } \partial\Omega$$

is negative, and then standard elliptic theory implies that  $[\mu \Delta + (m + 2b\bar{u})]^{-1}: L^p(\Omega) \rightarrow X$  exists as a bounded operator. This uses the assumption that  $m \in C^\alpha(\bar{\Omega})$ . It follows from the implicit function theorem that in some neighborhood  $f(m, \bar{u})$  in  $L^p \times X$  the relation  $F(\bar{m}, \bar{u}) = 0$  defines  $\bar{u} = \bar{u}(\bar{m}) \in X$  as  $\bar{m} \rightarrow m$  in  $L^p(\Omega)$ .

**Proof of Proposition 3.4.** The proof is based on Lemma 3.2 and the observation that if  $m(x) > 0$  on an open set then the principal eigenvalue  $\sigma_0$  of

$$\mu \Delta \psi + m(x)\psi = \sigma \psi \quad \text{in } \Omega$$

$$Bu = 0 \quad \text{on } \partial\Omega$$

satisfies

$$\sigma_0 > 0 \quad \text{if } \lambda_1(m(x)) > 0 \quad \text{and} \quad \mu < \frac{1}{\lambda_1(m)}$$

or for any  $\mu > 0$

$$\mu > 0 \quad \text{if } \int_{\Omega} m(x)dx > 0 \quad \text{and} \quad Bu = \frac{\partial u}{\partial \eta}.$$

(If

$$Bu = \frac{\partial u}{\partial \eta} \quad \text{and} \quad \int_{\Omega} m(x)dx < 0$$

then

$$\lambda_1(m) > 0; \quad \text{if } \int_{\Omega} m(x)dx = 0$$

then  $\sigma_0 = 0$ .) This point is discussed in [5, 32]. If  $Bu = \partial u / \partial \eta$ , assume for the moment that

$$\int_{\Omega} \left[ \frac{m_i - b_{ij}(m_j)_+}{b_{jj}} \right] dx \neq 0 \quad \text{for } i = 1, 2 \text{ and } j \neq i.$$

(The case where one of these integrals is zero requires a slightly different treatment and will be discussed at the end of this proof.) By (3.9) we have  $m_i(x) > 0$  on an open set for  $i = 1, 2$  so that  $\bar{u}_1$  and  $\bar{u}_2$  exist at least for  $\mu_1, \mu_2$  sufficiently small. Suppose that for

$$i = 1, 2 \quad \text{and} \quad j \neq i, \quad \lambda_1 \left( \frac{m_i - b_{ji}(m_j)_+}{b_{jj}} \right) > 0.$$

By Lemma 3.2,

$$\bar{u}_j \rightarrow \frac{(m_j)_+}{b_{jj}} \quad \text{in } L^p(\Omega)$$

for any  $p < \infty$ . However,  $\lambda_1(m(x))$  depends continuously on  $m$  relative to  $L^p(\Omega)$  for  $p$  sufficiently large. (This follows from the variational formulation of the eigenvalue problem and the fact that  $W^{1,p}$  embeds in  $L^2$  for some  $q > 2$ . See [4] and the references therein for further discussion.) Thus, there exists a  $\mu_j^*$  such that if  $\mu_j < \mu_j^*$  then

$$0 < \lambda_1(m_i - b_{ij}\bar{u}_j) < 2\lambda_1 \left( m_i - \frac{b_{ij}(m_j)_+}{b_{jj}} \right).$$

If

$$\mu_i < \frac{1}{2\lambda_1 \left( m_i - \frac{b_{ij}(m_j)_+}{b_{jj}} \right)} \quad \text{then } \sigma_i > 0.$$

Thus, if

$$\mu_i < \frac{1}{2\lambda_1 \left( m_i - \frac{b_{ij}(m_j)_+}{b_{jj}} \right)} \quad \text{and} \quad \mu_j < \mu_j^* \quad \text{then } \sigma_i > 0.$$

If

$$\mu_i < \min \left\{ \mu_i^*, \frac{1}{2\lambda_1 \left( m_i - \frac{b_{ij}(m_j)_+}{b_{jj}} \right)} \right\} \text{ for } i = 1, 2, j \neq i$$

then  $\sigma_i > 0$  for  $i = 1, 2$ .

