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Multiple Reversals of Competitive Dominance in Ecological Reserves via External Habitat Degradation*

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In this article we continue an examination of the consequences of habitat degradation on species interactions begun by Cantrell, Cosner and Fagan in Cantrell et al., *J. Math. Biol. 37*, 491–533 (1998). In Cantrell et al., *J. Math. Biol. 37*, 491–533 (1998), two competing species were thought to inhabit a pristine patch of habitat surrounded by "matrix" habitat whose level of degradation is variable. The dynamics of the species interactions was modeled by diffusive Lotka–Volterra competition equations in the patch supplemented by Robin boundary conditions on the interface between the pristine patch and the matrix habitat. Habitat degradation was incorporated into the model via a tunable hostility parameter in the boundary conditions. Analysis of the model showed that it is possible for a species to be competitively dominant in the pristine patch when the surrounding environs are only mildly unfavorable but to lose this advantage and be competitively inferior in the patch when matrix hostility is severe. In this article we address the question of just how delicately competitive advantage within the pristine patch depends on the level of degradation in the environs surrounding the pristine patch. We show that it is indeed possible for competitive advantage to reverse more than once as the level of degradation in the matrix habitat increases and also examine the effects thereof on the number and nature of equilibria through a detailed bifurcation analysis.

KEY WORDS: Reaction-diffusion; Lotka–Volterra; competition; bifurcation; population dynamics; competitive advantage.

1. INTRODUCTION

Predicting the consequences of habitat fragmentation and other spatial processes for ecological systems requires an understanding of the

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*Dedicated to Professor Shui-Nee Chow on the occasion of his 60th birthday.

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mechanisms through which those processes act locally. Habitat edges are natural byproducts of the process of fragmentation which serve to modify species interactions and hence ultimately, community composition and structure. Recently, Cantrell, Cosner and Fagan have been studying different avenues through which habitat edges change species interactions. In [6], they identified four principal ways by which edges may effect species interactions:

1. by alteration of species' moving patterns,
2. by differential induction of species' mortality,
3. through cross-boundary subsidies,
4. by the creation of novel opportunities for species interactions.

In further work [3–5,7], they employed reaction-diffusion models motivated by empirical examples to illustrate and explore these categories of edge-mediated effects.

As an example, in [4], Cantrell, Cosner and Fagan demonstrated how degrading the quality of the "matrix" habitat surrounding a habitat patch could reverse the nature of competitive two-species dynamics inside the patch so that a normally "inferior" species out competes a "superior" one. The model employed in [4] was a diffusive Lotka–Volterra model for two-species competition in a bounded habitat. It may be expressed as

$$\frac{\partial u_1}{\partial t} = D_1 \Delta u_1 + u_1[a_1 - u_1 - b_1 u_2], \tag{1.1}$$

$$\frac{\partial u_2}{\partial t} = D_2 \Delta u_2 + u_2[a_2 - b_2 u_1 - u_2] \quad \text{in } \Omega \times (0, \infty),$$

$$\left(1 - \frac{\beta}{\alpha_i + \beta}\right) \Delta u_i \cdot \eta + \frac{\beta}{\alpha_i + \beta} u_i = 0 \qquad \text{on } \partial\Omega \times (0, \infty), \tag{1.2}$$

$i = 1, 2$. Here u_i represents the population density of species i and Ω represents the habitat patch in question, where Ω is a bounded domain in $\mathbb{R}^k, k \in \{1, 2, 3\}$, with smooth boundary $\partial\Omega$, and η is the outerward unit normal vector on $\partial\Omega$. The diffusion coefficients (D_i), intrinsic per capita growth rates (a_i) and competition coefficients (b_i) in (1.1) were taken to be constants in [4]. The parameters $\alpha_i > 0$ in the boundary condition (1.2) were employed to allow for a differential response to the level of hostility of the "matrix" habitat surrounding Ω, which was captured by the parameter β. The model (1.1) and (1.2) was analyzed in [4] to determine if there were conditions on the parameters D_i, a_i, b_i and α_i and the domain Ω under which its predictions regarding the outcome of the competition could be altered by increasing the level of exterior hostility by increasing β. Note that β was allowed to range from 0 to $+\infty$, with the convention that $\beta/(\alpha_i + \beta)$ takes on the value 1, when $\beta = +\infty$.

