

Competitive reversals inside ecological reserves: the role of external habitat degradation

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Abstract. Habitat degradation is the slow – and often subtle – deterioration in habitat quality that accompanies human activities through increases in road density, pesticide use, hunting pressure, etc. Such degradation is of particular concern in fragmented habitats where economic or jurisdictional boundaries rather than ecological ones determine the level of exploitation adjoining habitat patches endure. To examine the consequences habitat degradation might have on species interactions, we posited a patch of pristine habitat surrounded by “matrix” habitat whose degradation level was variable. Using a coupled pair of diffusive Lotka–Volterra competition equations with Robin (mixed) boundary conditions, we modeled the dynamics of two competing species inhabiting the pristine patch and incorporated matrix degradation through a tunable “hostility” parameter representing species’ mortality rates in the matrix. We found that the numerical range of competition coefficients over which one species is the competitive dominant and the other inferior may grow or shrink as matrix

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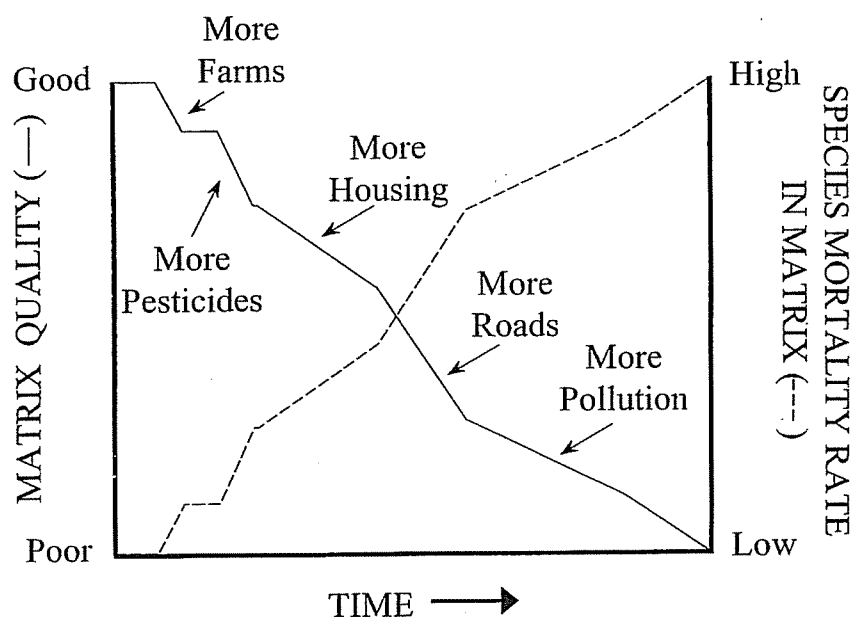


Fig. 1.1. Over time, intensification of human imprints on “matrix” habitat adjoining nature reserves (through such activities as road construction and pollution) can result in a progressive degradation of matrix quality. For species that unknowingly stray into matrix habitat from nature reserves, such decreased habitat quality often takes an ecological toll in the form of elevated mortality rates due to increased exposure to road traffic, toxic chemicals, or other species

intensify in the matrix habitat, they gradually reduce the quality of that region, making it more and more hostile to species in the remnants Fig. 1.1.

For example, species diversity of birds inhabiting remnant woodlots in Ontario, Canada, declined as the extent of housing development outside the forest fragments increased (Friesen et al. 1995). Because only one group of birds (neotropical migrants) appeared sensitive to the habitat changes, dramatic shifts in community composition were evident along the development gradient. Friesen et al. cite increased mortality from domesticated pets and other sources in the matrix habitat as one potential mechanism for the changes. Similarly, Angelstam (1986) suggests that Swedish forest birds suffered increased mortality from generalist predators (e.g., corvids, foxes) residing in matrix habitat as human activities make the habitat patch and its surroundings more and more dissimilar. In many ecological systems, progressive deterioration of the matrix habitat may be accompanied by a predictable pattern of species extinctions in remnant patches (e.g. Bierregaard et al. 1992). Species’ interactions and life-history traits (e.g., rates of

quality deteriorates. In some cases, degradation of the exterior habitat would bring about a complete competitive reversal *inside* the preserve. This result, wherein a formerly inferior species supplants a formerly dominant one – even inside the “protected” remnant patch itself – has policy implications for both nature reserve design and management of human activities outside park boundaries.

Key words: Competition – Edge effects – Reaction–diffusion – Lotka–Volterra – Ecological reserves

1 Introduction

In ecology, tremendous energy is devoted to understanding how landscape heterogeneity influences the dynamics of resident species. Habitat fragmentation – wherein human activities form isolated, remnant patches from historically dominant habitat types – is of particular concern because it often leads to precipitous declines in the abundance of resident species. Familiar examples of such fragmentation-induced declines include northern spotted owls (Thomas et al. 1990) and the “faunal collapse” that may occur in tropical forest fragments following isolation (Karr 1982; Lovejoy et al. 1983).

Typically, the human-modified “matrix” surrounding remnant habitat patches is of lower quality (for certain focal species) than the remnant patches themselves. This translates into an increased mortality risk for individuals that venture (or propagules that are dispersed) beyond the boundaries of the remnant patches. Such increased mortality risk in the matrix can threaten species with extinction as individual habitat patches are “drained” of their occupants (e.g., Bach 1984; Kareiva 1985) and as potential colonizers are killed on the journey from one isolated patch to another (e.g., Janzen 1986; Thomas et al. 1990).

Often landscape alterations like fragmentation and patch isolation are portrayed as an all or none event; that is two types of habitat exist: (1) isolated patches of pristine habitat (e.g., nature reserves) and (2) the modified matrix in which the relict patches are embedded. However, human activities often change ecological landscapes in more subtle ways, such as the slow degradation of habitat (Doak 1995). In this degradation scenario, human activities do not convert matrix habitat from its natural condition to condominiums in one step, but instead impact matrix habitat quality in a much more protracted fashion. As housing and highway construction, pollution, and similar activities

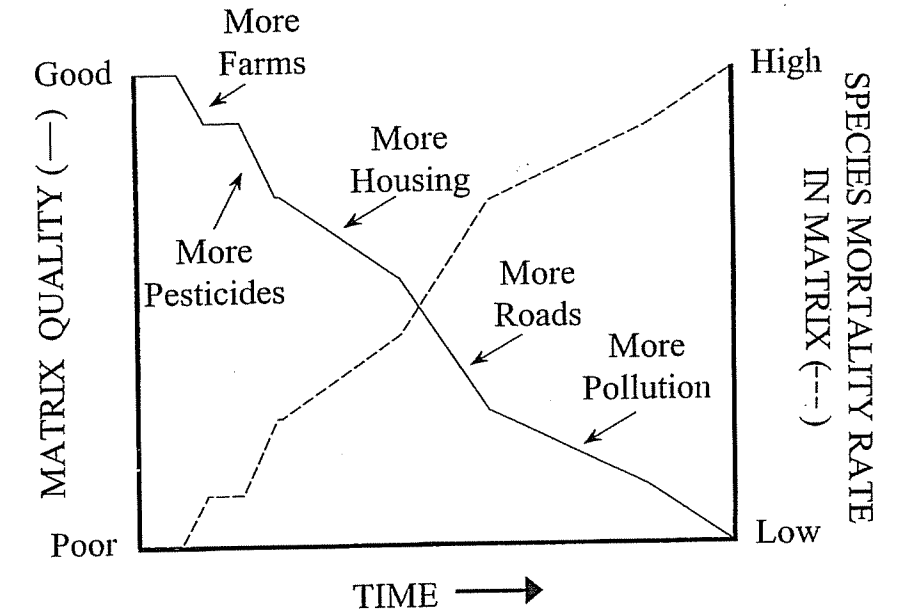


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reproduction and dispersal) are thought to critically determine extinction likelihoods in such cases.

Here we explore, at a theoretical level, the effects that the process of habitat degradation has on species coexistence. Specifically, we posit a patch of pristine habitat that is surrounded by matrix habitat. Populations of two competing species reside and reproduce in the pristine patch but can disperse (unknowingly) into the surrounding matrix. We then ask how degrading (or equivalently, increasing the hostility of) matrix habitat alters the outcome of the species' competitive interactions. Among other results, our analysis will show how a competitor that is inferior in the pristine core habitat when the matrix habitat is of high quality can become dominant over – and eventually replace – the other species as degradation in the surrounding matrix region proceeds. The occurrence of this competitive reversal is dependent on several factors including the size of the patch of pristine habitat, the growth and dispersal rates of the competing species, and the strength of their competitive interactions.

We shall model the dispersal and interactions of the competing species via a system of reaction – diffusion equations. Such models were introduced by Skellam (1951) and Kierstead and Slobodkin (1953) and have been widely used to describe spatial effects in population dynamics; see Holmes et al. (1994). In such models the degree of hostility of the environment outside a habitat patch is typically described via boundary conditions, i.e. conditions imposed on the solutions to the system at the boundary of the patch; see Ludwig et al. (1979). There have been numerous studies of the effects of habitat size, geometry, and composition on the interactions of competing species from the viewpoint of reaction – diffusion models; see for example Pacala and Roughgarden (1982), Mimura (1984), Mimura and Fife (1986), Mimura et al. (1991), and Cantrell and Cosner (1993), among many others. For additional references see Holmes et al. (1994). What is new in the present article is a careful analysis of how the boundary conditions (which reflect the hostility of the external environment) affect the outcome of competitive interactions.

2 Mathematical modelling and interpretation

The purpose of this section is two fold. First, we describe a mathematical framework that addresses how the coexistence of two competing species in a continuous habitat patch is affected by increasing the hostility of the exterior of the patch. Second, we summarize conclusions regarding competitive dominance and reversals of dominance that our subsequent analysis will support.

Providing a mathematical framework consists not only of introducing our two-species competition model but also of establishing the context for our analyses. To this end, we first discuss corresponding single species models and mathematical formulations of the related concepts of coexistence and invasibility.

2.1 Single species models

The single species models which we employ in this article are of the logistic form

$$\frac{\partial u}{\partial t} = D_{\text{in}} \nabla^2 u + r \left(\gamma(x) - \frac{u}{K} \right) u \quad \text{in } \Omega \times (0, \infty) \quad (2.1)$$

$$\alpha \frac{\partial u}{\partial \eta} + \beta u = 0 \quad \text{on } \partial \Omega \times (0, \infty), \quad (2.2)$$

where Ω is a bounded open connected set in one, two or three spatial dimensions representing a habitat for the species whose population density at locale $x \in \Omega$ and time $t \geq 0$ is given by $u = u(x, t)$. The parameters D_{in} , r and K occurring in (2.1) are standard ones, representing the diffusion rate for the species within Ω , the intrinsic growth rate for the species and its carrying capacity, respectively. The quantity $\gamma(x)$ does not exceed 1; it represents the possibility of spatial dependence in efficacy of reproductive growth. Here this heterogeneity is in response to spatial variation in competitive pressure with $\gamma(x)$ decreasing as the population density of the competitor and the intensity of competition at the locale x increases. Indeed, it is conceivable that $\gamma(x)$ is negative for some locales.

The parameters α and β in the boundary condition (2.2) are non-negative with $\alpha + \beta > 0$. The term $\frac{\partial u}{\partial \eta}$ is $\nabla u \cdot \eta$, where $\eta(x)$ is a unit outward normal along the boundary $\partial \Omega$ of Ω . Condition (2.2) allows us to vary the hostility of the environment surrounding the habitat patch. (We will refer to this external environment as the habitat “matrix”.) To see that such is the case, recall its derivation in the now classic paper of Ludwig, Aronson and Weinberger (Ludwig et al. 1979) on the spruce budworm. In this paper, Ω is a one dimensional habitat (i.e. a bounded open interval) surrounded by an infinite “sea” of hostile territory. Exterior to Ω , the population density u is subject to the growth law

$$\frac{\partial u}{\partial t} = D_{\text{out}} \nabla^2 u - su \quad (2.3)$$

where D_{out} is the diffusion rate of the species outside Ω and $s > 0$ is its death rate outside Ω . Matching densities and fluxes for an equilibrium to (2.1) and the unique bounded equilibrium for (2.3) leads to (2.2) with

$$\alpha = D_{\text{in}} \quad \text{and} \quad \beta = \sqrt{sD_{\text{out}}}. \quad (2.4)$$

Consequently, (2.2) is equivalent to

$$\frac{D_{\text{in}}}{\sqrt{D_{\text{out}}}} \nabla u \cdot \eta + \sqrt{su} = 0$$

on $\partial\Omega$ or

$$\sqrt{D} \nabla u \cdot \eta + \sqrt{su} = 0$$

when $D_{\text{in}} = D_{\text{out}} = D$. As a result, the parameter β in (2.2) may be interpreted as an indicator of how hostile the matrix is to the species in question. The extremal case $\beta = 0$ corresponds to a completely closed patch (i.e. one with a reflecting boundary). Since (2.2) can be written as

$$\frac{\alpha}{\beta} \nabla u \cdot \eta + u = 0$$

for $\beta > 0$ and $\frac{\alpha}{\beta} \rightarrow 0$ if $\alpha > 0$ is fixed and $\beta \rightarrow \infty$, the extremal case $\beta = \infty$ corresponds to an immediately lethal exterior.

Single species models of the form (2.1)–(2.2) are widely used and broadly accepted in the modelling of a population inhabiting a continuous habitat patch, dating back to the seminal papers of (Skellam 1951) and (Kierstead and Slobodkin 1953). The dynamics of such models are by now very well understood (see Cantrell and Cosner 1989). Namely, any positive initial population density profile which then propagates subject to (2.1)–(2.2) tends over time to an equilibrium solution of (2.1)–(2.2). The associated eigenvalue problem

$$\begin{aligned} D_{\text{in}} \nabla^2 \phi + r\gamma(x)\phi &= \sigma\phi \quad \text{in } \Omega \\ \alpha \nabla \phi \cdot \eta + \beta\phi &= 0 \quad \text{on } \partial\Omega \end{aligned} \quad (2.5)$$

will have a principal eigenvalue, characterized by the admission of a positive eigenfunction. The principal eigenvalue represents the fastest possible growth rate for the linear growth model corresponding to (2.1)–(2.2). If the principal eigenvalue σ for (2.5) is negative or zero, the only nonnegative equilibrium solution to (2.1)–(2.2) is identically zero, meaning that the species is extinct. On the other hand, when $\sigma > 0$, (2.1)–(2.2) admits a unique equilibrium solution that is positive in Ω ,

and moreover, all positive initial population density profiles then propagate to the positive equilibrium over time, a rather strong sense of the species persisting. (The idea that solutions starting near an unstable equilibrium of a reaction-diffusion equation are bounded below by solutions which increase monotonically toward another equilibrium was introduced by Aronson and Weinberger (1975) and given a more general and detailed formulation by Matano (1978, 1979).)