Suppose that  $B_i u = \partial u / \partial \eta$  and that

$$\int_{\Omega} \left[ m_i - \frac{b_{ij}(m_j)_+}{b_{jj}} \right] dx > 0.$$

Since

$$\bar{u}_j \rightarrow \frac{(m_j)_+}{b_{jj}} \text{ in } L^p(\Omega) \text{ as } \mu_j \rightarrow 0,$$

there exists  $\mu_j^*$  such that if  $\mu_j < \mu_j^*$  then  $\int_{\Omega} (m_i - b_{ij}\bar{u}_j) dx > 0$ , so that for  $\mu_j < \mu_j^*$  we have  $\sigma_i > 0$ . Finally, if

$$B_i u = \frac{\partial u}{\partial \eta} \text{ and } \int_{\Omega} \left[ m_i - \frac{b_{ij}(m_j)_+}{b_{jj}} \right] dx = 0,$$

choose  $\delta > 0$  such that

$$m_i - \frac{b_{ij}(m_j)_+}{b_{jj}} - \delta > 0$$

on an open set. Note that

$$\int_{\Omega} \left( m_i - \frac{b_{ij}(m_j)_+}{b_{jj}} - \delta \right) dx = -\delta |\Omega| < 0$$

so that

$$\lambda_1 \left( m_i - \frac{b_{ij}(m_j)_+}{b_{jj}} - \delta \right) > 0.$$

As before, there exists  $\mu_j^*$  such that for  $\mu_j < \mu_j^*$  we have

$$0 < \lambda_1 (m_i - b_{ij}\bar{u}_j - \delta) < 2\lambda_1 \left( m_i - \frac{b_{ij}(m_j)_+}{b_{jj}} - \delta \right).$$

If

$$\mu_i < \frac{1}{2\lambda_1 \left( m_i - \frac{b_{ij}(m_j)_+}{b_{jj}} - \delta \right)}$$

then  $\sigma_i^* > 0$  where  $\sigma_i^*$  is the principal eigenvalue of

$$\begin{aligned} \mu_i \Delta \psi + [m_i - b_{ij}\bar{u}_j - \delta] \psi &= \sigma \psi \text{ in } \Omega \\ B_i \psi &= 0 \text{ on } \partial \Omega. \end{aligned}$$

However,  $\sigma_i^* = \sigma - \delta$  so for  $\mu_j < \mu_j^*$  and

$$\mu_i < \frac{1}{2\lambda \left( m_i - \frac{b_{ij}(m_j)_+}{b_{jj}} \right)}$$

we have  $\sigma > 0$ . The case of  $\sigma_j$  is symmetric.

*Proof of Proposition 3.5.* The proof consists of showing that the hypotheses of Proposition 3.5 imply those of Lemma 2.3. We must show that the state with  $u_i = 0$  and  $u_j = \bar{u}_j$  is unstable and that there is no equilibrium with both components positive. The instability of the state with  $u_i = 0$  and  $u_j = \bar{u}_j$  follows from (3.9) wherever  $\mu_i$  and  $\mu_j$  are sufficiently small, so we need only show the nonexistence of a positive equilibrium in (3.2).