The analysis in [4] proceeded along the following lines. First of all, in any competition model, coexistence should require that each species persists in the absence of the other. Consequently, it is necessary to begin with the diffusive logistic problems

$$\begin{aligned}&\frac{\partial u_i}{\partial t} = D_i \Delta u_i + u_i[a_i - u_i] \quad \text{in } \Omega \times (0,\infty),\\&\left(1 - \frac{\beta}{\alpha_i + \beta}\right) \nabla u_i \cdot \eta + \frac{\beta}{\alpha_i + \beta} u_i = 0 \quad \text{on } \partial\Omega \times (0,\infty),\end{aligned} \tag{1.3}$$

$i = 1, 2$. The dynamics of (1.3) are well-understood (e.g., see [2]). Namely, positive solutions to (1.3) converge over time in $C^{1+\alpha}(\bar{\Omega})$ to a unique positive equilibrium solution, denoted $\theta_{\beta/(\alpha_i+\beta)}$, provided that the principal eigenvalue σ_i is positive in the problem

$$\begin{aligned}&D_i \Delta z + a_i z = \sigma_i z \quad \text{in } \Omega,\\&\left(1 - \frac{\beta}{\alpha_i + \beta}\right) \nabla z \cdot \eta + \frac{\beta}{\alpha_i + \beta} z = 0 \quad \text{on } \partial\Omega\end{aligned} \tag{1.4}$$

and converge to 0 over time if $\sigma_i \le 0$. It is a simple matter to calculate that

$$\sigma_i = a_i - D_i \lambda^1 \left(\Omega, \frac{\beta}{\alpha_i + \beta}\right), \tag{1.5}$$

where $\lambda = \lambda^1(\Omega, (\beta/(\alpha_i + \beta)))$ is the principal eigenvalue in the problem

$$\begin{aligned}&-\Delta w = \lambda w \quad \text{in } \Omega,\\&\left(1 - \frac{\beta}{\alpha_i + \beta}\right) \nabla w \cdot \eta + \frac{\beta}{\alpha_i + \beta} w = 0 \quad \text{on } \partial\Omega.\end{aligned} \tag{1.6}$$

Consequently, $\sigma_i > 0$ in (1.4) is equivalent to

$$\frac{a_i}{D_i} > \lambda^1 \left(\Omega, \frac{\beta}{\alpha_i + \beta}\right). \tag{1.7}$$

Since $\lambda^1(\Omega, (\beta/(\alpha_i + \beta)))$ is monotonically increasing in β, by (1.7) one may guarantee that (1.3) predicts persistence of each species in the absence of the other for all $\beta \in [0, \infty]$ provided

$$\frac{a_i}{D_i} > \lambda^1(\Omega, 1) \tag{1.8}$$

for $i = 1, 2$.

The globally attracting positive equilibrium solution to (1.3), which exists for any β assuming (1.8), effectively functions as a (spatially varying) carrying capacity for the species' density. It follows as in [8] that species 1 is predicted by (1.1) and (1.2) to persist if it always increases its density when it is introduced into the habitat patch Ω at low densities while species 2 is present in Ω at its carrying capacity $\theta_{\beta/(\alpha_2+\beta)}$ in the absence of species 1, and *vice versa* for species 2. Mathematically, these requirements are again expressed as having positive principal eigenvalues for suitable elliptic operators. Specifically, species 1 is expected to persist if the principal eigenvalue $\tilde{\sigma}_1$ is positive in

$$\begin{aligned} &D_1\Delta\phi_1+\left(a_1-b_1\theta_{\frac{\beta}{\alpha_2+\beta}}\right)\phi_1=\tilde{\sigma}_1\phi_1 \quad \text{in } \Omega,\\ &\left(1-\tfrac{\beta}{\alpha_1+\beta}\right)\nabla\phi_1\cdot\eta+\tfrac{\beta}{\alpha_1+\beta}\phi_1=0 \quad \text{on } \partial\Omega \end{aligned} \tag{1.9}$$

and species 2 is expected to persist if the principal eigenvalue $\tilde{\sigma}_2$ is positive in

$$\begin{aligned} &D_2\Delta\phi_2+\left(a_2-b_2\theta_{\frac{\beta}{\alpha_1+\beta}}\right)\phi_2=\tilde{\sigma}_2\phi_2 \quad \text{in } \Omega,\\ &\left(1-\tfrac{\beta}{\alpha_2+\beta}\right)\nabla\phi_2\cdot\eta+\tfrac{\beta}{\alpha_2+\beta}\phi_2=0 \quad \text{on } \partial\Omega. \end{aligned} \tag{1.10}$$