2.2 Competition models

We shall consider the diffusive Lotka–Volterra competition model

$$\begin{aligned} \frac{\partial U_1}{\partial t} &= D_1 \nabla^2 U_1 + r_1 \left[1 - \frac{U_1}{K_1} - \frac{B_1}{K_1} U_2 \right] U_1 \\ \frac{\partial U_2}{\partial t} &= D_2 \nabla^2 U_2 + r_2 \left[1 - \frac{B_2 U_1}{K_2} - \frac{U_2}{K_2} \right] U_2 \end{aligned} \quad (2.6)$$

in $\Omega \times (0, \infty)$, subject to

$$\alpha_i \nabla U_i \cdot \eta + \beta U_i = 0 \quad (2.7)$$

on $\partial\Omega \times (0, \infty)$. Here Ω is once again a bounded open connected set in one, two or three space dimensions and $U_i = U_i(x, t)$ represents the population density of the i th species at locale $x \in \Omega$ and time $t > 0$. D_i , r_i , K_i , α_i , and β are as in Sect. 2.1, while B_1 scales the competitive impact of U_2 on U_1 and B_2 scales the competitive impact of U_1 on U_2 . As we will elaborate on shortly, we assume the competitors' mortality rates in the matrix can vary independently but in proportion to the overall level of matrix hostility.

In ecology, equations of this form are a traditional way of representing spatially-distributed populations of competing species. Ecologists regularly estimate these equations' variables – or, at least, closely associated quantities – from field data. For example, diffusion coefficients can be estimated from local scale experimental data (Kareiva 1983; Cain 1990; Fagan 1997) or from landscape scale spread rates (Andow et al. 1990; Okubo 1980). Intraspecific and interspecific competition rates, although often difficult to acquire, are also estimable from ecological data (e.g. Gause 1934).

In order to analyze how increasing β influences coexistence in (2.6)–(2.7), it is mathematically advantageous to rescale U_1 and U_2 . We let $u_1 = \frac{r_1 U_1}{K_1}$ and $u_2 = \frac{r_2 U_2}{K_2}$. A simple calculation shows that (2.6)–(2.7) is

then equivalent to

$$\frac{\partial u_1}{\partial t} = D_1 \nabla^2 u_1 + [a_1 - u_1 - b_1 u_2] u_1 \quad (2.8)$$

$$\frac{\partial u_2}{\partial t} = D_2 \nabla^2 u_2 + [a_2 - b_2 u_1 - u_2] u_2$$

in $\Omega \times (0, \infty)$,

$$\alpha_i \nabla u_i \cdot \eta + \beta u_i = 0 \quad (2.9)$$

in $\partial\Omega \times (0, \infty)$.

Here D_i , α_i and β are as in Sect. 2.1, $a_i = r_i$, and b_1 and b_2 are normalizations of the original competition parameters B_1 and B_2 . Specifically,

$$b_1 = B_1 \left(\frac{r_1 K_2}{K_1 r_2} \right), \quad b_2 = B_2 \left(\frac{r_2 K_1}{K_2 r_1} \right) \quad (2.10)$$

Further, we assume that the two species' death rates in the habitat matrix may differ, yet both be proportional to some overarching level of matrix mortality (e.g., road density, pesticide contamination). This approach makes biological sense because species may vary widely in their sensitivity to a complex process such as habitat degradation (Lovejoy et al. 1989; Bierregaard et al. 1992). From this assumption and (2.4), (2.9) is equivalent to

$$0 = (D_{in})_i \nabla u_i \cdot \eta + \sqrt{c_i s (D_{out})_i} u_i \quad (2.11)$$

where c_i is the hostility proportionality constant.

Since (2.11) can be written as

$$0 = \frac{(D_{in})_i}{\sqrt{c_i (D_{out})_i}} \nabla u_i \cdot \eta + \sqrt{s} u_i,$$

we take $\alpha_i = (D_{in})_i / \sqrt{c_i (D_{out})_i}$ and $\beta = \sqrt{s}$ in (2.9). Thus when we increase matrix hostility, we are specifically increasing the overall death rate in the matrix.

By arranging the boundary conditions in this way, we are assuming that the boundary between the remnant habitat and the surrounding, degraded area is an "invisible" one that is not detectable by the resident species. Thus, species neither shun nor are unduly attracted to the surrounding area. This assumption is certainly plausible for many species and situations where factors such as increased hunting pressure, pesticide contamination, or pollution are responsible for the degradation of the matrix habitat (Janzen 1986; Doak 1995). These

forms of degradation are much more subtle than processes like deforestation that create a visible, physical boundary to which some species might respond. Buechner (1987) tabulates examples of mortality factors facing several charismatic vertebrate species that unknowingly venture from U.S. National Parks into more hostile surrounding areas.

We will show how species' sensitivity to the hostility of the area surrounding a remnant habitat patch can lead to a competitive reversal as the extent of degradation intensifies. This type of result, wherein a formerly inferior species supplants a formerly dominant one – even inside the "protected" remnant patch itself – has policy implications for both nature reserve design and management of human activities outside park boundaries. As we describe next, we shall measure the effect of such increasing matrix hostility on coexistence in (2.8)–(2.9) through the normalized competition parameters b_1 and b_2 of (2.10).

2.3 Coexistence and invasibility

We shall say that the model (2.8)–(2.9) predicts coexistence of the species represented by u_1 and u_2 provided there are functions V_1 and V_2 on $\bar{\Omega}$ with $V_i(x) > 0$ in Ω , $i = 1, 2$, so that any solution to (2.8)–(2.9) with

$$u_i(x, 0) \geq 0 \quad \text{in } \Omega \quad (2.12)$$

$i = 1, 2$, satisfies

$$u_i(x, t) \geq V_i(x) \quad \text{in } \bar{\Omega} \quad (2.13)$$

$i = 1, 2$, for $t \geq t_0 = t_0(u_1(x, 0), u_2(x, 0))$. The functions V_1 and V_2 can be considered *asymptotic floors* for the population densities in (2.8)–(2.9). Whenever V_1 and V_2 exist, they, of course, depend on the parameters D_i , a_i , b_i , α_i and β in (2.8)–(2.9). However, for any fixed selection of parameters such that V_1 and V_2 exist, the time it takes a solution to exceed and remain above the asymptotic floor depends only upon the initial population density profile. It is clear that if (2.8)–(2.9) admits a single globally attracting componentwise positive equilibrium, then the model predicts coexistence as we have defined it. However, our notion of coexistence allows for more complicated dynamics; for instance, multiple componentwise positive equilibria are possible. If the system admits stable equilibria of the form $(u_1, 0)$ or $(0, u_2)$, then clearly our notion of coexistence cannot obtain. Consequently, in this context, stable equilibria of the form $(u_1, 0)$ or $(0, u_2)$ are of interest only as a possibility to be ruled out.

Coexistence must imply the persistence of each species in the absence of the other, harking back to the discussion in Sect. 2.1. As

noted there, in order for the model

$$\frac{\partial u_i}{\partial t} = D_i \nabla^2 u_i + u_i(a_i - u_i) \quad \text{in } \Omega \times (0, \infty) \quad (2.14)$$

$$\alpha_i \nabla u_i \cdot \eta + \beta u_i = 0 \quad \text{on } \partial\Omega \times (0, \infty), \quad (2.15)$$

to predict persistence, we require that the relations

$$D_i \nabla^2 \phi_i + a_i \phi_i = \sigma_i \phi_i \quad \text{in } \Omega$$

$$\alpha_i \nabla \phi_i \cdot \eta + \beta \phi_i = 0 \quad \text{on } \partial\Omega$$

$$\phi_i > 0 \quad \text{in } \Omega$$

imply $\sigma_i > 0$. A straightforward calculation shows that

$$-\nabla^2 \phi_i = \left(\frac{a_i - \sigma_i}{D_i} \right) \phi_i.$$

If we now let λ_1^{β/a_i} denote the unique λ for which

$$-\nabla^2 \phi = \lambda \phi \quad \text{in } \Omega$$

$$\alpha_i \nabla \phi \cdot \eta + \beta \phi = 0 \quad \text{on } \partial\Omega$$

admits a positive eigenfunction, then λ_1^{β/a_i} is nonnegative and $\frac{a_i - \sigma_i}{D_i} = \lambda_1^{\beta/a_i}$. Consequently, $\sigma_i > 0$ is equivalent to $\frac{a_i}{D_i} > \lambda_1^{\beta/a_i}$, so that either is a necessary precondition for coexistence in (2.8)–(2.9). Biologically, the inequality $\frac{a_i}{D_i} > \lambda_1^{\beta/a_i}$ indicates that persistence of a species in the absence of its competitor is possible only when the ratio of its reproductive and dispersal rates exceeds a certain critical value, which is related to the size and shape of the habitat patch and varies as degradation proceeds in the matrix surrounding the habitat patch. In particular, we shall show that λ_1^{β/a_i} decreases with increasing β .

Given that each species can persist in the absence of the other, what conditions are necessary for invasion by the other species? To this end, suppose now that $\frac{a_i}{D_i} > \lambda_1^{\beta/a_i}$, $i = 1, 2$. Then, as in Sect. 2.1, we have a unique globally attracting positive solution, denoted u_i^* , to (2.14)–(2.15). Suppose we were to have an initial profile $(u_1(x, 0), u_2(x, 0))$ for (2.8)–(2.9) with $u_1(x, 0)$ near 0 and $u_2(x, 0)$ near $u_2^*(x)$. Suppose also that $\phi > 0$ in

$$D_1 \nabla^2 \phi + (a_1 - b_1 u_2^*(x)) \phi = \sigma \phi \quad \text{in } \Omega \quad (2.16)$$

$$\alpha_1 \nabla \phi \cdot \eta + \beta \phi = 0 \quad \text{on } \partial\Omega$$

implies that $\sigma < 0$. Let (u_1, u_2) be the solution to (2.8)–(2.9) corresponding to $(u_1(x, 0), u_2(x, 0))$. Then

$$\begin{aligned} \frac{\partial u_1}{\partial t} &= D_1 \nabla^2 u_1 + u_1(a_1 - b_1 u_2^*(x)) - u_1(b_1[u_2 - u_2^*(x)] + u_1) \\ &\leq D_1 \nabla^2 u_1 + u_1(a_1 - b_1 u_2^*(x) + \varepsilon) \end{aligned} \quad (2.17)$$

for $t > 0$ so long as $|b_1(u_2 - u_2^*) + u_1|$ remains less than ε . (The smaller ε , the closer $u_1(x, 0)$ is to 0 and $u_2(x, 0)$ is to $u_2^*(x)$.) Suppose $\varepsilon < |\sigma|$. It is easy to calculate that $w(x, t) = e^{(\sigma + \varepsilon)t} \phi(x)$ satisfies

$$\begin{aligned} \frac{\partial w}{\partial t} &= D_1 \nabla^2 w + w(a_1 - b_1 u_2^*(x) + \varepsilon) \quad \text{in } \Omega \times (0, \infty), \\ \alpha_1 \nabla w \cdot \eta + \beta w &= 0 \quad \text{on } \partial\Omega \times (0, \infty). \end{aligned} \quad (2.18)$$

If $K > 0$ is such that

$$u_1(x, 0) \leq K \phi(x)$$

then a well-known comparison principle (see e.g. Cosner and Lazer 1984 or Cantrell et al. 1993b) implies that

$$u_1(x, t) \leq K e^{(\sigma + \varepsilon)t} \phi(x) \quad (2.19)$$

for $t > 0$ so long as $|b_1(u_2 - u_2^*) + u_1| < \varepsilon$. Since $\sigma + \varepsilon < 0$, (2.19) implies that $u_1(x, t)$ decays exponentially if $(u_1(x, 0), u_2(x, 0))$ is sufficiently near $(0, u_2^*(x))$. In such a case, (2.8)–(2.9) predicts that species 2 excludes species 1 if the initial densities are near $(0, u_2^*(x))$.

In the preceding, species 1 could not increase in density if introduced into the habitat at a low density with the u_2 density near its carrying capacity. In other words, $\sigma < 0$ in (2.16) means that species 2 is not invasible at carrying capacity by species 1. Indeed, in such a case, the density of species 1 decays exponentially toward extinction and (2.8)–(2.9) does not predict coexistence as we have defined it. Consequently, if we are to expect (2.8)–(2.9) to predict coexistence, it seems reasonable to hypothesize (in addition to the persistence of each species in the absence of the other) that species i is invasible at carrying capacity by species j , $i, j = 1, 2$, $i \neq j$. Mathematically, we must then require (in addition to $\frac{a_i}{D_i} > \lambda_1^{\beta/a_i}$, $i = 1, 2$) that $\sigma_i > 0$ when the eigenvalue problem

$$D_i \nabla^2 \phi + (a_i - b_i u_j^*(x)) \phi = \sigma_i \phi \quad \text{in } \Omega \quad (2.20)$$

$$\alpha_i \nabla \phi \cdot \eta + \beta \phi = 0 \quad \text{on } \partial\Omega$$

admits a positive solution, $i = 1, 2$, $i \neq j$. It then follows from Corollary 3.7 of Cantrell et al. (1993a) that (2.8)–(2.9) predicts coexistence.

The results of Cantrell et al. (1993a) may consequently be regarded as giving mathematical precision to the ecological dictum "invasibility implies coexistence". This notion of invasibility is described and studied numerically in Pacala and Roughgarden (1982).

Now consider (2.20). If $b_i = 0$, $\sigma > 0$ is equivalent to $\frac{a_i}{D_i} > \lambda_1^{\beta/\alpha_i}$, the requirement that each species persist in the absence of the other. (Of course, such is certainly to be expected, since $b_i = 0$ corresponds to no competitive impact of species j on species i .) Suppose now that $b_i < b'_i$ and that σ_i , σ'_i and ϕ , ϕ' are the corresponding eigenvalues and eigenfunctions in (2.20). In this case $\sigma_i > \sigma'_i$. To see that such is the case, multiply the equation

$$D_i \nabla^2 \phi + (a_i - b_i u_j^*(x)) \phi = \sigma_i \phi$$

by ϕ' and the equation

$$D_i \nabla^2 \phi' + (a_i - b'_i u_j^*(x)) \phi' = \sigma'_i \phi'$$

by ϕ , integrate and subtract. We obtain

$$D_i \int_{\Omega} [\phi' \Delta \phi - \phi \Delta \phi'] - (b_i - b'_i) \int_{\Omega} u_j^* \phi \phi' = (\sigma_i - \sigma'_i) \int_{\Omega} \phi \phi'.$$

Green's Second Identity implies

$$\begin{aligned} D_i \int_{\Omega} [\phi' \Delta \phi - \phi \Delta \phi'] &= D_i \int_{\partial \Omega} [\phi' \nabla \phi \cdot \eta - \phi \nabla \phi' \cdot \eta] \\ &= D_i \int_{\partial \Omega} \phi' \left(-\frac{\beta}{\alpha_i} \phi \right) - \phi \left(-\frac{\beta}{\alpha_i} \phi' \right) \\ &= 0. \end{aligned}$$

Consequently, $(b'_i - b_i) \int_{\Omega} u_j^* \phi \phi' = (\sigma_i - \sigma'_i) \int_{\Omega} \phi \phi'$, and so if $b_i < b'_i$, then $\sigma_i > \sigma'_i$. Thus increasing b_i lowers σ_i in (2.20). Moreover, it can be shown that σ_i is a smooth function of b_i with $\lim_{b_i \rightarrow \infty} \sigma_i = -\infty$. (We shall address this point in our next section.) The implication is that there is a critical value \bar{b}_i so that

$$\begin{aligned} \sigma_i &> 0 && \text{if } 0 \leq b_i < \bar{b}_i \\ \sigma_i &= 0 && \text{if } b_i = \bar{b}_i \\ \sigma_i &< 0 && \text{if } b_i > \bar{b}_i \end{aligned}$$

Consequently, species j at its carrying capacity u_j^* is invisable by species i , $i \neq j$, so long as $b_i < \bar{b}_i$, while species j excludes species i at low densities if $b_i > \bar{b}_i$. From the preceding discussion, it seems reasonable to regard \bar{b}_i as a measure of the threshold capacity of species i to persist in the face of competition from species j , $j \neq i$. Note that u_j^* depends on

D_j , a_j , α_j and β , but not on b_j . It follows that \bar{b}_i depends on all parameters in (2.8)–(2.9) except b_j , $j \neq i$. Suppose D_i , a_i , and α_i are fixed for $i = 1, 2$. Then $\bar{b}_1(\beta) > \bar{b}_2(\beta)$ indicates that species 1 can withstand more intense competition from species 2 than *vice versa*.