Suppose that  $(u_1^*, u_2^*)$  is an equilibrium of (3.2) with both components positive. Clearly  $u_j^*$  is a subsolution of

$$\begin{aligned} \frac{\partial u}{\partial t} &= \mu_j \Delta u + (m_j - b_{jj}u_j)u \text{ in } \Omega \\ B_j u &= 0 \text{ on } \partial \Omega. \end{aligned} \quad (\text{A.1})$$

Since (A.1) has  $\bar{u}_j$  as its unique equilibrium and admits any sufficiently large constant as a supersolution, it follows that  $u_j^* \leq \bar{u}_j$ . Thus,  $u_i^*$  is a supersolution to

$$\begin{aligned} \frac{\partial u}{\partial t} &= \mu_i \Delta u + (m_i - b_{ij}\bar{u}_j - b_{ii}u)u \text{ in } \Omega \\ B_i u &= 0 \text{ on } \partial \Omega. \end{aligned} \quad (\text{A.2})$$

By (3.9) we have  $\sigma_i > 0$  for  $\mu_i$  and  $\mu_j$  sufficiently small where  $\sigma_i$  is the principal eigenvalue of

$$\begin{aligned} \mu_i \Delta \Psi + (m_i - b_{ij}\bar{u}_j) \Psi &= \sigma \Psi \text{ in } \Omega \\ B_i \Psi &= 0 \text{ on } \partial \Omega. \end{aligned}$$

If  $\Psi_i > 0$  is the eigenfunction with  $\sigma_i$ , then  $\gamma \Psi_i$  is a subsolution of (A.2) for  $\gamma > 0$  sufficiently small. Thus (A.2) has a unique positive equilibrium  $u_i \leq u_i^*$ . Finally,  $u_j^*$  must then be a subsolution of

$$\begin{aligned} \frac{\partial u}{\partial t} &= \mu_j \Delta u + (m_j - b_{ji}u_i - b_{jj}u)u \text{ in } \Omega \\ B_j u &= 0 \text{ on } \partial \Omega. \end{aligned} \quad (\text{A.3})$$

As  $\mu_j \rightarrow 0$  we have  $\bar{u}_j \rightarrow (m_j)_+ / b_{jj}$  in  $L^p(\Omega)$  for all  $p$  by Lemma 3.2. Thus  $u_i \rightarrow u_i^{**}$  in  $C^{1+\alpha}(\bar{\Omega})$  as  $\mu_j \rightarrow 0$  by Lemma 3.3, where  $u_i^{**}$  is the positive equilibrium of

$$\begin{aligned} \frac{\partial u}{\partial t} &= \mu_i \Delta u + \left( m_i - \frac{b_{ij}(m_j)_+}{b_{jj}} - b_{ii}u \right) u \text{ in } \Omega \\ B_i u &= 0 \text{ on } \partial \Omega. \end{aligned} \quad (\text{A.4})$$

(The existence of  $u_i^{**}$  for  $\mu_i$  small is guaranteed by Lemma 2.6 since (3.9) implies that  $m_i - (b_{ij}(m_j)_+)/b_{jj} > 0$  on a set of positive measure.) Hence for any  $\varepsilon > 0$  there is  $\bar{\mu}_j > 0$  such that  $\|\bar{u}_i - u_i^{**}\|_{C^1(\bar{\Omega})} < \varepsilon$  for  $\mu_j < \bar{\mu}_j$ . By Lemma 3.2,

$$u_i^{**} \rightarrow \frac{\left[ m_i - \frac{b_{ij}(m_j)_+}{b_{jj}} \right]_+}{b_{ii}} \quad \text{in } L^p(\Omega) \text{ as } \mu_i \rightarrow 0.$$

Since  $b_{ji}$  is bounded the principal eigenvalue  $\sigma_j^*$  of

$$\begin{aligned} \mu_j \Delta \Psi + [m_j - b_{ji} u_i^{**}] \Psi &= \sigma \Psi \quad \text{in } \Omega \\ B_j \Psi &= 0 \quad \text{on } \partial \Omega \end{aligned}$$

depends continuously on  $u_i^{**}$  relative to  $L^p(\Omega)$  for large  $p$ . (This follows from the variational formulation of the eigenvalue problem and the embedding of  $W^{1,2}$  into  $L^q$  for some  $q > 2$ .) Thus for any  $\varepsilon > 0$  there exists  $\mu_i^* > 0$  so that if  $\mu_i < \mu_i^*$  then  $\sigma_j^* < \sigma_j^{**} + \varepsilon$ , where  $\sigma_j^{**}$  is the principal eigenvalue of

$$\mu_j \Delta \Psi + \left\{ \frac{m_j - b_{ji} \left[ m_i - \frac{(m_j)_+ b_{ij}}{b_{jj}} \right]_+}{b_{ii}} \right\} \Psi = \sigma \Psi \quad \text{in } \Omega \\ B_j \Psi = 0 \quad \text{on } \partial \Omega$$