Notice now that for fixed selections of the parameters D_i, a_i, α_i and $\beta, \tilde{\sigma}_1$ and $\tilde{\sigma}_2$ are decreasing in b_1 and b_2, respectively, and indeed that there are unique values $\bar{b}_1=\bar{b}_1(D_1,D_2,a_1,a_2,\alpha_1,\alpha_2,\beta)>0$ and $\bar{b}_2=\bar{b}_2(D_1,D_2,a_1,a_2,\alpha_1,\alpha_2,\beta)>0$ so that $\tilde{\sigma}_1=0$ when $b_1=\bar{b}_1$ and $\tilde{\sigma}_2=0$ when $b_2=\bar{b}_2$. Consequently, the model (1.1) and (1.2) predicts persistence of species 1 when $b_1<\bar{b}_1$ and persistence of species 2 when $b_2<\bar{b}_2$. If $b_1>\bar{b}_1, \tilde{\sigma}_1<0$ and then species 1 tends toward extinction in (1.1) and (1.2) if the initial configuration of the ecological system is $(u_1, \theta_{\beta/(\alpha_2+\beta)})$, where $u_1 \ll 1$, with an analogous result for species 2. Thus, species 1 has a competitive advantage over species 2 whenever $b_1<\bar{b}_1$ but $b_2>\bar{b}_2$. Likewise, species 2 has the advantage if $b_2<\bar{b}_2$ but $b_1>\bar{b}_1$.

For fixed configurations of D_i, a_i and $\alpha_i, \bar{b}_1$ and $\bar{b}_2$ may now be regarded as functions of β on $[0,\infty]$. Theorem 3.1 of [4] guarantees that $\bar{b}_1(\beta)$ and $\bar{b}_2(\beta)$ are differentiable in β on $[0,\infty]$. Suppose now that

$$a_1>a_2. \tag{1.11}$$

An easy calculation reveals that

$$\bar{b}_1(0)=\frac{a_1}{a_2}>\frac{a_2}{a_1}=\bar{b}_2(0). \tag{1.12}$$

It follows from (1.11) and (1.12) and the differentiability of $\bar{b}_1(\beta)$ and $\bar{b}_2(\beta)$ that if $b_1=1=b_2$, then $b_1<\bar{b}_1(\beta)$ and $b_2>\bar{b}_2(\beta)$ for all sufficiently small β. Under the assumptions

$$\frac{a_2}{D_2} > \frac{a_1}{D_1} > \lambda^1(\Omega, 1) \tag{1.13}$$

and

$$\frac{a_1 - a_2}{D_1 - D_2} < \lambda^1(\Omega, 1), \tag{1.14}$$

Theorem 6.2 of [4] guarantees that

$$\bar{b}_1(\infty) < \frac{a_2}{a_1} < \frac{a_1}{a_2} < \bar{b}_2(\infty). \tag{1.15}$$

Consequently, assuming (1.11), (1.13) and (1.14) it follows from (1.15) and the continuity of $\bar{b}_1(\beta)$ and $\bar{b}_2(\beta)$ that if $b_1 = 1 = b_2$, then $b_1 > \bar{b}_1(\beta)$ and $b_2 < \bar{b}_2(\beta)$ for all sufficiently large β. So under assumptions (1.11), (1.13) and (1.14), if $b_1 = 1 = b_2$, species 1 has the competitive advantage in the model (1.1) and (1.2) when the level of hostility of the "matrix" habitat surrounding Ω is low, whereas species 2 has the competitive advantage when the level of hostility of the "matrix" habitat surrounding Ω is high. Thus there is a reversal of competitive advantage *inside the habitat patch* Ω *brought about solely* by a sufficient increase in the level of degradation in the "matrix" habitat surrounding Ω.