What we shall explore in the body of this paper is how changes in β affect the relative positions of $\bar{b}_1(\beta)$ and $\bar{b}_2(\beta)$ under various assumptions on the remaining parameters. In this way, we will examine how increasing the hostility of the matrix influences competition between the two species within the habitat patch, Ω .

2.4 Interpretation

In this last subsection, we briefly illustrate some of the conclusions regarding interspecific competition that can be extracted from our analysis of the relative values of the two species' "competition thresholds", \bar{b}_1 and \bar{b}_2 , as functions of β on $[0, \infty]$. We shall address this issue in greater detail at the end of this article.

Consider Figs. 2.1(a) and (b), which illustrate two contrasting scenarios for the relative values of $\bar{b}_1(\beta)$ and $\bar{b}_2(\beta)$. Our subsequent analysis

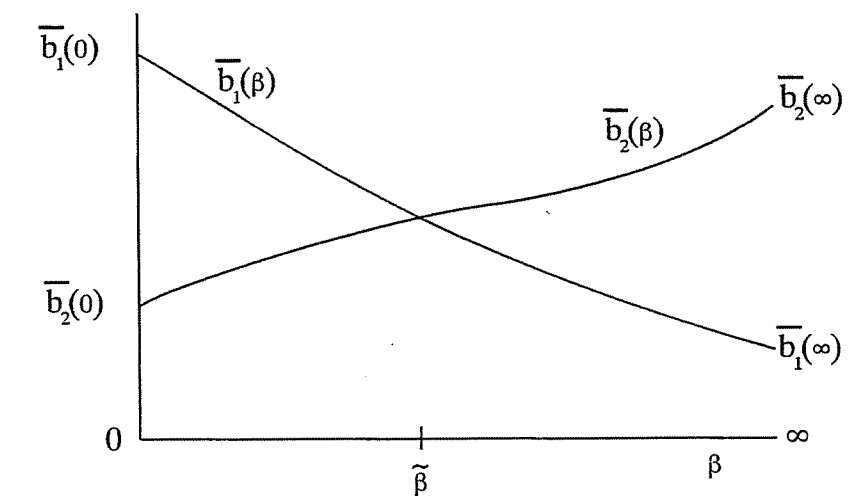


Fig. 2.1a. In this graph β represents the degree of hostility of the matrix surrounding a habitat patch and $\bar{b}_i(\beta)$ represents the maximum level of competition that species i can sustain from species j and still be predicted to persist for any positive initial density. This particular scenario shows a reversal of competitive advantage as β increases. The graph is a schematic representation of the simplest possible case of reversal of competitive advantage. We cannot rule out the possibility of multiple crossings of the two curves which would indicate multiple reversals

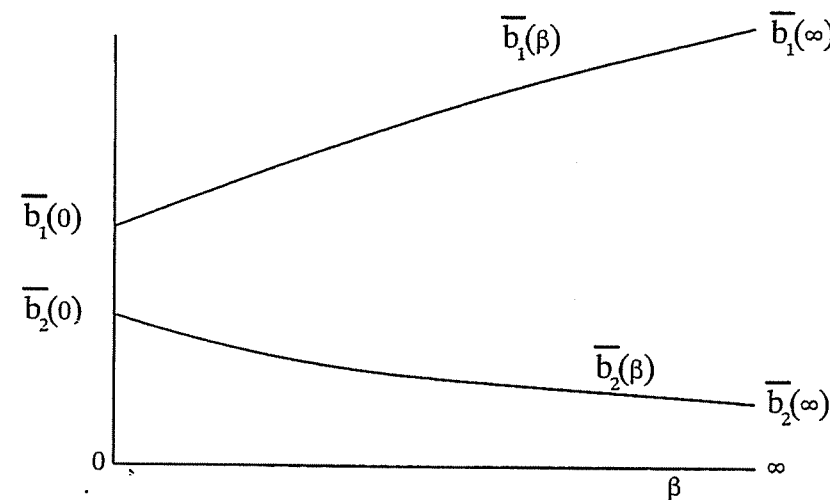


Fig. 2.1b. Again, β represents the degree of hostility of the matrix surrounding a habitat patch and $\bar{b}_i(\beta)$ represents the maximum level of competition that species i can sustain from species j and still be predicted to persist for any positive initial density. This scenario shows no reversal of competitive advantage as β increases, and in fact shows the advantage of species 1 to be increasing with β

demonstrates that both scenarios in essence occur for appropriate (and different) choices of the remaining parameters.

These two scenarios reflect how tremendously complex the relationships between the two species' competition thresholds and the severity of matrix hostility can be. In the scenario illustrated by Fig. 2.1(a), suppose that b_1 and b_2 lie in the interval $(\max\{\bar{b}_2(0), \bar{b}_1(\infty)\}, \bar{b}_1(\beta))$. Then for β small, $b_1 < \bar{b}_1(\beta)$ while $b_2 > \bar{b}_2(\beta)$; hence, species 1 can invade species 2 at carrying capacity, while species 2 at low densities is excluded by species 1 at carrying capacity. In other words, if the hostility of the region surrounding the habitat patch is low, species 1 has a clear competitive advantage. For moderate values of β , $b_1 < \bar{b}_1(\beta)$ and $b_2 < \bar{b}_2(\beta)$, so that each species can invade the other at carrying capacity and we have coexistence of the two species. But then for large values of β (i.e. the matrix is a very hostile environment), $b_1 > \bar{b}_1(\beta)$ and $b_2 < \bar{b}_2(\beta)$; consequently, the competitive advantage shifts to species 2. Contrast the preceding possibility with the scenario illustrated in Fig. 2.1(b). Then if species 1 can invade species 2 at carrying capacity when there is little matrix hostility, it retains that ability as β increases, whereas if species 2 cannot invade species 1 at carrying capacity for small β , it never gains the ability to do so as β increases. Consequently, in the scenario illustrated by Fig. 2.1(b), if

species 2 does not hold a competitive advantage in a closed habitat, it cannot gain an advantage as the hostility of the habitat matrix increases.

Because modifications to matrix habitat may have far reaching effects on remnant patches such as changing critical ecological processes like decay rates for carrion and dung (Klein 1989) or success rates for plant pollination and seed set (Aizen and Feinsinger 1994), it is important to understand the possible mechanisms through which external modifications can impinge on the functioning of ecological communities (e.g., Janzen 1983; Cantrell and Cosner 1993). Our analyses illustrate one plausible mechanism through which the consequences of human-generated landscape heterogeneity extend far beyond simple reductions in species abundance. Namely, we show how the slow degradation of matrix habitat adjoining a protected nature reserve can reverse the outcome of two species' competitive interactions *inside* the reserve: a competitive dominant becomes inferior and *vice versa*. At the community level, such degradation-induced competitive reversals could ultimately change the ecological structure and composition of a supposedly secure reserve.

3 Mathematical preliminaries

In the preceding section, we showed a way to formulate mathematically how competition between two species in a habitat patch may be affected by increasing the hostility of the surrounding matrix to the species in question. Specifically, we plan to study how the critical parameters \bar{b}_i , $i = 1, 2$, vary with increases in the matrix hostility parameter β . The definition of $\bar{b}_1 = \bar{b}_1(\beta)$ and $\bar{b}_2 = \bar{b}_2(\beta)$ in Sect. 2.3 implies that they are the unique positive numbers for which the boundary value problems

$$D_1 \nabla^2 \phi_1 + (a_1 - \bar{b}_1 u_2^*(x)) \phi_1 = 0 \quad \text{in } \Omega \quad (3.1)$$

$$\alpha_1 \nabla \phi_1 \cdot \eta + \beta \phi_1 = 0 \quad \text{on } \partial \Omega$$

and

$$D_2 \nabla^2 \phi_2 + (a_2 - \bar{b}_2 u_1^*(x)) \phi_2 = 0 \quad \text{in } \Omega \quad (3.2)$$

$$\alpha_2 \nabla \phi_2 \cdot \eta + \beta \phi_2 = 0 \quad \text{on } \partial \Omega$$

admit solutions ϕ_1 and ϕ_2 , respectively, which are positive on the habitat patch Ω . (Here $\frac{a_i}{D_i} > \lambda_1^{\beta/a_i}$ and $u_i^*(x)$ is the corresponding positive

single species equilibrium, as in the preceding section.) Observe that (3.1) and (3.2) can be expressed as

$$-\nabla^2 \phi_1 + \frac{\bar{b}_1}{D_1} u_2^*(x) \phi_1 = \frac{a_1}{D_1} \phi_1 \quad \text{in } \Omega$$

$$\alpha_1 \nabla \phi_1 \cdot \eta + \beta \phi_1 = 0 \quad \text{on } \partial\Omega \quad (3.3)$$

and

$$-\nabla^2 \phi_2 + \frac{\bar{b}_2}{D_2} u_1^*(x) \phi_2 = \frac{a_2}{D_2} \phi_2 \quad \text{in } \Omega$$

$$\alpha_2 \nabla \phi_2 \cdot \eta + \beta \phi_2 = 0 \quad \text{on } \partial\Omega \quad (3.4)$$

respectively.

The results and conclusions in the remainder of this paper depend upon a detailed understanding of (3.3) and (3.4). More specifically, they depend upon a thorough quantitative and qualitative analysis of how u_i^* , \bar{b}_i and ϕ_i in (3.3) and (3.4) vary with increasing β . However, only a portion of the mathematical analysis, *per se*, is directly used in drawing biologically interpretable conclusions. The rest of the analysis consists of the derivation of properties (e.g. monotonicity) and estimates needed to support the main arguments. A separation between the two parts of the mathematical analysis serves to highlight our biologically interpretable conclusions and allow a reader with biological interests to focus his or her attention there. To this end, we devote this section to stating, as simply as possible and in context, the background results that we will use in the analysis of the next three sections, and defer the proofs of said results to the Appendix. Our hope is that by so doing, our main results will be both essentially mathematically self-contained and biologically meaningful.

Our first observation is the following:

Theorem 3.1. *Suppose $\beta_0 \in [0, \infty]$ and that $\frac{a_i}{D_i} > \lambda_1^{\beta_0/a_i}$ for $i = 1, 2$. Let $(\bar{b}_1, u_2^*, \phi_1)$ be as in (3.3) and $(\bar{b}_2, u_1^*, \phi_2)$ be as in (3.4) with $\int_{\Omega} \phi_i^2 = 1$ for $i = 1, 2$. Then the maps from $[0, \infty] \rightarrow [0, \infty) \times C^1(\bar{\Omega}) \times C^1(\bar{\Omega})$ given by $\beta \rightarrow (\bar{b}_1, u_2^*(\beta), \phi_1(\beta))$ and $\beta \rightarrow (\bar{b}_2, u_1^*(\beta), \phi_2(\beta))$ are differentiable at β_0 .*

It is worthwhile to note that Theorem 3.1 is significant in two ways. First of all, it includes the important fact that $\{(\beta, \bar{b}_i(\beta)) : \beta \in [0, \infty)\}$ is a smooth curve with the property that $\lim_{\beta \rightarrow \infty} \bar{b}_i(\beta) = \bar{b}_i(\infty)$, $i = 1, 2$. Second, it justifies the calculations we make of $\bar{b}_i(0)$ in Sect. 5 to examine the effect of the onset of exterior hostility.

Now return to (3.3) and (3.4). Observe that both boundary value problems are of the form

$$-\nabla^2 \psi + q\psi = \lambda\psi \quad \text{in } \Omega$$

$$\nabla \psi \cdot \eta + \gamma\psi = 0 \quad \text{on } \partial\Omega \quad (3.5)$$

with $q = \frac{\bar{b}_1}{D_1} u_2^*$ in (3.3) and $\frac{\bar{b}_2}{D_2} u_1^*$ in (3.4), $\lambda = \frac{a_1}{D_1}$ in (3.3) and $\frac{a_2}{D_2}$ in (3.4), and $\gamma = \frac{\beta}{\alpha_1}$ in (3.3) and $\frac{\beta}{\alpha_2}$ in (3.4). Let $\lambda_1^{\gamma}(q)$ denote the so-called principal eigenvalue for (3.5); i.e., the unique value of λ for which (3.5) admits an eigenfunction which is positive in Ω . Notice that $\lambda_1^{\gamma}(0)$ is the same quantity as the previously employed λ_1^{γ} . Basic to our subsequent results is our next observation.

Theorem 3.2. *The principal eigenvalue $\lambda_1^{\gamma}(q)$ of (3.5) satisfies:*

- (i) *If q_1 and q_2 are continuous functions on $\bar{\Omega}$, $\gamma \geq 0$ and $q_1 \leq q_2$ then $\lambda_1^{\gamma}(q_1) \leq \lambda_1^{\gamma}(q_2)$. If $q_1 \not\equiv q_2$, then $\lambda_1^{\gamma}(q_1) < \lambda_1^{\gamma}(q_2)$.*
- (ii) *If $0 \leq \gamma_1 < \gamma_2$ and q is a continuous function on $\bar{\Omega}$, then $\lambda_1^{\gamma_1}(q) < \lambda_1^{\gamma_2}(q)$.*

It is a well-known fact that the principal eigenvalue for the Laplace operator subject to homogeneous Neumann boundary data (i.e. reflecting boundary conditions) is 0. In our notation, this fact is expressed as $\lambda_1^0(0) = 0$. It follows from (ii) that $\lambda_1^{\gamma}(0)$ increases strictly as matrix hostility γ increases and that $\lambda_1^{\infty}(0)$, the principal eigenvalue in the case of absorbing or Dirichlet boundary data, is the largest such quantity. Notice that this ordering should be intuitive in light of the observation in the preceding section that species with density u_i persists in the absence of competition (with exterior hostility level γ) when $\frac{a_i}{D_i}$, the ratio of intrinsic growth rate to diffusion rate, exceeds $\lambda_1^{\gamma}(0)$ and in light of the expectation that survival should be the least likely with a completely lethal exterior.