By (3.10)  $\sigma_j^{**} < 0$ . Returning to (A.3), let  $\bar{\sigma}_j$  denote the principal eigenvalue to

$$\begin{aligned} \mu_j \Delta \Psi + \{m_j - b_{ji} \bar{u}_i\} \Psi &= \sigma \Psi \quad \text{in } \Omega \\ B_j \Psi &= 0 \quad \text{on } \partial \Omega. \end{aligned}$$

We have  $\bar{u}_i \geq u_i^{**} - \varepsilon$ , so if  $\mu_j < \bar{\mu}_j$  then  $\bar{\sigma}_j \leq \sigma_j^* + \varepsilon \sup b_{ji}$  by standard eigenvalue comparison results. For  $\mu_i < \mu_i^*$  we have  $\sigma_j^* \leq \sigma_j^{**} + \varepsilon$  so  $\bar{\sigma}_j \leq \sigma_j^{**} + \varepsilon + \varepsilon \sup b_{ji}$ . It follows that for  $\varepsilon > 0$  sufficiently small,  $\bar{\sigma}_j < 0$  so by the remarks following Lemma 2.6 all positive solutions of (A.3) must approach zero as  $t \rightarrow \infty$ . Since  $u_j^*$  is a subsolution to (A.3), we must have  $u_j^* \rightarrow 0$  as  $t \rightarrow \infty$ , contradicting the assumption that  $u_j^* > 0$  in  $\Omega$ . Thus, under hypothesis (3.10) there can be no positive equilibrium for (3.2), and it now follows from (3.9) and (3.10) that all positive solutions of (3.2) must approach  $(\bar{u}, 0)$  as  $t \rightarrow \infty$  provided  $\mu_1$  and  $\mu_2$  are sufficiently small.

*Proof of Proposition 3.6 (Sketch).* The proof that  $\sigma_j > 0$  for  $\mu_j$  small and  $\mu_i$  large if (3.15) holds is essentially the same as that of Proposition 3.4, except that the fact that

$$\bar{u}_i \rightarrow \frac{\bar{m}_i}{\bar{b}_{ii}} \quad \text{as } \mu_i \rightarrow \infty$$

is used in place of the fact that

$$\bar{u}_i \rightarrow \frac{(m_i)_+}{b_{ii}} \quad \text{as } \mu_i \rightarrow 0.$$

To see that (3.14) implies  $\sigma_i > 0$  for  $\mu_i$  large and  $\mu_j$  small we simply take the limit of the integral in (3.4) as  $\mu_j \rightarrow \infty$ . (The convergence in (3.6) and (3.7) can be taken in  $L^p(\Omega)$  for any  $p < \infty$ .) Since  $\bar{u}_i \rightarrow \bar{m}_i/\bar{b}_{ii}$ , which is a constant the result is that as  $\mu_i \rightarrow \infty$  and  $\mu_j \rightarrow 0$ ,

$$\begin{aligned} \int (b_{ii} \bar{u}_i - b_{ij} \bar{u}_j) \bar{u}_i^2 dx &\rightarrow \left( \frac{\bar{m}_i}{\bar{b}_{ii}} \right)^2 \int \left[ b_{ii} \left( \frac{\bar{m}_i}{\bar{b}_{ii}} \right) - \frac{b_{ij}(m_j)_+}{b_{jj}} \right] dx \\ &= \left( \frac{\bar{m}_i}{\bar{b}_{ii}} \right)^2 \left[ \left( \frac{\bar{m}_i}{\bar{b}_{ii}} \right) \int b_{ii} dx - \int \left( \frac{b_{ij}(m_j)_+}{b_{jj}} \right) dx \right] \\ &= \left( \frac{\bar{m}_i}{\bar{b}_{ii}} \right)^2 \left[ \bar{m}_i - \int \left( \frac{b_{ij}(m_j)_+}{b_{jj}} \right) dx \right]. \end{aligned}$$