Theorem 6.2 of [4] guarantees an ultimate reversal of competitive advantage in (1.1) and (1.2). However, the result in Theorem 6.2 of [4] does not rule out the possibility that the competitive advantage in (1.1) and (1.2) might switch back and forth between species 1 and species 2 a number of times before ultimately belonging to species 2. This observation raises a very interesting question, both ecologically and mathematically. Namely, just how sensitive might the competitive advantage in a model such as (1.1) and (1.2) be to the level of degradation in the "matrix" habitat surrounding the habitat patch Ω? In particular, can competitive advantage in such models reverse more than once as the level of degradation in the "matrix" habitat surrounding Ω increases?

It seems reasonable to suppose that if the two competitors are similar to one another, the sensitivity of the system to the level of degradation in the surrounding "matrix" should be higher than in a case in which they are less similar. Consequently, we will look for the phenomenon of multiple reversals of competitive advantage in a Lotka–Volterra system which is only a slight perturbation of a situation in which the competitors are identical. Specifically we will examine the system

$$\begin{aligned} &\frac{\partial u}{\partial t} = \Delta u + u[1 + \varepsilon g - u -] \\ & \qquad\qquad\qquad\qquad\qquad \text{in } \Omega \times (0, \infty), \\ &\frac{\partial v}{\partial t} = \Delta v + v[1 - u - v] \\ &(1-s)\nabla u \cdot \eta + su = 0 = (1-s)\nabla v \cdot \eta + sv \quad \text{on } \partial\Omega \times (0, \infty), \end{aligned} \tag{1.16}$$

where s ranges over [0,1]. Notice that when $\varepsilon = 0$, (1.16) reduces to

$$\begin{aligned} &\frac{\partial u}{\partial t} = \Delta u + u(1 - u - v) \\ & \qquad\qquad\qquad\qquad\qquad \text{in } \Omega \times (0, \infty), \\ &\frac{\partial v}{\partial t} = \Delta v + v(1 - u - v) \\ &(1-s)\nabla u \cdot \eta + su = 0 = (1-s)\nabla v \cdot \eta + sv \quad \text{on } \partial\Omega \times (0, \infty). \end{aligned} \tag{1.17}$$

If $\lambda^1(\Omega, 1) < 1, \theta_s > 0$ exists for all $s \in [0, 1]$. Since

$$\begin{aligned} &\Delta\theta_s + \theta_s(1 - \theta_s) = 0 \quad \text{in } \Omega \\ &(1-s)\nabla\theta_s \cdot \eta + s\theta_s = 0 \quad \text{on } \partial\Omega, \end{aligned}$$

it follows that

$$\bar{b}_1(s) = \bar{b}_2(s) = 1 \tag{1.18}$$

in (1.17) for all $s \in [0, 1]$, and neither species ever holds a competitive advantage in the sense we have described. Notice also that equilibria to (1.17) satisfy

$$\begin{aligned} &\Delta u + u(1 - u - v) = 0 \\ & \qquad\qquad\qquad\qquad \text{in } \Omega, \\ &\Delta v + v(1 - u - v) = 0 \\ &(1-s)\nabla u \cdot \eta + su = 0 = (1-s)\nabla v \cdot \eta + sv \quad \text{on } \partial\Omega. \end{aligned} \tag{1.19}$$

By adding the Equations in (1.19), we see that $w = u + v$ satisfies

$$\begin{aligned} &\Delta w + w(1 - w) = 0 \quad \text{in } \Omega, \\ &(1-s)\nabla w \cdot \eta + sw = 0 \quad \text{on } \partial\Omega. \end{aligned}$$

Hence, if u and v are nonnegative, $u + v = \theta_s$. So by (1.19), u and v each solves the eigenvalue problem

$$\begin{aligned} &\Delta z + z(1 - \theta_s) = \sigma z \quad \text{in } \Omega, \\ &(1-s)\nabla z \cdot \eta + sz = 0 \quad \text{on } \partial\Omega, \end{aligned}$$

with $\sigma = 0$. The definition of θ_s then guarantees that $u = \tau\theta_s$ and $v = (1 - \tau)\theta_s$ for some $\tau \in [0, 1]$. Consequently, for each $s \in [0, 1]$, (1.17) has the one parameter family

$$\{(\tau\theta_s, (1-\tau)\theta_s) : \tau \in [0, 1]\} \tag{1.20}$$

of componentwise-nonnegative equilibria.