Our results in Sect. 6 demonstrating or prohibiting a shift in competitive balance depend upon an analysis of the quantities $\lambda_1^{\beta/a_1}(\frac{\bar{b}_1}{D_1} u_2^*)$ and $\lambda_1^{\beta/a_2}(\frac{\bar{b}_2}{D_2} u_1^*)$, an analysis which is facilitated by the following additional information concerning u_1^* and u_2^* . Let γ be nonnegative and let $a > \lambda_1^{\gamma}(0)$. As in Sect. 2, there is then a unique positive solution to the boundary value problem

$$-\nabla^2 u = u(a - u) \quad \text{in } \Omega$$

$$\nabla u \cdot \eta + \gamma u = 0 \quad \text{on } \partial\Omega. \quad (3.6)$$

Let us denote this solution by θ_a^{γ} . Then θ_a^{γ} is defined for $\gamma \geq 0$ and $a > \lambda_1^{\gamma}(0)$ and we have:

Theorem 3.3. (i) *θ_a^{γ} is an increasing function of a and a decreasing function of γ .*

- (ii) $\theta_a^\gamma \leq a$ for any $\gamma \geq 0$ and $a > \lambda_1^\gamma(0)$.
- (iii) $\lambda_1^\gamma(\theta_a^\gamma) = a$ for any $\gamma \geq 0$ and $a > \lambda_1^\gamma(0)$.
- (iv) $u_i^*(\beta) = D_i \theta_{a_i/D_i}^{\beta/\alpha_i}$ for any $\beta \geq 0$ and a_i, D_i such that $\frac{a_i}{D_i} > \lambda_1^{\beta/\alpha_i}(0)$, $i = 1, 2$.

As a consequence of Theorem 3.3(iv), the quantities crucial to our analysis in Sect. 6 are $\lambda_1^{\beta/\alpha_1}(\bar{b}_1 \frac{D_2}{D_1} \theta_{a_2/D_2}^{\beta/\alpha_2})$ and $\lambda_1^{\beta/\alpha_2}(\bar{b}_2 \frac{D_1}{D_2} \theta_{a_1/D_1}^{\beta/\alpha_1})$. Hence we require estimates on quantities of the form $\lambda_1^\gamma(e\theta_a^\gamma)$, where e is a constant and $(e\theta_a^\gamma)$ plays the role of q . We have:

Theorem 3.4. Suppose that $0 \leq \gamma_1 \leq \gamma_2$.

- (i) Let $e > 0$ and $a > \lambda_1^{\gamma_1}(0)$. Then if $e < 1$,

$$ae + \lambda_1^{\gamma_2}(0)(1 - e) \leq \lambda_1^{\gamma_2}(e\theta_a^{\gamma_1}) \leq \lambda_1^{\gamma_2}(0) + ae \quad (3.7)$$

while if $e > 1$

$$a < \lambda_1^{\gamma_2}(e\theta_a^{\gamma_1}) \leq \lambda_1^{\gamma_2}(0) + ae. \quad (3.8)$$

- (ii) Let $e > 0$ and $a > \lambda_1^{\gamma_2}(0)$. Then if $e < 1$,

$$\lambda_1^{\gamma_1}(0) < \lambda_1^{\gamma_1}(e\theta_a^{\gamma_2}) < a \quad (3.9)$$

while if $e > 1$,

$$\lambda_1^{\gamma_1}(e\theta_a^{\gamma_2}) \leq ae + (1 - e)\lambda_1^{\gamma_1}(0). \quad (3.10)$$

4 Some exceptional cases

An additional consequence of Theorem 3.1 is that if $\frac{a_1}{D_1} > \lambda_1^\infty(0)$ and $\frac{a_2}{D_2} > \lambda_1^\infty(0)$, then $b_1(\beta)$ and $b_2(\beta)$ are necessarily bounded functions of $\beta \in [0, \infty]$. Biologically, this fact can be interpreted as indicating that if both species can persist in the absence of the other in a habitat patch with a highly lethal exterior, then changes in exterior hostility could at most yield a limited increase in the overall level of competition compatible with coexistence.

However, it is not difficult to see that if, for instance, $\frac{a_2}{D_2} < \lambda_1^\infty(0) < \frac{a_1}{D_1}$, such is no longer the case. Indeed, since $\lambda_1^0(0) = 0$ and $\lambda_1^{\beta/\alpha_2}(0)$ increases strictly in β , there must be a unique value of $\beta \in (0, \infty)$, say β_0 , for which $\frac{a_2}{D_2} > \lambda_1^{\beta_0/\alpha_2}(0)$ for $\beta \in [0, \beta_0)$, $\frac{a_2}{D_2} = \lambda_1^{\beta_0/\alpha_2}(0)$, and $\frac{a_2}{D_2} < \lambda_1^{\beta/\alpha_2}(0)$ for $\beta > \beta_0$. Consequently, species 2 goes extinct at the level of exterior hostility corresponding to β_0 quite independent of any competitive effect from species 1. So, as β increases toward β_0 , the equilibrium density $u_2^*(\beta)$ tends toward zero and species 1 persists even if the competitive impact species 2 on it (as measured by b_1) becomes indefinitely large. On the other hand, species 2 becomes extinct even with no competition from species 1. See Fig. 4.1.

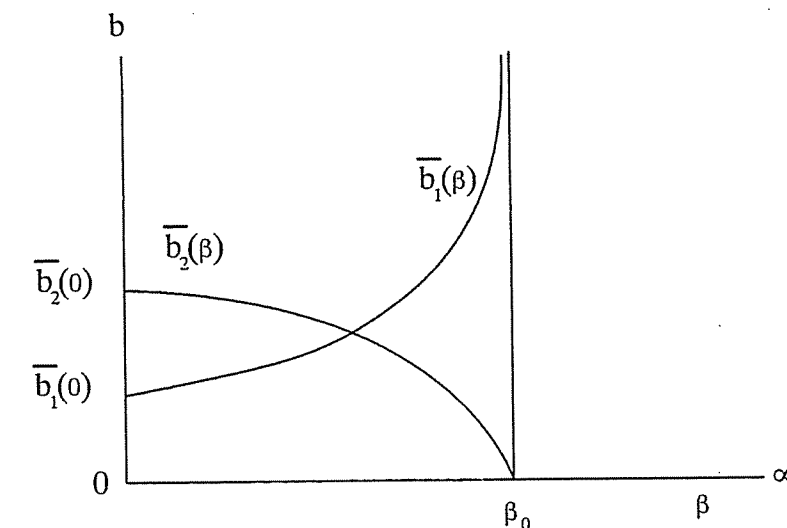


Fig. 4.1. As in Fig. 2.1, β represents the degree of hostility of the matrix surrounding a habitat patch and $\bar{b}_i(\beta)$ represents the maximum level of competition that species i can sustain from species j and still be predicted to persist for any positive initial density. This graph depicts a scenario where species 2 cannot persist when β is too large, even in the absence of species 1. As β becomes so large that species 2 cannot ever persist, the amount of competition that species 1 can sustain from species 2 approaches infinity. This is the only scenario we studied where the total level of competition which could be sustained seemed to increase with β ; however, the reason why species 1 can sustain strong competition from species 2 is that species 2 is tending toward extinction for reasons independent of the interaction between species

As we shall see in Sect. 5, the introduction of matrix hostility usually impacts species' competitive rankings rather than increasing the intensity of competition they can withstand. Matrix hostility can in fact influence competitive rankings even when the two species have the same growth rates, diffusion rates, and competitive impacts and are thus "competitively balanced" in a closed habitat. If these well-matched species exhibit different responses to matrix hostility, then, under some circumstances, the introduction of matrix hostility may initiate a disruption of their competitive balance. However, in one exceptional case, the introduction of exterior hostility into the system may actually have no impact at all on the competitive balance. To see this possibility, let us assume perfectly matched species having $a_1 = a_2$, $D_1 = D_2$ and $\alpha_1 = \alpha_2$. Theorem 3.3(iv) tells us that $u_1^*(\beta) = D_1 \theta_{a_1/D_1}^{\beta/\alpha_1} = D_2 \theta_{a_2/D_2}^{\beta/\alpha_2} = u_2^*(\beta)$. Consequently, $\frac{b_1}{D_1} u_2^*(\beta) = b_1 \theta_{a_1/D_1}^{\beta/\alpha_1}$ and $\frac{b_2}{D_2} u_1^*(\beta) = b_2 \theta_{a_2/D_2}^{\beta/\alpha_2}$. Since $\lambda_1^{\beta/\alpha_i}(\theta_{a_i/D_i}^{\beta/\alpha_i}) = \frac{a_i}{D_i}$ by Theorem 3.3(iii), it follows from (3.3) and (3.4) that $\bar{b}_1(\beta) \equiv 1$ and $\bar{b}_2(\beta) \equiv 1$. So, in this admittedly

highly special case, the introduction of exterior hostility has no impact on species' competitive rankings nor on the intensity of competition compatible with coexistence.

5 The effect of introducing exterior hostility

Closed habitats correspond to reflecting (i.e. homogeneous Neumann) boundary data. In this case, the unique positive solution to the boundary value problem (3.6) used in defining $u_i^*(0)$ is the constant a . Theorem 3.3(iv) then implies that $u_1^*(0) = a_1$ and $u_2^*(0) = a_2$. Biologically, this fact can be interpreted as saying that in the absence of boundary dissipation, the population of each species spreads itself uniformly throughout the habitat patch. With $u_1^*(0) = a_1$ and $u_2^*(0) = a_2$, the critical equations (3.3) and (3.4) also have the property that positive eigenfunctions are necessarily constant. A cursory examination of (3.3) and (3.4) shows that $\bar{b}_1 = \bar{b}_1(0)$ and $\bar{b}_2 = \bar{b}_2(0)$ must satisfy $\bar{b}_1 \frac{a_2}{D_1} = \frac{a_1}{D_1}$ and $\bar{b}_2 \frac{a_1}{D_2} = \frac{a_2}{D_2}$ which of course yields

$$\bar{b}_1(0) = \frac{a_1}{a_2}, \quad \bar{b}_2(0) = \frac{a_2}{a_1}. \quad (5.1)$$

So long as $a_1 \neq a_2$, we have $\bar{b}_1(0) \neq \bar{b}_2(0)$ and, as noted in Sect. 2, one of the species has a clear competitive advantage if the competition rates b_1, b_2 lie in the interval between $\bar{b}_1(0)$ and $\bar{b}_2(0)$. For instance, if $a_1 > a_2$ and $\frac{a_2}{a_1} < b_1, b_2 < \frac{a_2}{a_2}$, species 1 can invade the habitat patch when species 2 is at carrying capacity while if species 2 is introduced in small numbers with species 1 at carrying capacity, species 2 will die out.

We can measure the effect of introducing exterior hostility effects via the derivatives $\bar{b}_i(0)$ and $\bar{b}_i(\beta)$. For instance, in the situation just described, if $\bar{b}_1(0) > 0$ and $\bar{b}_2(0) < 0$ the range of values for competition coefficients for which species 1 holds a competitive advantage over species 2 expands for small values of β , while if $\bar{b}_1(0) < 0$ and $\bar{b}_2(0) > 0$, it contracts. We shall see that unless $\bar{b}_1(0) = 0 = \bar{b}_2(0)$, we have $\bar{b}_1(0) \cdot \bar{b}_2(0) < 0$, so that one of the preceding alternatives obtains. More precisely, we have the following result.

Theorem 5.1. *Let $\bar{b}_i(\beta)$ be as defined in Sect. 2.3. Then*

$$\bar{b}_1(0) = \left(\frac{a_1 \alpha_1}{D_1} - \frac{a_2 \alpha_2}{D_2} \right) \frac{(D_1 D_2) |\partial \Omega|}{(a_2^2 \alpha_1 \alpha_2) |\Omega|} \quad (5.2)$$

and

$$\bar{b}_2(0) = \left(\frac{a_2 \alpha_2}{D_2} - \frac{a_1 \alpha_1}{D_1} \right) \frac{(D_1 D_2) |\partial \Omega|}{(a_1^2 \alpha_1 \alpha_2) |\Omega|}. \quad (5.3)$$

Consequently, unless $\frac{a_1 \alpha_1}{D_1} - \frac{a_2 \alpha_2}{D_2} = 0$, $\bar{b}_1(0)$ and $\bar{b}_2(0)$ we have opposite signs.

Proof. We shall derive (5.2) only, as the derivation of (5.3) is analogous. To calculate $\bar{b}_1(0)$, we consider (3.3) with ϕ_1 satisfying $\int_{\Omega} \phi_1^2 = 1$ and (3.6) with $a = \frac{a_2}{D_2}$ and $\gamma = \frac{\beta}{a_2}$. Employing Theorem 3.1, we differentiate each with respect to β , and let $' = \frac{d}{d\beta}$. So doing, we obtain

$$-\nabla^2 \phi_1' = \left(\frac{a_1}{D_1} - \frac{\bar{b}_1 \bar{u}_2}{D_1} \right) \phi_1' - \frac{\bar{b}_1 \bar{u}_2 \phi_1}{D_1} - \frac{\bar{b}_1 \bar{u}_2' \phi_1}{D_1} \quad \text{in } \Omega \quad (5.4)$$

$$\alpha_1 \nabla \phi_1' \cdot \eta + \beta \phi_1' + \phi_1 = 0 \quad \text{on } \partial \Omega$$

and

$$-\nabla^2 \bar{u}_2' = \left(\frac{a_2}{D_2} - \frac{2\bar{u}_2}{D_2} \right) \bar{u}_2' \quad \text{in } \Omega \quad (5.5)$$

$$\alpha_2 \nabla \bar{u}_2' \cdot \eta + \beta \bar{u}_2' + \bar{u}_2 = 0 \quad \text{on } \partial \Omega$$

Next, multiply (5.4) by ϕ_1 and (3.3) by ϕ_1' , integrate both and subtract. The net result is

$$\int_{\Omega} (\phi_1' \nabla^2 \phi_1 - \phi_1 \nabla^2 \phi_1') dx = - \int_{\Omega} \left(\bar{b}_1 \frac{\bar{u}_2}{D_1} \phi_1^2 + \bar{b}_1 \frac{\bar{u}_2'}{D_1} \phi_1^2 \right) dx. \quad (5.6)$$

Apply Green's Second Identity to the left hand side of (5.6) and simplify the resulting equation to show that $\bar{b}_1(\beta)$ is given by the formula

$$\bar{b}_1(\beta) = \frac{-\frac{D_1}{\alpha_1} \int_{\partial \Omega} \phi_1^2(\beta) dS - \bar{b}_1(\beta) \int_{\Omega} \bar{u}_2(\beta) \phi_1^2(\beta) dx}{\int_{\Omega} \bar{u}_2(\beta) \phi_1^2(\beta) dx}. \quad (5.7)$$

We know that $\bar{u}_2(0) = a_2$ and $\bar{b}_1(0) = \frac{a_1}{a_2}$. Moreover, since $\phi_1(0)$ is constant and $\int_{\Omega} \phi_1^2(0) dx = 1$, $\phi_1(0) = \frac{1}{\sqrt{|\Omega|}}$, where $|\Omega|$ denotes the volume (or area) of Ω . Consequently, we may obtain a formula for $\bar{b}_1(0)$ in terms of the coefficients D_i, a_i , and α_i provided we can do so for $\int_{\Omega} \bar{u}_2'(0) dx$.