Thus, (3.14) implies that (3.4) holds for  $\mu_i$  large and  $\mu_j$  small, so  $\sigma_i > 0$ .

*Proof of Proposition 3.7 (sketch).* The idea is the same as in the proof of Proposition 3.5, with only the limiting behavior of the various equilibria changing. Suppose (3.14), and (3.16) hold; then  $\sigma_i > 0$  for  $\mu_i$  large and  $\mu_j$  small. As in the proof of Proposition 3.5, an equilibrium  $(u_1^*, u_2^*)$  satisfies  $u_j^* \leq \bar{u}_j$  and  $u_1^* \geq \underline{u}_1$  where  $\bar{u}_j$  and  $\underline{u}_1$  are the equilibria of (A.1) and (A.2) respectively, and it follows that  $u_j^*$  is a subsolution of (A.3). Since

$$\bar{u}_j \rightarrow \frac{(m_j)_+}{b_{jj}} \quad \text{as } \mu_j \rightarrow 0$$

and

$$\underline{u}_1 \rightarrow \frac{\int (m_1 - b_{1j} \bar{u}_j) dx}{\int b_{11}} = \frac{(\bar{m}_1 - \int b_{1j} \bar{u}_j) dx}{\bar{b}_{11}} \quad \text{as } \mu_i \rightarrow \infty,$$

it follows that for  $\mu_j$  small and  $\mu_i$  large the principal eigenvalue  $\bar{\sigma}_j$  of (A.5) is negative provided (3.16) holds.

Suppose (3.15) and (3.17) hold. The argument is essentially the same, except for the observation that the principal eigenvalue for

$$\begin{aligned} \mu_i \Delta \Psi + [m_i - b_{ij} \underline{u}_j] \Psi &= \sigma \Psi \quad \text{in } \Omega \\ B_i \Psi &= 0 \quad \text{on } \partial \Omega \end{aligned}$$

(with  $B_i \Psi = \partial \Psi / \partial \eta$ ) is negative for  $\mu_i > (1/\lambda_1(m_i - b_{ij} \underline{u}_j))$  provided  $\int (m_i - b_{ij} \underline{u}_j) dx < 0$ . (Here  $\underline{u}_j$  replaces  $\bar{u}_j$  in the proof of Proposition 3.5). Thus, we do not need a pointwise condition to show that there can be no equilibrium  $(u_1^*, u_2^*)$  positive for large  $\mu_i$ . In this case

$$\bar{u}_i \rightarrow \frac{\bar{m}_i}{\bar{b}_{ii}} \quad \text{and} \quad \underline{u}_j \rightarrow \frac{(m_j - b_{ji} \bar{u}_i)_+}{b_{jj}} \quad \text{as } \mu_j \rightarrow 0$$

so a condition implying  $\int (m_i - b_{ij} \underline{u}_j) dx < 0$  for  $\mu_i$  large and  $\mu_j$  small is given by (3.17).