The perturbed system (1.16) is completely determined by the choice of the funciton g. The remainder of this article is devoted to the question of whether there exist functions g for which (1.16) exhibits mulitple reversals of competitive advantage as the hostility of the "matrix" habitat surrounding Ω (which is measured by s) increases. In Section 2, we make a detailed examination of the dynamics of the perturbed system (1.16) for small positive ε and for $s \in [0, 1]$, leading to appropriate conditions on the funciton g and the carrying capacity densities θ_s so that (1.16) does exhibit multiple reversals of competitive advantage between the two competitors as s varies from 0 to 1. In this case, as distinct from the results in [4], the competitive advantage that one species has over the other is necessarily independent of initial configurations of species densities. In other words, when one of the species has the advantage, it competitively excludes the other over time. Moreover, the analysis shows explicitly how, under appropriate conditions on g and the θ_s, the regions in (ε, s) space in which one species excludes the other in (1.16) are bordered by values for which (1.16) admits a unique globally attracting componentwise positive equilibrium. These results require a very careful unfolding of the sheet of solutions described by (1.20) near appropriate values of s. In Section 3, we show how to guarantee the existence of a suitable perturbation g, and we conclude with a brief discussion of the ramifications of the results in Section 4.

2. THE DYNAMICS OF THE PERTURBED SYSTEM

Throughout this section, we assume that $1 > \lambda^1(\Omega, 1)$ and that g in (1.16) is Hölder continuous on $\bar{\Omega}$ with exponent $\alpha \in (0, 1)$ (i.e., $g \in C^\alpha(\bar{\Omega})$ for some $\alpha \in (0, 1)$). When $\varepsilon \neq 0$, $(0, \theta_s)$ remains an equilibrium solution to (1.16) for any ε and for all $s \in [0, 1]$. However, the remainder of the one-parameter family (1.20) of equilibrium solutions to (1.17), namely $\{(\tau\theta_s, (1-\tau)\theta_s) : \tau \in (0, 1]\}$, *are not* equilibrium solutions to (1.16). If $v = 0$, (1.16) reduces to the diffusive logistic problem

$$\begin{aligned} \frac{\partial u}{\partial t} &= \Delta u + (1 + \varepsilon g - u)u \quad \text{in } \Omega, \\ (1-s)\nabla u \cdot \eta + su &= 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{2.1}$$

The dynamics of (2.1) are the same as (1.3); positive solutions to (2.1) converge over time in $C^1(\bar{\Omega})$ to a unique globally attracting positive equilibrium solution $\tilde{u}_{\varepsilon,s}$ provided the principal eigenvalue σ is positive in the eigenvalue problem

$$\begin{aligned} &\Delta\phi + (1+\varepsilon g)\phi = \sigma\phi \quad \text{in } \Omega, \\ &(1-s)\nabla\phi\cdot\eta + s\phi = 0 \quad \text{on } \partial\Omega \end{aligned} \tag{2.2}$$

and converge over time in $C^1(\bar{\Omega})$ to 0 if $\sigma \le 0$. Since $g \in C^\alpha(\bar{\Omega}), \varepsilon g \ge -|\varepsilon|\|g\|_\infty$ and we have by an eigenvalue comparison principle that

$$\begin{aligned} \sigma &\ge 1 - |\varepsilon|\|g\|_\infty - \lambda^1(\Omega, s) \\ &\ge 1 - |\varepsilon|\|g\|_\infty - \lambda^1(\Omega, 1) \\ &> 0 \end{aligned}$$

provided that $|\varepsilon|$ is sufficiently small. So in that which follows, we assume $|\varepsilon|$ to be small enough so that $\tilde{u}_{\varepsilon,s}$ exists and is the globally attracting equilibrium for (2.1) for all $s \in [0, 1]$.