We now go back to (5.5) for the purpose of calculating $\int_{\Omega} \bar{u}_2'(0) dx$. Since $\bar{u}_2(0) = a_2$, (5.5) simplifies to

$$-\nabla^2 \bar{u}_2'(0) = -\frac{a_2}{D_2} \bar{u}_2'(0) \quad \text{in } \Omega \quad (5.8)$$

$$\alpha_2 \nabla \bar{u}_2'(0) \cdot \eta = -a_2 \quad \text{on } \partial \Omega$$

Hence by (5.8) and Green's Second Identity,

$$\begin{aligned} \int_{\Omega} \bar{u}'_2(0) dx &= \frac{D_2}{a_2} \oint_{\partial\Omega} \nabla \bar{u}'_2(0) \cdot \eta dS \\ &= \frac{D_2}{a_2} \oint_{\partial\Omega} \frac{-a_2}{\alpha_2} ds \\ &= -\frac{D_2}{\alpha_2} |\partial\Omega|. \end{aligned}$$

Consequently, when $\beta = 0$, (5.7) becomes

$$\begin{aligned} \bar{b}'_1(0) &= \frac{-\frac{D_1}{\alpha_1} \frac{|\partial\Omega|}{|\Omega|} - \frac{a_1}{a_2} \left(-\frac{D_2}{\alpha_2} \frac{|\partial\Omega|}{|\Omega|} \right)}{a_2} \\ &= \left(\frac{-D_1 a_2 \alpha_2 + a_1 D_2 \alpha_1}{a_2^2 \alpha_1 \alpha_2} \right) \left| \frac{\partial\Omega}{\Omega} \right| \\ &= \left(\frac{a_1 \alpha_1}{D_1} - \frac{a_2 \alpha_2}{D_2} \right) \left(\frac{D_1 D_2}{a_2^2 \alpha_1 \alpha_2} \right) \left| \frac{\partial\Omega}{\Omega} \right|. \end{aligned} \quad (5.9)$$

Reiterating, unless $\frac{a_1 \alpha_1}{D_1} - \frac{a_2 \alpha_2}{D_2} = 0$, $\bar{b}'_1(0)$ and $\bar{b}'_2(0)$ have opposite signs. Thus the onset of matrix hostility usually increases the "competition threshold" of one species and reduces that of the other, and so has the tendency to exaggerate or diminish the competitive advantage for one of the species described previously. Notice that the magnitude of the effect of introducing matrix hostility depends explicitly on the perimeter to area (or surface area to volume) ratio $|\partial\Omega|/|\Omega|$. We explore in the next section the possibility of a "reversal of fortune" due to increasing matrix hostility.

6 A "reversal of fortune" or not

Our aim in this section is to demonstrate that both the tendencies at the onset of exterior hostility observed in the preceding section may extend over the entire range of the exterior hostility parameter β . Recall that if $\bar{b}_1(\beta) > \bar{b}_2(\beta)$ for some β , then species 1 enjoys a competitive advantage over species 2 so long as the competition parameters b_1, b_2 lie in the interval $(\bar{b}_2(\beta), \bar{b}_1(\beta))$. The competitive advantage switches if $\bar{b}_2(\beta) > \bar{b}_1(\beta)$ and b_1, b_2 lie in $(\bar{b}_1(\beta), \bar{b}_2(\beta))$. We will first give conditions on a_i, D_i and α_i under which we can demonstrate that $\bar{b}_1(0) > \bar{b}_2(0)$ and $\bar{b}_1(\beta) > \bar{b}_1(0)$ and $\bar{b}_2(\beta) < \bar{b}_2(0)$ for all $\beta > 0$. Under

such conditions, $(\bar{b}_2(0), \bar{b}_1(0)) \subseteq (\bar{b}_2(\beta), \bar{b}_1(\beta))$ for all $\beta > 0$ and the competitive advantage held by species 1 in a closed habitat is enhanced by increasing the exterior hostility parameter from 0 to β . We then posit conditions on a_i, D_i and α_i under which we can show that $\bar{b}_1(0) > \bar{b}_2(0)$ but $\bar{b}_1(\beta) < \bar{b}_1(0)$ and $\bar{b}_2(\beta) > \bar{b}_2(0)$ for all $\beta > 0$. In this case, if $\bar{b}_2(\beta) < \bar{b}_1(\beta)$, $(\bar{b}_2(\beta), \bar{b}_1(\beta)) \subseteq (\bar{b}_2(0), \bar{b}_1(0))$ and the range of values for competition coefficients under which species 1 holds a competitive advantage is diminished by increasing the exterior hostility parameter from 0 to β . If $\bar{b}_2(\beta) > \bar{b}_1(\beta)$, the competitive advantage actually switches to species 2. We show that such a switch can occur, depending on the principal eigenvalue $\lambda_1^\infty(0)$. This last finding demonstrates that the *size* and *geometry* of the habitat patch are significant factors in any "reversal of fortune" due to increasing exterior hostility. We shall return to this point at the end of the section.

As our chief aim is to demonstrate that increasing exterior hostility can lead either to the exaggeration of the competitive advantage that exists in a closed habitat or to its reversal, we have not attempted at this point an analysis of all possible configurations of the parameters a_i, D_i and $\alpha_i, i = 1, 2$. Rather we have isolated two sets of conditions which serve our main purpose. Our first result is as follows.

Theorem 6.1. *Suppose that*

$$\frac{a_1}{D_1} > \frac{a_2}{D_2} > \lambda_1^\infty(0), \quad D_1 > D_2, \quad \alpha_1 > \alpha_2. \quad (6.1)$$

Then for any $\beta > 0$, $\bar{b}_1(\beta)$ and $\bar{b}_2(\beta)$ satisfy

$$\begin{aligned} \bar{b}_1(\beta) &\geq \frac{a_1 - D_1 \lambda_1^{\beta/\alpha_1}(0)}{a_2 - D_2 \lambda_1^{\beta/\alpha_1}(0)} > \frac{a_1}{a_2} > 1 \\ &> \frac{a_2}{a_1} > \frac{a_2 - D_2 \lambda_1^{\beta/\alpha_2}(0)}{a_1 - D_1 \lambda_1^{\beta/\alpha_2}(0)} \geq \bar{b}_2(\beta). \end{aligned} \quad (6.2)$$

In particular, the numerical range of values for competition coefficient b_1, b_2 for which species 1 holds a competitive advantage expands from $(\frac{a_2}{a_1}, \frac{a_1}{a_2})$ in the case of a closed habitat to at least

$$\left(\frac{a_2 - D_2 \lambda_1^{\beta/\alpha_2}(0)}{a_1 - D_1 \lambda_1^{\beta/\alpha_2}(0)}, \frac{a_1 - D_1 \lambda_1^{\beta/\alpha_1}(0)}{a_2 - D_2 \lambda_1^{\beta/\alpha_1}(0)} \right)$$

when the exterior hostility parameter takes the value $\beta > 0$.

Proof. Notice that $\frac{a_1}{D_1} > \frac{a_2}{D_2}$ and $D_1 > D_2$ imply that $\frac{a_1}{a_2} > \frac{D_1}{D_2} > 1$. Since $\bar{b}_1(0) = \frac{a_1}{a_2}$ and $\bar{b}_2(0) = \frac{a_2}{a_1}$, species 1 holds the competitive advantage in a closed habitat (i.e. when $\beta = 0$).

We now examine $\bar{b}_1(\beta)$ and $\bar{b}_2(\beta)$ for $\beta > 0$. Let us first consider $\bar{b}_1(\beta)$. We have from (3.3) and Theorem 3.3(iv) that $\bar{b}_1 = \bar{b}_1(\beta)$ satisfies

$$\lambda_1^{\beta/\alpha_1} \left(\bar{b}_1 \frac{D_2}{D_1} \theta_{a_2/D_2}^{\beta/\alpha_2} \right) = \frac{a_1}{D_1}. \quad (6.3)$$

Observe that (6.1) implies that $\bar{b}_1 \frac{D_2}{D_1} > 1$. Suppose to the contrary that $\bar{b}_1 \frac{D_2}{D_1} \leq 1$. Then

$$\bar{b}_1 \frac{D_2}{D_1} \theta_{a_2/D_2}^{\beta/\alpha_1} \leq \theta_{a_2/D_2}^{\beta/\alpha_1},$$

so that Theorem 3.2(i) implies that

$$\lambda_1^{\beta/\alpha_1} \left(\bar{b}_1 \frac{D_2}{D_1} \theta_{a_2/D_2}^{\beta/\alpha_1} \right) \leq \lambda_1^{\beta/\alpha_1} \left(\theta_{a_2/D_2}^{\beta/\alpha_1} \right).$$

But now Theorem 3.3(iii) implies

$$\lambda_1^{\beta/\alpha_1} \left(\theta_{a_2/D_2}^{\beta/\alpha_1} \right) = \frac{a_2}{D_2}.$$

Hence

$$\frac{a_2}{D_2} \geq \lambda_1^{\beta/\alpha_1} \left(\bar{b}_1 \frac{D_2}{D_1} \theta_{a_2/D_2}^{\beta/\alpha_2} \right).$$

Because $\alpha_1 > \alpha_2$ by (6.1), $\frac{\beta}{\alpha_1} < \frac{\beta}{\alpha_2}$. So Theorem 3.3(i) implies that

$$\bar{b}_1 \frac{D_2}{D_1} \theta_{a_2/D_2}^{\beta/\alpha_1} > \bar{b}_1 \frac{D_2}{D_1} \theta_{a_2/D_2}^{\beta/\alpha_2} \quad \text{on } \Omega.$$

Consequently, Theorem 3.2(i) implies

$$\lambda_1^{\beta/\alpha_1} \left(\bar{b}_1 \frac{D_2}{D_1} \theta_{a_2/D_2}^{\beta/\alpha_1} \right) > \lambda_1^{\beta/\alpha_1} \left(\bar{b}_1 \frac{D_2}{D_1} \theta_{a_2/D_2}^{\beta/\alpha_2} \right) = \frac{a_1}{D_1}$$

by (6.3). We are now led to the conclusion that $\frac{a_2}{D_2} > \frac{a_1}{D_1}$, a contradiction to (6.1). So $\bar{b}_1 \frac{D_2}{D_1} > 1$.

We may now employ the estimates of Theorem 3.4(ii) with

$$\gamma_1 = \frac{\beta}{\alpha_1}, \quad \gamma_2 = \frac{\beta}{\alpha_2}, \quad e = \bar{b}_1 \frac{D_2}{D_1} > 1 \quad \text{and} \quad a = \frac{a_2}{D_2}.$$

By (3.16), we have

$$\frac{a_1}{D_1} = \lambda_1^{\beta/\alpha_1} \left(\bar{b}_1 \frac{D_2}{D_1} \theta_{a_2/D_2}^{\beta/\alpha_2} \right) \leq \frac{a_2}{D_2} \left(\bar{b}_1 \frac{D_2}{D_1} \right) + \left(1 - \bar{b}_1 \frac{D_2}{D_1} \right) \lambda_1^{\beta/\alpha_1}(0). \quad (6.4)$$

From (6.4), we obtain that

$$\bar{b}_1(\beta) \geq \frac{a_1 - D_1 \lambda_1^{\beta/\alpha_1}(0)}{a_2 - D_2 \lambda_1^{\beta/\alpha_1}(0)}. \quad (6.5)$$

Now consider $\bar{b}_2(\beta)$. By (3.4) and Theorem 3.3(iv),

$$\lambda_1^{\beta/\alpha_2} \left(\bar{b}_2 \frac{D_1}{D_2} \theta_{a_1/D_1}^{\beta/\alpha_1} \right) = \frac{a_2}{D_2} \quad (6.6)$$

where $\bar{b}_2 = \bar{b}_2(\beta)$. If

$$\bar{b}_2 \frac{D_1}{D_2} \geq 1, \quad \bar{b}_2 \frac{D_1}{D_2} \theta_{a_1/D_1}^{\beta/\alpha_1} \geq \theta_{a_1/D_1}^{\beta/\alpha_1}.$$

Because

$$\frac{\beta}{\alpha_1} < \frac{\beta}{\alpha_2}, \quad \theta_{a_1/D_1}^{\beta/\alpha_1} > \theta_{a_1/D_1}^{\beta/\alpha_2} \quad \text{on } \Omega.$$

Consequently, (6.6) and Theorem 3.2(i) imply that

$$\begin{aligned} \frac{a_2}{D_2} &= \lambda_1^{\beta/\alpha_2} \left(\bar{b}_2 \frac{D_1}{D_2} \theta_{a_1/D_1}^{\beta/\alpha_1} \right) \\ &\geq \lambda_1^{\beta/\alpha_2} \left(\theta_{a_1/D_1}^{\beta/\alpha_1} \right) \\ &> \lambda_1^{\beta/\alpha_2} \left(\theta_{a_1/D_1}^{\beta/\alpha_2} \right). \end{aligned}$$

Because $\lambda_1^{\beta/\alpha_2}(\theta_{a_1/D_1}^{\beta/\alpha_2}) = \frac{a_1}{D_1}$ by Theorem 3.3(iii), we obtain $\frac{a_2}{D_2} > \frac{a_1}{D_1}$, contradicting (6.1). Hence $\bar{b}_2 \frac{D_1}{D_2} < 1$.

We now apply the estimates of Theorem 3.4(i) with

$$\gamma_1 = \beta/\alpha_1, \quad \gamma_2 = \beta/\alpha_2, \quad e = \bar{b}_2 \frac{D_1}{D_2} \quad \text{and} \quad a = \frac{a_1}{D_1}.$$

From (3.7), we have

$$\left(\frac{a_1}{D_1} \right) \left(\bar{b}_2 \frac{D_1}{D_2} \right) + \lambda_1^{\beta/\alpha_2}(0) \left(1 - \bar{b}_2 \frac{D_1}{D_2} \right) \leq \lambda_1^{\beta/\alpha_2} \left(\bar{b}_2 \frac{D_1}{D_2} \theta_{a_1/D_1}^{\beta/\alpha_1} \right) = \frac{a_2}{D_2}. \quad (6.7)$$

It follows from (6.7) that

$$\bar{b}_2(\beta) \leq \frac{a_2 - D_2 \lambda_1^{\beta/\alpha_2}(0)}{a_1 - D_1 \lambda_1^{\beta/\alpha_2}(0)}. \quad (6.8)$$

So if (6.3) holds, we have from (6.4) and (6.8) that

$$\bar{b}_2(\beta) \leq \frac{a_2 - D_2 \lambda_1^{\beta/\alpha_2}(0)}{a_1 - D_1 \lambda_1^{\beta/\alpha_2}(0)}$$

while

$$\bar{b}_1(\beta) \geq \frac{a_1 - D_1 \lambda_1^{\beta/\alpha_1}(0)}{a_2 - D_2 \lambda_1^{\beta/\alpha_1}(0)}$$

The function

$$f(x) = \frac{a_2 - D_2 x}{a_1 - D_1 x}$$

has derivative

$$f'(x) = \frac{\left(\frac{a_2}{D_2} - \frac{a_1}{D_1}\right)(D_1 D_2)}{(a_1 - D_1 x)^2} \quad \text{on} \left(0, \frac{a_1}{D_1}\right).$$

By (6.1), $f'(x) < 0$. Since Theorem 3.2(ii) guarantees that $\lambda_1^{\beta/\alpha_2}(0)$ increases in β , the quantity

$$\frac{a_2 - D_2 \lambda_1^{\beta/\alpha_2}(0)}{a_1 - D_1 \lambda_1^{\beta/\alpha_2}(0)} = f(\lambda_1^{\beta/\alpha_2}(0))$$

decreases as β increases. Similarly,

$$\frac{a_1 - D_1 \lambda_1^{\beta/\alpha_1}(0)}{a_2 - D_2 \lambda_1^{\beta/\alpha_1}(0)}$$

increases as β increases and the proof is complete. \square

We now consider a different configuration of the parameters a_i, D_i and $\alpha_i, i = 1, 2$, under which a competitive reversal is sometimes possible. We have the following result.