*Proof of Proposition 3.12.* By Lemma 2.6 we have  $\sigma_j < 0$  if

$$\mu_j > \frac{1}{\lambda_1 \left( r_j \left[ 1 - \frac{\alpha_{ji} \bar{u}_i}{k_j} \right] \right)}$$

provided that

$$\int \left( 1 - \frac{\alpha_{ji} \bar{u}_i}{k_j} \right) dx < 0.$$

Recall that

$$\mu_i \Delta \bar{u}_i + r_i \left( 1 - \frac{\bar{u}_i}{k_i} \right) \bar{u}_i = 0$$

so that

$$\int_{\Omega} \left( 1 - \frac{\bar{u}_i}{k_i} \right) dx = -\frac{\mu_i}{r_i} \int_{\Omega} \frac{\Delta \bar{u}_i}{\bar{u}_i} dx.$$

However

$$\frac{\Delta \bar{u}_i}{\bar{u}_i} = \nabla \cdot \frac{\nabla \bar{u}_i}{\bar{u}_i} + \frac{|\nabla \bar{u}_i|^2}{\bar{u}_i^2}$$

so that since  $\partial \bar{u}_i / \partial \eta = 0$  on  $\partial \Omega$  we have

$$\begin{aligned} \int_{\Omega} \left( 1 - \frac{\bar{u}_i}{k_i} \right) dx &= -\frac{\mu_i}{r_i} \int_{\Omega} \left[ \left( \nabla \cdot \left( \frac{\nabla \bar{u}_i}{\bar{u}_i} \right) \right) + \frac{|\nabla \bar{u}_i|^2}{\bar{u}_i^2} \right] dx \\ &= -\frac{\mu_i}{r_i} \oint_{\partial \Omega} \left( \frac{1}{\bar{u}_i} \frac{\partial \bar{u}_i}{\partial \eta} \right) ds - \frac{\mu_i}{r_i} \int_{\Omega} \frac{|\nabla \bar{u}_i|^2}{\bar{u}_i^2} dx \\ &= -\frac{\mu_i}{r_i} \int_{\Omega} \frac{|\nabla \bar{u}_i|^2}{\bar{u}_i^2} dx < 0 \end{aligned}$$

By (3.27) we have

$$\begin{aligned} \int_{\Omega} \left( 1 - \frac{\alpha_{ji} \bar{u}_i}{k_j} \right) dx &< \int_{\Omega} \left( 1 - \frac{\gamma \bar{u}_i}{k_i} \right) dx \\ &= (1 - \gamma) |\Omega| + \gamma \int_{\Omega} \left( 1 - \frac{\bar{u}_i}{k_i} \right) dx \\ &< 0 \end{aligned}$$

for  $\gamma$  sufficiently close to 1. It follows from Lemma 2.6 that if  $\mu_j$  is sufficiently large then  $\sigma_j < 0$ .

*Proof of Theorem 4.1.* It follows from [29] and [3] that

$$\lambda_1 \left( -d + e(x) f \left( \frac{a}{b} \right) \right) \leq \frac{\int_{\Omega} |\nabla h|^2}{\int_{\Omega} \left( -d + e(x) f \left( \frac{a}{b} \right) \right) h^2}$$

for all  $h \in W_0^{1,2}(\Omega)$  ( $h \in W^{1,2}(\Omega)$  if  $B = \partial/\partial \eta$ ) so that  $\int_{\Omega} (-d + e(x) f(a/b)) h^2 > 0$ . Let  $\phi > 0$  on  $\Omega_0$  be an eigenfunction for (4.5). Define

$$\tilde{\phi}(x) = \begin{cases} \phi(x) & x \in \Omega_0 \\ 0 & x \in \bar{\Omega} \setminus \Omega_0. \end{cases}$$

Then  $\tilde{\phi} \in W_0^{1,2}(\Omega)$  and since  $-d + e(x) f(a/b) \geq -d + e^* f(a/b) > \lambda_1(\Omega_0) > 0$  on  $\Omega_0$  a.e.,  $\int_{\Omega} (-d + e(x) f(a/b)) \tilde{\phi}^2 > 0$ . Hence

$$\begin{aligned} \lambda_1 \left( -d + e(x) f \left( \frac{a}{b} \right) \right) &\leq \frac{\int_{\Omega} |\nabla \tilde{\phi}|^2}{\int_{\Omega} \left( -d + e(x) f \left( \frac{a}{b} \right) \right) \tilde{\phi}^2} \\ &= \frac{\int_{\Omega_0} |\nabla \phi|^2}{\int_{\Omega_0} \left( -d + e(x) f \left( \frac{a}{b} \right) \right) \phi^2}. \end{aligned}$$

Since  $\phi$  satisfies (4.5),

$$\int_{\Omega_0} |\nabla \phi|^2 = \int_{\Omega_0} -\phi \Delta \phi = \lambda_1(\Omega_0) \int_{\Omega_0} \phi^2,$$

so that

$$\begin{aligned} \lambda_1 \left( -d + e(x) f \left( \frac{a}{b} \right) \right) &\leq \frac{\lambda_1(\Omega_0) \int_{\Omega_0} \phi^2}{\int_{\Omega_0} \left( -d + e(x) f \left( \frac{a}{b} \right) \right) \phi^2} \\ &\leq \frac{\lambda_1(\Omega_0) \int_{\Omega_0} \phi^2}{\left( -d + e^* f \left( \frac{a}{b} \right) \right) \int_{\Omega_0} \phi^2} \\ &< 1. \end{aligned}$$

*Proof of Theorem 4.2.* Let  $\phi > 0$  satisfy

$$\begin{aligned} -\Delta \phi &= \lambda_1 \left( -d + e(x) f \left( \frac{a}{b} \right) \right) \left( -d + e(x) f \left( \frac{a}{b} \right) \right) \phi && \text{in } \Omega \\ \phi &= 0 && \text{on } \partial \Omega \end{aligned}$$

Then

$$\begin{aligned} \lambda_1 \left( -d + e(x) f \left( \frac{a}{b} \right) \right) &= \frac{\int_{\Omega} |\nabla \phi|^2}{\int_{\Omega} \left( -d + e(x) f \left( \frac{a}{b} \right) \right) \phi^2} \\ &\geq \frac{\int_{\Omega} |\nabla \phi|^2}{\int_{\Omega_1} \left( -d + e_* f \left( \frac{a}{b} \right) \right) \phi^2} + \frac{\int_{\Omega - \Omega_1} \left( -d + \bar{e} f \left( \frac{a}{b} \right) \right) \phi^2}{\int_{\Omega} \left( -d + e(x) f \left( \frac{a}{b} \right) \right) \phi^2} \\ &\geq \lambda_1(m_{\Omega_1}), \end{aligned}$$

where

$$m_{\Omega_1} = \begin{cases} -d + e_* f\left(\frac{a}{b}\right) & \text{on } \Omega_1 \\ -d + \bar{e} f\left(\frac{a}{b}\right) & \text{on } \Omega \setminus \Omega_1 \end{cases}$$

and  $\lambda(m_{\Omega_1})$  is the unique positive value so that

$$\begin{aligned} -\Delta z &= \lambda m_{\Omega_1} z & \text{in } \Omega \\ z &= 0 & \text{on } \partial\Omega \end{aligned}$$

admits a positive solution. (Note that the preceding made use of the fact that  $\int_{\Omega} m_{\Omega_1} \phi^2 \geq \int_{\Omega} (-d + e(x)f(a/b)) \phi^2 > 0$ .) By the proof of [4, Theorem 3.9], we can construct a rearrangement  $m_{\Omega_2}$ , given by

$$m_{\Omega_2} = \begin{cases} -d + e_* f\left(\frac{a}{b}\right) & \text{on } \Omega_2 \\ -d + \bar{e} f\left(\frac{a}{b}\right) & \text{on } \Omega \setminus \Omega_2 \end{cases}$$

so that  $|\Omega_2| = |\Omega_1|$ ,  $\lambda(m_{\Omega_2}) \geq \lambda_1(m_{\Omega_2})$  and the eigenfunction corresponding to  $\lambda_1(m_{\Omega_2})$  has  $\partial\Omega_2$  as a level set. It then follows by symmetrization as discussed in [1] that  $\lambda_1(m_{\Omega_2}) \geq \lambda_1(m_*)$  as in [4, Remark 3.10].

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