Theorem 6.2. *Suppose that*

$$\frac{a_2}{D_2} > \frac{a_1}{D_1} > \lambda_1^\infty(0), \quad a_1 > a_2. \quad (6.9)$$

Then

$$\bar{b}_1(\infty) \leq \frac{a_1 - D_1 \lambda_1^\infty(0)}{a_2 - D_2 \lambda_1^\infty(0)} \quad \text{and} \quad \bar{b}_2(\infty) \geq \frac{a_2 - D_2 \lambda_1^\infty(0)}{a_1 - D_1 \lambda_1^\infty(0)}. \quad (6.10)$$

If $\lambda_1^\infty(0) > \frac{a_1 - a_2}{D_1 - D_2}$, then for sufficiently large $\beta > 0$, $\bar{b}_1(\beta) < \bar{b}_2(\beta)$. In this case, the competitive advantage held by species 1 when the competition coefficients b_1, b_2 lie in $\left(\frac{a_2}{a_1}, \frac{a_1}{a_2}\right)$ switches to a competitive advantage for species 2 for competition coefficients b_1, b_2 in $(\bar{b}_1(\beta), \bar{b}_2(\beta))$. If

$$\lambda_1^\infty(0) > \frac{a_1^2 - a_2^2}{a_1 D_1 - a_2 D_2} > \left(\frac{a_1 - a_2}{D_1 - D_2}, \left(\frac{a_2}{a_1}, \frac{a_1}{a_2}\right)\right) \subseteq (\bar{b}_1(\beta), \bar{b}_2(\beta))$$

and the range of values for competition coefficients for which species 2 holds a competitive advantage when the matrix hostility is high subsumes the range of values for competition coefficients for which species 1 holds a competitive advantage in a closed habitat.

Remark. Again, it is the case that

$$\bar{b}_1(0) = \frac{a_1}{a_2} > \frac{a_2}{a_1} = \bar{b}_2(0),$$

and species 1 holds a competitive advantage when the competition coefficients b_1, b_2 lie in the interval $\left(\frac{a_2}{a_1}, \frac{a_1}{a_2}\right)$. If $\bar{b}_1(\infty) < \bar{b}_2(\infty)$, then extreme exterior hostility switches the competitive advantage to species 2. More specifically, when $\bar{b}_1(\infty) < \bar{b}_2(\infty)$, $\bar{b}_1(\beta) < \bar{b}_2(\beta)$ for all large β by Theorem 3.1, so that species 2 is at an advantage when the competition coefficients b_1, b_2 lie in the interval $(\bar{b}_1(\beta), \bar{b}_2(\beta))$.

Proof. Let us first consider $\bar{b}_1(\infty)$. We have from (3.3) and Theorem 3.3(iv) that $\bar{b}_1 = \bar{b}_1(\infty)$ satisfies

$$\lambda_1^\infty\left(\bar{b}_1 \frac{D_2}{D_1} \theta_{a_2/D_2}^\infty\right) = \frac{a_1}{D_1}. \quad (6.11)$$

If $\bar{b}_1 \frac{D_2}{D_1} \geq 1$, $\bar{b}_1 \frac{D_2}{D_1} \theta_{a_2/D_2}^\infty \geq \theta_{a_2/D_2}^\infty$ and (6.11) and Theorem 3.2(i) imply that

$$\begin{aligned} \frac{a_1}{D_1} &= \lambda_1^\infty\left(\bar{b}_1 \frac{D_2}{D_1} \theta_{a_2/D_2}^\infty\right) \\ &\geq \lambda_1^\infty(\theta_{a_2/D_2}^\infty). \end{aligned}$$

Since $\lambda_1^\infty(\theta_{a_2/D_2}^\infty) = \frac{a_2}{D_2}$ by Theorem 3.3(iii), we obtain a contradiction to (6.9). Hence $\bar{b}_1 \frac{D_2}{D_1} < 1$.

We now employ the estimates of Theorem 3.4(i) with

$$\gamma_1 = \infty, \quad \gamma_2 = \infty, \quad e = \bar{b}_1 \frac{D_2}{D_1} \quad \text{and} \quad a = \frac{a_2}{D_2}.$$

From (3.7), we have

$$\frac{a_1}{D_1} = \lambda_1^\infty\left(\bar{b}_1 \frac{D_2}{D_1} \theta_{a_2/D_2}^\infty\right) \geq \frac{a_2}{D_2} \left(\bar{b}_1 \frac{D_2}{D_1}\right) + \lambda_1^\infty(0) \left(1 - \bar{b}_1 \frac{D_2}{D_1}\right). \quad (6.12)$$

It follows from (6.12) that

$$\bar{b}_1(\infty) \leq \frac{a_1 - D_1 \lambda_1^\infty(0)}{a_2 - D_2 \lambda_1^\infty(0)}. \quad (6.13)$$

Now consider $\bar{b}_2(\infty)$. Again, from (3.4) and Theorem 3.3(iv), we have

$$\lambda_1^\infty\left(\bar{b}_2 \frac{D_1}{D_2} \theta_{a_1/D_1}^\infty\right) = \frac{a_2}{D_2} \quad (6.14)$$

where $\bar{b}_2 = \bar{b}_2(\infty)$. If $\bar{b}_2 \frac{D_1}{D_2} \leq 1$, $\bar{b}_2 \frac{D_1}{D_2} \theta_{a_1/D_1}^\infty \leq \theta_{a_1/D_1}^\infty$, and (6.14) and Theorem 3.2(i) imply

$$\frac{a_2}{D_2} = \lambda_1^\infty \left(\bar{b}_2 \frac{D_1}{D_2} \theta_{a_1/D_1}^\infty \right) \leq \lambda_1^\infty(\theta_{a_1/D_1}^\infty).$$

Again, Theorem 3.3(iii) implies that $\lambda_1^\infty(\theta_{a_1/D_1}^\infty) = \frac{a_1}{D_1}$ and we contradict (6.9). Consequently, $\frac{b_2 D_1}{D_2} > 1$.

We may now apply once more the estimates of Theorem 3.4(ii), this time with

$$\gamma_1 = \infty, \quad \gamma_2 = \infty, \quad e = \bar{b}_2 \frac{D_1}{D_2} \quad \text{and} \quad a = \frac{a_1}{D_1}.$$

We have from (3.10) that

$$\frac{a_2}{D_2} = \lambda_1^\infty \left(\bar{b}_2 \frac{D_1}{D_2} \theta_{a_1/D_1}^\infty \right) \leq \frac{a_1}{D_1} \left(\bar{b}_2 \frac{D_1}{D_2} \right) + \left(1 - \bar{b}_2 \frac{D_1}{D_2} \right) \lambda_1^\infty(0). \quad (6.15)$$

It follows from (6.15) that

$$\bar{b}_2(\infty) \geq \frac{a_2 - D_2 \lambda_1^\infty(0)}{a_1 - D_1 \lambda_1^\infty(0)}. \quad (6.16)$$

So if (6.9) holds, (6.13) and (6.16) give (6.10). By (6.9), the function $f(x) = \frac{a_2 - D_2 x}{a_1 - D_1 x}$ is increasing on $(0, \frac{a_1}{D_1})$ and its reciprocal $\frac{a_1 - D_1 x}{a_2 - D_2 x}$ is decreasing. At a minimum, we are guaranteed that extreme exterior hostility reduces the numerical range of values for competition coefficients b_1 , b_2 under which species 1 enjoys a competitive advantage. When

$$\frac{a_1 - D_1 \lambda_1^\infty(0)}{a_2 - D_2 \lambda_1^\infty(0)} < 1 < \frac{a_2 - D_2 \lambda_1^\infty(0)}{a_1 - D_1 \lambda_1^\infty(0)},$$

there is a switch in competitive advantage to species 2. It is easy to calculate that such a switch takes place for β large when

$$\lambda_1^\infty(0) > \frac{a_1 - a_2}{D_1 - D_2}. \quad (6.17)$$

If the value of $\lambda_1^\infty(0)$ is large enough, we will have

$$\left(\frac{a_2}{a_1}, \frac{a_1}{a_2} \right) \subseteq (\bar{b}_1(\beta), \bar{b}_2(\beta)) \quad (6.18)$$

so that the range of values for competition coefficients b_1, b_2 for which species 2 enjoys a competitive advantage when matrix hostility is high $((\bar{b}_1(\beta), \bar{b}_2(\beta)))$ actually subsumes the range of values for b_1, b_2 for which species 1 enjoys a competitive advantage in a closed habitat $(\frac{a_2}{a_1}, \frac{a_1}{a_2})$. It

is not difficult to see that (6.18) holds once $\lambda_1^\infty(0)$ is large enough to have

$$\frac{a_1 - D_1 \lambda_1^\infty(0)}{a_2 - D_2 \lambda_1^\infty(0)} < \frac{a_2}{a_1}.$$

This requires

$$\lambda_1^\infty(0) > \frac{a_1^2 - a_2^2}{a_1 D_1 - a_2 D_2}. \quad (6.19)$$

Remark. We may interpret (6.17) and (6.19) as saying that the geometry of the habitat Ω is such that very little of its interior is effectively buffered from the hostility of exterior. It is important to recognize that both the size and the shape of the habitat factor into the value $\lambda_1^\infty(0)$.

Examples. We shall now illustrate Theorems 6.1 and 6.2 with examples based on parameter values that might be plausible for small mammals; see Okubo et al. (1989). We shall assume that the parameters in (2.6) are

$$r_1 = 1.5 \text{ yr}, \quad B_1 = 1.0, \quad K_1 = 60 \text{ individuals/km}^2 \quad (6.20)$$

$$r_2 = 1.0 \text{ yr}, \quad B_2 = 1.0, \quad K_2 = 40 \text{ individuals/km}^2$$

so that under the rescaling (2.10) we have

$$a_1 = 1.5, \quad b_1 = 1.0, \quad a_2 = 1.0, \quad b_2 = 1.0. \quad (6.21)$$

For these parameter values species 1 would exclude species 2 in a closed homogeneous environment, since $\bar{b}_1(0) = 1.5 > 1 = b_1 = b_2 > 2/3 = \bar{b}_2(0)$. What happens as the exterior hostility increases and/or there is greater dispersal across the boundary depends on the diffusion coefficients. We first consider the hypotheses (6.1) and (6.9) of Theorems 6.1 and 6.2 respectively. For (6.1) to hold for a_1, a_2 as in (6.21) requires $1 < D_1/D_2 < 1.5$; for (6.9) to hold requires $D_1/D_2 > 1.5$. Thus, the scenario corresponding to the coefficients in (6.21) shifts from that described by Theorem 6.1 to that described by Theorem 6.2 when $D_1 = 1.5D_2$.

To illustrate Theorem 6.1, suppose that

$$D_1 = 1.0 \text{ km}^2/\text{yr}, \quad D_2 = 0.75 \text{ km}^2/\text{yr}. \quad (6.22)$$

Hypothesis (6.1) is satisfied under (6.21) and (6.22), provided $\alpha_1 > \alpha_2$. For simplicity, let us assume that species 2 is four times as susceptible to mortality in the hostile exterior as species 1 and that the diffusion rates of both species are the same inside and outside of the patch. In

that case we have $c_2 = 4c_1$ in (2.11) so that $\alpha_1 = 2\alpha_2 \geq \alpha_2$. Under these hypotheses Theorem 6.1 will hold provided $a_2/D_2 > \lambda_1^\infty(0)$, i.e. $4/3 > \lambda_1^\infty(0)$. To examine what this last requirement means, note that for a square with area A we have $\lambda_1^\infty(0) = 2\pi^2/A$. Thus, if A is the area in km^2 of a square patch, Theorem 6.1 will hold if $A > 3\pi^2/2 \approx 14 \text{ km}^2$. (This is the smallest square that could support species 2 in the case of a boundary that is immediately lethal, i.e. as $\beta \rightarrow \infty$.) More generally, for a rectangle whose area is A and whose sides have ratio S , $\lambda_1^\infty(0) = \pi^2(\sqrt{S} + 1/\sqrt{S})/A$. Thus, if the rectangle is four times as long as it is wide we would need $A > 27\pi^2/8 \approx 33 \text{ km}^2$. (The requirement that $a_2/D_2 > \lambda_1^\infty(0)$ is needed to insure that species 2 can persist in the absence of species 1 as $\beta \rightarrow \infty$.) Under the above assumptions Theorem 6.1 implies that $\bar{b}_1 > 1.5 > 1 = b_1 = b_2 = 1 > 0.67 > \bar{b}_2$ for all values of β . Thus, species 1 can always invade a patch inhabited by species 2, but species 2 can never invade a patch inhabited by species 1. Suppose that A is chosen so that $\lambda_1^\infty(0) = 1$; if the patch is a square this would require $A = 2\pi^2 \approx 20$. Then by Theorem 6.1 we would have $\bar{b}_1(\infty) \geq 2$ and $\bar{b}_2(\infty) \leq 0.5$.

To illustrate Theorem 6.2 we need only change D_2 . Suppose that

$$D_1 = 1.0 \text{ km}^2/\text{yr} \quad \text{and} \quad D_2 = 0.25 \text{ km}^2/\text{yr}. \quad (6.23)$$

In this case Theorem 6.2 holds provided that $a_1/D_1 = 1.5 > \lambda_1^\infty(0)$. In the case of a square patch that will be true if $A \geq 4\pi^2/3 \approx 13 \text{ km}^2$. Under these hypotheses we have $\bar{b}_1(0) = 1.5 > 1 = b_1 = b_2 = 1 > 2/3 = \bar{b}_2(0)$. However, if we take A so that $\lambda_1^\infty(0) = 1$ (for a square this means $A \approx 20$), we have $\bar{b}_1(\infty) \leq 2/3 < 1 = b_1 = b_2 = 1 < 3/2 \leq \bar{b}_2(\infty)$. Thus in this case, species 1 excludes species 2 when $\beta = 0$ but as $\beta \rightarrow \infty$ species 2 can invade a patch inhabited by species 1 and species 1 cannot invade a patch inhabited by species 2, so the balance of competition has shifted.

In cases where $\lambda_1^\infty(0)$ is too large to satisfy (6.1) or (6.9), one or both populations will be unable to persist alone as $\beta \rightarrow \infty$. This would lead to the type of situation illustrated in Fig. 4.1 if $a_1/D_1 > a_2/D_2$, and to the same thing with the roles of the two species reversed if $a_2/D_2 > a_1/D_1$.

Since the outcome of competition depends not just on \bar{b}_1 and \bar{b}_2 but on how b_1 and b_2 are related to \bar{b}_1 and \bar{b}_2 , there are various other possible scenarios which might occur. For example, if b_1 and b_2 are sufficiently small and the patch is sufficiently large the two species will coexist for all values of β . Our results on the behavior of \bar{b}_1 and \bar{b}_2 could be used to analyze many of the possible scenarios, but we shall not attempt to do that here.

7 Summary and conclusions

This work formalizes one mechanism through which habitat disruption can fundamentally alter the nature of species interactions. Specifically, we have shown here how habitat degradation outside of a nature preserve might have devastating impacts on competitive relationships of species inside the preserve. We modeled the dynamics of two competing species using a coupled pair of diffusive Lotka–Volterra competition equations applicable to one, two or three dimensional reserves. Including Robin (mixed) boundary conditions in our PDE system allowed us to study the impacts of matrix degradation through a tunable “hostility” parameter that reflected species mortality rates in the matrix. We formulated a measure of the threshold capacity of each species to persist in the face of competition from the other species and found that these competitive thresholds varied with increasing matrix hostility. Consequently, the numerical range of competition coefficients over which one species is competitive dominant and the other inferior grew or shrank as matrix quality deteriorated. Perhaps the most startling result is that degradation of the exterior habitat was often sufficient to bring about a competitive reversal *inside* the preserve. Whether or not the competitive reversal occurred depended on the intensity of the two species’ competitive interactions, their rates of reproduction and dispersal inside the preserve, and the geometry of the preserve itself.

Our analyses here were motivated by the fact that ecologists are increasingly concerned about the preservation of species *interactions* (as well as species’ abundances) in habitats disturbed by human activities (e.g., Janzen 1983, 1986; Klein 1989; Aizen and Feinsinger 1994). From a management standpoint, our work suggests just how difficult it may be to maintain the basic nature of species interactions when degraded matrix habitat is an important part of the landscape. It is worth noting at this point that the concepts and methodology outlined here in the context of two species diffusive Lotka–Volterra competition can in principle be extended not only to competitive interactions other than Lotka–Volterra but also to other types of species interactions such as predation or even sometimes mutualism. In the case of a diffusive Lotka–Volterra predator–prey system, preliminary investigation indicates a rather complex response of the long term dynamics of the system to increased degradation of matrix habitat.

One potential solution is to devise reserves large enough to reduce residents’ contacts with the hostile matrix habitat. The tradeoff, of course, is that a single large reserve may preclude protection of different species elsewhere. Alternatively, some researchers have suggested

“buffer zones” (regions surrounding nature preserves designed to lessen the influences of human impacts) as one possible solution. However, buffer zones themselves may generate similar disruptive effects on species interaction if reserve inhabitants exhibit differential abilities to utilize the surrounding habitat for reproduction or feeding (Janzen 1983; Cantrell and Cosner 1993).

Here, we have focused on scenarios in which human activities alter habitat “quality” by increasing mortality risk. However, human-caused habitat disruption can impact sets of interacting species through a diversity of mechanisms. For instance, in many ecosystems, some species are less willing than others to cross particular habitat boundaries. Among other attributes, these differential boundary responses can depend on species’ habitat usage (e.g., arboreal vs. terrestrial mammals (Laurence 1991)), species evolutionary milieu (native vs. exotic pollinators (Aizen and Feinsinger 1994)), or even something as subtle as temporally varying predation risk (rodent foraging at edges linked to moon phases (Bowers and Dooley 1993)). In such cases, non-dispersing species (and species intimately linked to non-dispersing species through pollination predation, etc.) could be at a distinct disadvantage in ecosystems where patch edges are abundant. These kinds of asymmetries in species responses to habitat changes set the stage for disrupting whole suites of biological interactions, many of which may have coevolved (Lovejoy et al. 1983; Bierregaard et al. 1992). Consequently, the impacts of human modifications to natural habitats are likely to be quite complex and extend much further than “simple” changes in the abundance of a particular favored species.

Because habitat destruction, fragmentation, and degradation are continuing at an unprecedented rate, there is a pressing need for research relating such complicated spatial processes to the dynamics of interacting species. In this regard, theory addressing the roles of habitat boundaries and patchiness to species interactions can help formalize verbal arguments and outline new areas for field workers. In many of these situations, approaches similar to the “patch-and-boundary” model presented here could be instructive as we strive to understand how human habitat modifications alter species interactions.

Appendix A

Proof of Theorem 3.1

The operator $-D\nabla^2 u + c(x)u$ in Ω , where $c(x) \geq 0$, enjoys the same properties when it is supplemented by Robin boundary data,

$\nabla u \cdot \eta + \beta u$ on $\partial\Omega$, $\beta \geq 0$, as it does when it is supplemented by Dirichlet boundary data. Several properties are pertinent to the present discussion. First of all, boundary value problems of the form

$$-D\nabla^2 u + c(x)u = f(x) \quad \text{in } \Omega \quad \nabla u \cdot \eta + \beta u = \phi(x) \quad \text{on } \partial\Omega \quad (\text{A.1})$$

are uniquely solvable with $u \in C^{2,\alpha}(\bar{\Omega})$ provided $f \in C^\alpha(\bar{\Omega})$ and $\phi \in C^{1,\alpha}(\partial\Omega)$ (Gilbarg and Trudinger 1977). Second, if $\phi(x) \equiv 0$ and $f(x) \geq 0$, then $u > 0$ in Ω ; i.e., the operator admits a maximum principle (Protter and Weinberger 1967). As a consequence, the eigenvalue problem

$$\begin{aligned} -D\nabla^2 w + c(x)w &= \sigma w \quad \text{in } \Omega \\ \nabla w \cdot \eta + \beta w &= 0 \quad \text{on } \partial\Omega \end{aligned} \quad (\text{A.2})$$

has a principal eigenvalue; i.e., there is a unique σ (which is in fact positive) for which (A.2) admits a positive solution (Hess 1991). Moreover, this eigenvalue can be realized variationally as in (Courant and Hilbert 1953).

We first establish that the maps $\beta \rightarrow u_1^*(\beta)$ and $\beta \rightarrow u_2^*(\beta)$ are differentiable on $[0, \infty)$. We consider $u_1^*(\beta)$. Define a map $\Phi: C^{2,\alpha}(\bar{\Omega}) \times [0, \infty) \rightarrow C^\alpha(\bar{\Omega}) \times C^{1,\alpha}(\partial\Omega)$ by

$$\Phi(u, \beta) = (D_1 \nabla^2 u + (a_1 - u)u, \alpha_1 \nabla u \cdot \eta + \beta u). \quad (\text{A.3})$$

Then

$$\left[\frac{\partial}{\partial u} \Phi(u, \beta) \right] w = (D_1 \nabla^2 w + (a_1 - 2u)w, \alpha_1 \nabla w \cdot \eta + \beta w). \quad (\text{A.4})$$

Suppose now for some $\beta \geq 0$ that $u = u_1^*(\beta)$, as defined in (2.14)–(2.15). Then $\Phi(u, \beta) = 0$. Moreover, the definition of $u_1^*(\beta)$ forces the principal eigenvalue in

$$\begin{aligned} -D_1 \nabla^2 w + (u_1^*(\beta) - a_1)w &= \lambda w \quad \text{in } \Omega \\ \alpha_1 \nabla w \cdot \eta + \beta w &= 0 \quad \text{on } \partial\Omega \end{aligned}$$

to be 0. Consequently, because $u_1^*(\beta) > 0$ in Ω , the principal eigenvalue in

$$\begin{aligned} -D_1 \nabla^2 w + (2u_1^*(\beta) - a_1)w &= \lambda w \quad \text{in } \Omega \\ \alpha_1 \nabla w \cdot \eta + \beta w &= 0 \quad \text{on } \partial\Omega \end{aligned}$$

is positive. It follows that $\left[\frac{\partial}{\partial \beta} \Phi(u_1^*(\beta), \beta) \right]$ is a linear homeomorphism and the differentiability of $u_1^*(\beta)$ follows from the implicit function theorem. A precisely analogous argument gives the result for $u_2^*(\beta)$.

Now consider the linear problem

$$\begin{aligned} D_1 \nabla \phi + [a_1 - b_1 u_2^*(\beta)] &= 0 \quad \text{in } \Omega \\ \alpha_1 \nabla \phi \cdot \eta + \beta \phi &= 0 \quad \text{on } \partial \Omega. \end{aligned} \quad (\text{A.5})$$

Define a map $\psi: C^{2,\alpha}(\bar{\Omega}) \times [0, \infty) \times [0, \infty) \rightarrow C^\alpha(\bar{\Omega}) \times \mathbb{R} \times C^{1,\alpha}(\partial \Omega)$ by

$$\psi(\phi, b, \beta) = \left(D_1 \nabla^2 \phi + (a_1 - b u_2^*(\beta)) \phi, \int_\Omega \phi^2 - 1, \alpha_1 \nabla \phi \cdot \eta + \beta \phi \right) \quad (\text{A.6})$$

Then

$$\begin{aligned} \left[\frac{\partial \Psi}{\partial(\phi, b)}(\phi, b, \beta) \right](\rho, c) \\ = \left(D_1 \nabla^2 \rho + (a_1 - b u_2^*(\beta)) \rho - c u_2^*(\beta) \phi, 2 \int_\Omega \phi \rho, \alpha_1 \nabla \rho \cdot \eta + \beta \rho \right) \end{aligned} \quad (\text{A.7})$$

Let $(\phi, b, \beta) = (\phi_1(b), \bar{b}_1(\beta), \beta)$. Then $\psi(\phi, b, \beta) = 0$. If now $\left[\frac{\partial \Psi}{\partial(\phi, b)} \psi(\phi, b, \beta) \right](\rho, c) = 0$, then

$$D_1 \nabla^2 \rho + (a_1 - \bar{b}_1 u_2^*(\beta)) \rho - c u_2^*(\beta) \phi = 0 \quad (\text{A.8})$$

$$\int_\Omega \phi \rho = 0 \quad (\text{A.9})$$

$$\alpha_1 \nabla \rho \cdot \eta + \beta \rho = 0. \quad (\text{A.10})$$

Because $D_1 \nabla \phi + [a_1 - \bar{b}_1 u_2^*(\beta)] \phi = 0$ in Ω with $\alpha_1 \nabla \phi \cdot \eta + \beta \phi = 0$ on $\partial \Omega$ and $\phi > 0$ in Ω , (A.8) and (A.10) are solvable only if $\int_\Omega (c u_2^*(\beta) \phi) \phi = 0$. Since $u_2^*(\beta) > 0$ in Ω and $\phi > 0$ in Ω , $c = 0$. In that case, (A.8) and (A.10) imply that $\rho = k \phi$ where k is a constant. But then (A.9) implies that $k \int_\Omega \phi^2 = 0$, hence $k = 0$. So $\left[\frac{\partial \Psi}{\partial(\phi, b)}(\phi, b, \beta) \right]$ is injective.

Now consider

$$D_1 \nabla^2 \rho + [a_1 - b u_2^*(\beta)] \rho + c u_2^*(\beta) \phi = f \quad (\text{A.11})$$

$$\int_\Omega \rho \phi = g \quad (\text{A.12})$$

$$\alpha_1 \nabla \rho \cdot \eta + \beta \rho = h \quad (\text{A.13})$$

where $f \in C^\alpha(\bar{\Omega})$, $g \in \mathbb{R}$, and $h \in C^{1,\alpha}(\partial \Omega)$. The Fredholm alternative implies that (A.11) and (A.13) will have a solution ρ provided $f - c u_2^*(\beta) \phi$ is orthogonal to ϕ in $L^2(\Omega)$. Consequently, (A.11) and (A.13) may be solved if

$$\int_\Omega f \phi = c \int_\Omega u_2^*(\beta) \phi^2. \quad (\text{A.14})$$

From (A.14), we require

$$c = \frac{\int_\Omega f \phi}{\int_\Omega u_2^*(\beta) \phi^2}.$$

If ρ_0 is a solution of (A.11) and (A.13), so is $\rho_0 + k \phi$ where k is a constant. For such a solution to also solve (A.12) we need $\int_\Omega \rho_0 \phi + k \int_\Omega \phi^2 = g$. As $\phi > 0$ in Ω , we can solve to get

$$k = \frac{g - \int_\Omega \rho_0 \phi}{\int_\Omega \phi^2}.$$

Consequently, $\left[\frac{\partial \Psi}{\partial(\phi, b)}(\phi, b, \beta) \right]$ is surjective. The implicit function theorem guarantees that $\phi_1(\beta)$ and $\bar{b}_1(\beta)$ are differentiable in β on $[0, \infty)$.

To extend the result to the case $\beta = \infty$, i.e., the Dirichlet case, rewrite the boundary condition as $\alpha_1 \gamma \nabla u \cdot \eta + u = 0$ where $\gamma = \frac{1}{\beta}$ and argue as before.

Proof of Theorem 3.2

(i) Let ψ_i denote a positive eigenfunction for (3.5) corresponding to $\lambda_1^i(q_i)$. Then

$$-\nabla^2 \psi_1 + q_1 \psi_1 = \lambda_1^i(q_1) \psi_1 \quad \text{in } \Omega \quad (\text{A.15})$$

and

$$-\nabla^2 \psi_2 + q_2 \psi_2 = \lambda_1^i(q_2) \psi_2 \quad \text{in } \Omega \quad (\text{A.16})$$

with $\nabla \psi_i \cdot \eta + \gamma \psi_i = 0$ on $\partial \Omega$, $i = 1, 2$. Multiply (A.15) by ψ_2 and (A.16) by ψ_1 , integrate over Ω and subtract. We obtain

$$\begin{aligned} - \int_\Omega [\psi_2 \nabla^2 \psi_1 - \psi_1 \nabla^2 \psi_2] + \int_\Omega (q_1 - q_2) \psi_1 \psi_2 \\ = [\lambda_1^i(q_1) - \lambda_1^i(q_2)] \int_\Omega \psi_1 \psi_2. \end{aligned} \quad (\text{A.17})$$

Green's Second Identity yields

$$\begin{aligned} \int_\Omega [\psi_2 \nabla^2 \psi_1 - \psi_1 \nabla^2 \psi_2] &= \int_{\partial \Omega} \psi_2 \nabla \psi_1 \cdot \eta - \psi_1 \nabla \psi_2 \cdot \eta \\ &= \int_{\partial \Omega} [\psi_2 (-\gamma \psi_1) - \psi_1 (-\gamma \psi_2)] \\ &= 0. \end{aligned}$$

Consequently, (A.17) reduces to

$$\int_{\Omega} (q_1 - q_2) \psi_1 \psi_2 = [\lambda_1^\gamma(q_1) - \lambda_1^\gamma(q_2)] \int_{\Omega} \psi_1 \psi_2. \quad (\text{A.18})$$

Part (i) follows readily from (A.18).

(ii) Let ψ_i now denote a positive eigenfunction for (3.5) corresponding to $\lambda_1^\gamma(q)$. Proceeding in a manner analogous to the proof of (i), we obtain

$$(\gamma_1 - \gamma_2) \int_{\partial\Omega} \psi_1 \psi_2 = [\lambda_1^{\gamma_1}(q) - \lambda_1^{\gamma_2}(q)] \int_{\Omega} \psi_1 \psi_2. \quad (\text{A.19})$$

Part (ii) is now immediate from (A.19).

Proof of Theorem 3.3

(i) Let θ_a^γ be as in (3.6). Suppose that $a' > a > \lambda_1^\gamma(0)$ for some fixed $\gamma \geq 0$. Then

$$\begin{aligned} -\nabla^2 \theta_a &= \theta_a(a - \theta_a) \\ &\leq \theta_a(a' - \theta_a) \end{aligned}$$

in Ω , with $\nabla \theta_a \cdot \eta + \gamma \theta_a = 0$ on $\partial\Omega$. Consequently, θ_a is a strict lower solution to

$$\begin{aligned} -\nabla^2 u &= u(a' - u) \quad \text{in } \Omega \\ \nabla u \cdot \eta + \gamma u &= 0 \quad \text{on } \partial\Omega. \end{aligned} \quad (\text{A.20})$$

Because any constant larger than a' is an upper solution to (A.20), we have $\theta_a^\gamma \leq \theta_a$ in Ω by the method of upper and lower solutions.

Now consider $\gamma' > \gamma \geq 0$ and assume $a > \lambda_1^{\gamma'}(0)$. Recall that $\lambda_1^{\gamma'}(0) > \lambda_1^\gamma(0)$, so that $a > \lambda_1^\gamma(0)$ as well. Then $\theta_a^{\gamma'}$ satisfies

$$\begin{aligned} -\nabla^2 \theta_a^{\gamma'} &= \theta_a^{\gamma'}(a - \theta_a^{\gamma'}) \quad \text{in } \Omega \\ \nabla \theta_a^{\gamma'} \cdot \eta + \gamma' \theta_a^{\gamma'} &= 0 \quad \text{on } \partial\Omega \end{aligned} \quad (\text{A.21})$$

The boundary condition in (A.21) yields

$$\nabla \theta_a^{\gamma'} \cdot \eta + \gamma \theta_a^{\gamma'} = (\gamma - \gamma') \theta_a^{\gamma'}$$

which is negative. Hence $\theta_a^{\gamma'}$ is a strict lower solution to

$$\begin{aligned} -\nabla^2 u &= u(a - u) \quad \text{in } \Omega \\ \nabla u \cdot \eta + \gamma u &= 0 \quad \text{on } \partial\Omega. \end{aligned} \quad (\text{A.22})$$

Because, once again, any constant larger than a is an upper solution to (A.22), $\theta_a^{\gamma'} < \theta_a^\gamma$ in Ω by the method of upper and lower solutions.

(ii) An application of the maximum principle (Protter and Weinberger 1967) as in (Cantrell and Cosner 1989, p. 301) readily yields this result.

(iii) By (3.6), θ_a^γ satisfies

$$\begin{aligned} -\nabla^2 u + \theta_a^\gamma u &= au \quad \text{in } \Omega \\ \nabla u \cdot \eta + \gamma u &= 0 \quad \text{on } \partial\Omega. \end{aligned}$$

Because $\theta_a^\gamma > 0$, it now follows from (3.5) that $a = \lambda_1^\gamma(\theta_a^\gamma)$.

(iv) By definition $u_i^* = u_i^*(\beta)$ is the unique positive equilibrium solution to (2.14)–(2.15). Consequently,

$$\begin{aligned} -D_i \nabla^2 u_i^* &= u_i^*(a_i - u_i^*) \quad \text{in } \Omega \\ \nabla u_i^* \cdot \eta + \frac{\beta}{\alpha_i} u_i^* &= 0 \quad \text{on } \partial\Omega. \end{aligned}$$

If we divide both sides of the top equation by D_i^2 and both sides of the bottom equation by D_i , we have

$$\begin{aligned} -\nabla^2 \left(\frac{u_i^*}{D_i} \right) &= \left(\frac{u_i^*}{D_i} \right) \left(\frac{a_i}{D_i} - \frac{u_i^*}{D_i} \right) \quad \text{in } \Omega \\ \nabla \left(\frac{u_i^*}{D_i} \right) \cdot \eta + \frac{\beta}{\alpha_i} \left(\frac{u_i^*}{D_i} \right) &= 0 \quad \text{on } \partial\Omega. \end{aligned}$$

It now follows from (3.6) that $u_i^*(\beta) = D_i \theta_{a_i/D_i}^{\beta/\alpha_i}$.

Proof of Theorem 3.4

(i) Let us first consider the defining equations for $\lambda_1^\gamma(e\theta_a^\gamma)$ namely

$$\begin{aligned} -\nabla^2 \psi_e + e\theta_a^\gamma \psi_e &= \lambda_1^\gamma(e\theta_a^\gamma) \psi_e \quad \text{in } \Omega \\ \nabla \psi_e \cdot \eta + \gamma \psi_e &= 0 \quad \text{on } \partial\Omega \end{aligned} \quad (\text{A.23})$$

where we normalize ψ_e by the assumption that $\int_{\Omega} \psi_e^2 = 1$. Fix a value $e_1 > 0$ and let $e_2 \geq 0$ be another value of e . Multiply the first equation in (A.23) for $e = e_1$ by ψ_{e_2} . Then integrate to obtain

$$\lambda_1^\gamma(e_1 \theta_a^\gamma) \int_{\Omega} \psi_{e_1} \psi_{e_2} = \int_{\Omega} \psi_{e_2} (-\nabla^2 \psi_{e_1}) + e_1 \int_{\Omega} \theta_a^\gamma \psi_{e_1} \psi_{e_2}. \quad (\text{A.24})$$

Green's Second Identity implies that

$$\begin{aligned} \int_{\Omega} \psi_{e_2} (-\nabla^2 \psi_{e_1}) - (-\nabla^2 \psi_{e_2}) \psi_{e_1} &= \int_{\partial\Omega} \psi_{e_2} (-\nabla \psi_{e_1} \cdot \eta) - (-\nabla \psi_{e_2} \cdot \eta) \psi_{e_1} \\ &= \int_{\partial\Omega} \gamma \psi_{e_1} \psi_{e_2} - \gamma \psi_{e_1} \psi_{e_2} \\ &= 0 \end{aligned}$$

Consequently, (A.24) becomes

$$\begin{aligned} \lambda_1^\gamma(e_1 \theta_a^\gamma) \int_{\Omega} \psi_{e_1} \psi_{e_2} &= \int_{\Omega} (-\nabla^2 \psi_{e_2}) \psi_{e_1} + e_1 \int_{\Omega} \theta_a^\gamma \psi_{e_1} \psi_{e_2} \\ &= \lambda_1^\gamma(e_2 \theta_a^\gamma) \int_{\Omega} \psi_{e_1} \psi_{e_2} - e_2 \int_{\Omega} \theta_a^\gamma \psi_{e_1} \psi_{e_2} + e_1 \int_{\Omega} \theta_a^\gamma \psi_{e_1} \psi_{e_2}. \end{aligned}$$

Hence we obtain that

$$[\lambda_1^\gamma(e_1 \theta_a^\gamma) - \lambda_1^\gamma(e_2 \theta_a^\gamma)] \int_{\Omega} \psi_{e_1} \psi_{e_2} = (e_1 - e_2) \int_{\Omega} \theta_a^\gamma \psi_{e_1} \psi_{e_2}. \quad (\text{A.25})$$

Now set $e_1 = e$ and $e_2 = 0$ in (A.25). Then

$$[\lambda_1^\gamma(e \theta_a^\gamma) - \lambda_1^\gamma(0)] \int_{\Omega} \psi_e \psi_0 = e \int_{\Omega} \theta_a \psi_e \psi_0.$$

Theorem 3.3(ii) guarantees that $\theta_a \leq a$. Consequently,

$$\lambda_1^\gamma(e \theta_a^\gamma) \int_{\Omega} \psi_e \psi_0 \leq \lambda_1^\gamma(0) \int_{\Omega} \psi_e \psi_0 + ae \int_{\Omega} \psi_e \psi_0,$$

from which it follows that

$$\lambda_1^\gamma(e \theta_a^\gamma) \leq \lambda_1^\gamma(0) + ae. \quad (\text{A.26})$$

It is important to recognize that the two critical elements in establishing (A.26) are having ψ_{e_1} and ψ_{e_2} satisfy the same boundary condition (so that $\int_{\partial\Omega} \psi_{e_2} (\nabla \psi_{e_1} \cdot \eta) = \int_{\partial\Omega} \psi_{e_1} (\nabla \psi_{e_2} \cdot \eta)$) and knowing that $\theta_a^\gamma \leq a$. These elements continue to hold if we consider $\lambda_1^{\gamma_2}(e \theta_a^{\gamma_2})$ in place of $\lambda_1^\gamma(e \theta_a^\gamma)$, and as a consequence, so does the analysis leading to (A.26). Hence we have that

$$\lambda_1^{\gamma_2}(e \theta_a^{\gamma_2}) \leq \lambda_1^{\gamma_2}(0) + ae \quad (\text{A.27})$$

whenever $0 \leq \gamma_1 \leq \gamma_2$ and $e > 0$, establishing the right inequality in both (3.7) and (3.8).

Now return to (A.25). Dividing by $(e_1 - e_2) \int_{\Omega} \psi_{e_1} \psi_{e_2}$ yields

$$\frac{\lambda_1^\gamma(e_1 \theta_a^\gamma) - \lambda_1^\gamma(e_2 \theta_a^\gamma)}{e_1 - e_2} = \frac{\int_{\Omega} \theta_a^\gamma \psi_{e_1} \psi_{e_2}}{\int_{\Omega} \psi_{e_1} \psi_{e_2}}. \quad (\text{A.28})$$

An argument similar to that for Theorem 3.1 shows that ϕ_e is continuous in e . Consequently, we may pass to the limit as $e_2 \rightarrow e_1$ in (A.28) to obtain

$$\frac{d}{de_1} [\lambda_1^\gamma(e_1 \theta_a^\gamma)] = \int_{\Omega} \theta_a^\gamma \psi_{e_1}^2 > 0. \quad (\text{A.29})$$

It follows from Theorem 3.3(iii) that $\lambda_1^\gamma(e \theta_a^\gamma) < a$ when $0 < e < 1$ and $\lambda_1^\gamma(e \theta_a^\gamma) > a$ when $e > 1$.

Next notice that we may rewrite (A.23) as

$$e \theta_a^\gamma \psi_e = \nabla^2 \psi_e + \lambda_1^\gamma(e \theta_a^\gamma) \psi_e \quad (\text{A.30})$$

Multiplying (A.30) by ψ_e and dividing by e yields

$$\theta_a^\gamma \psi_e^2 = \frac{1}{e} [\psi_e \nabla^2 \psi_e + \lambda_1^\gamma(e \theta_a^\gamma) \psi_e^2].$$

Integrating this result, we obtain from (A.29) that

$$\begin{aligned} \frac{d}{de} \{\lambda_1^\gamma(e \theta_a^\gamma)\} &= \int_{\Omega} \theta_a^\gamma \psi_e^2 \\ &= \frac{1}{e} \int_{\Omega} \psi_e \nabla^2 \psi_e + \lambda_1^\gamma(e \theta_a^\gamma) \int_{\Omega} \psi_e^2 \\ &= \frac{1}{e} \left[\lambda_1^\gamma(e \theta_a^\gamma) + \int_{\Omega} \psi_e \nabla^2 \psi_e \right] \\ &= \frac{1}{e} \left[\lambda_1^\gamma(e \theta_a^\gamma) + \int_{\partial\Omega} \psi_e \nabla \psi_e \cdot \eta - \int_{\Omega} |\nabla \psi_e|^2 \right] \\ &= \frac{1}{e} \left[\lambda_1^\gamma(e \theta_a^\gamma) - \int_{\partial\Omega} \gamma \psi_e^2 - \int_{\Omega} |\nabla \psi_e|^2 \right] \end{aligned} \quad (\text{A.31})$$

The variational characterization of $\lambda_1^\gamma(0)$ (Courant and Hilbert 1953) guarantees that

$$\int_{\Omega} |\nabla \psi_e|^2 + \gamma \int_{\partial\Omega} \psi_e^2 \geq \lambda_1^\gamma(0)$$

so that (A.31) yields

$$\frac{d}{de} \{\lambda_1^\gamma(e \theta_a^\gamma)\} - \frac{1}{e} \lambda_1^\gamma(e \theta_a^\gamma) \leq -\frac{1}{e} \lambda_1^\gamma(0). \quad (\text{A.32})$$

Proceeding as in (Cantrell and Cosner 1987), we obtain from (A.32) that

$$\frac{e \frac{d}{de} \{\lambda_1 \gamma(e\theta_a^\gamma)\} - \lambda_1^\gamma(e\theta_a^\gamma)}{e^2} \leq \frac{-\lambda_1^\gamma(0)}{e^2}$$

or equivalently that

$$\frac{d}{de} \left\{ \frac{\lambda_1^\gamma(e\theta_a^\gamma)}{e} \right\} \leq \frac{d}{de} \left\{ \frac{\lambda_1^\gamma(0)}{e} \right\} \quad (\text{A.33})$$

Now assume that $0 < e < 1$. Integrate (A.33) from e to 1 to obtain

$$\lambda_1^\gamma(\theta_a^\gamma) - \frac{\lambda_1^\gamma(e\theta_a^\gamma)}{e} \leq \lambda_1^\gamma(0) - \frac{\lambda_1^\gamma(0)}{e}. \quad (\text{A.34})$$

Since $\lambda_1^\gamma(\theta_a^\gamma) = a$ by Theorem 3.3(iii), (A.34) can be rewritten

$$ae + (1 - e)\lambda_1^\gamma(0) \leq \lambda_1^\gamma(e\theta_a^\gamma) \quad (\text{A.35})$$

if $0 < e < 1$.

Now let $0 \leq \gamma_1 \leq \gamma_2$ and consider $\lambda_1^{\gamma_2}(e\theta_a^{\gamma_1})$. Theorem 3.3(i) implies that $\theta_a^{\gamma_2} \leq \theta_a^{\gamma_1}$ in Ω , so that

$$\lambda_1^{\gamma_2}(e\theta_a^{\gamma_2}) \leq \lambda_1^{\gamma_2}(e\theta_a^{\gamma_1}). \quad (\text{A.36})$$

If $e \in (0, 1)$, the left hand inequality in (3.7) follows now from (A.35) and (A.36). If $e > 1$, the left hand inequality in (3.8) follows from (A.29) and (A.36).

(ii) Note that $\lambda_1^{\gamma_1}(e\theta_a^{\gamma_2}) \leq \lambda_1^{\gamma_1}(e\theta_a^{\gamma_1})$ by the same reasoning as for (A.36). Since (A.29) implies $\lambda_1^{\gamma_1}(e\theta_a^{\gamma_2}) < a$ if $e < 1$, (3.9) follows.

To obtain (3.10), consider (A.33) once more. Assume $e > 1$, and integrate between 1 and e to obtain

$$\frac{\lambda_1^\gamma(e\theta_a^\gamma)}{e} - \lambda_1^\gamma(\theta_a^\gamma) \leq \frac{\lambda_1^\gamma(0)}{e} - \lambda_1^\gamma(0). \quad (\text{A.37})$$

Using the fact that $\lambda_1^\gamma(\theta_a^\gamma) = a$, we may rewrite (A.37) as

$$\lambda_1^\gamma(e\theta_a^\gamma) \leq ae + (1 - e)\lambda_1^\gamma(0). \quad (\text{A.38})$$

Since $\lambda_1^{\gamma_1}(e\theta_a^{\gamma_2}) \leq \lambda_1^{\gamma_1}(e\theta_a^{\gamma_1})$, (3.10) is now immediate.

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