Our first task is to estimate the values $\bar{b}_1(\varepsilon, s)$ and $\bar{b}_2(\varepsilon, s)$ for which the principal eigenvalues $\sigma_1(\varepsilon, s)$ and $\sigma_2(\varepsilon, s)$ in the problems

$$\begin{aligned} &\Delta\phi_{\varepsilon,s} + (1+\varepsilon g - \bar{b}_1(\varepsilon, s)\theta_s)\phi_{\varepsilon,s} = \sigma_1(\varepsilon, s)\phi_{\varepsilon,s} \quad \text{in } \Omega, \\ &(1-s)\nabla\phi_{\varepsilon,s}\cdot\eta + s\phi_{\varepsilon,s} = 0 \text{ on } \partial\Omega, \end{aligned} \tag{2.3}$$

$$\begin{aligned} &\Delta\psi_{\varepsilon,s} + (1 - \bar{b}_2(\varepsilon, s)\tilde{u}_{\varepsilon,s})\psi_{\varepsilon,s} = \sigma_2(\varepsilon, s)\psi_{\varepsilon,s} \quad \text{in } \Omega, \\ &(1-s)\nabla\psi_{\varepsilon,s}\cdot\eta + s\psi_{\varepsilon,s} = 0 \text{ on } \partial\Omega \end{aligned} \tag{2.4}$$

are both zero. For the moment, regard $s \in [0, 1]$ as fixed. It follows as in [4] that $\tilde{u}_{\varepsilon,s}, \bar{b}_1(\varepsilon, s), \bar{b}_2(\varepsilon, s)$ are differentiable in ε for $|\varepsilon|$ small and that if $\phi_{\varepsilon,s}$ and $\psi_{\varepsilon,s}$ are normalized by the requirements

$$\int_\Omega \phi_{\varepsilon,s}^2 \, dx = 1 = \int_\Omega \psi_{\varepsilon,s}^2 \, dx$$

so are $\phi_{\varepsilon,s}$ and $\psi_{\varepsilon,s}$. Indeed, one may modify the arguments in [4] slightly so as to have these functions differentiable in ε for $|\varepsilon|$ small to any desired order. Consequently, we have the following expansions which are valid for

$|\varepsilon|$ small:

$$\bar{b}_1(\varepsilon, s) = 1 + \varepsilon r_1(s) + 0(\varepsilon^2), \tag{2.5}$$

$$\phi_{\varepsilon,s} = \frac{\theta_s}{\|\theta_s\|_2} + \varepsilon\rho_1(s) + 0(\varepsilon^2), \tag{2.6}$$

$$\tilde{u}_{\varepsilon,s} = \theta_s + \varepsilon u_1(s) + 0(\varepsilon^2), \tag{2.7}$$

$$\bar{b}_2(\varepsilon, s) = 1 + \varepsilon r_2(s) + 0(\varepsilon^2), \tag{2.8}$$

$$\psi_{\varepsilon,s} = \frac{\theta_s}{\|\theta_s\|_2} + \varepsilon\rho_2(s) + 0(\varepsilon^2). \tag{2.9}$$

We wish to determine $r_1(s)$ and $r_2(s)$. To find $r_1(s)$, substitute (2.5) and (2.6) into (2.3). After simplification we obtain that $\rho_1(s)$ satisfies

$$\begin{aligned} &\Delta\rho_1(s) + (1-\theta_s)\rho_1(s) = \frac{(r_1(s)\theta_s - g)\theta_s}{\|\theta_s\|_2} \quad \text{in } \Omega, \\ &(1-s)\nabla\rho_1(s)\cdot\eta + s\rho_1(s) = 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{2.10}$$

Multiplying (2.10) by θ_s, integrating and employing the Divergence Theorem gives

$$0 = r_1(s)\int_\Omega \theta_s^3 \mathrm{d}x - \int_\Omega g\theta_s^2 \mathrm{d}x$$

so that

$$r_1(s) = \int_\Omega g\theta_s^2 \mathrm{d}x \Big/ \int_\Omega \theta_s^3 \mathrm{d}x. \tag{2.11}$$

To find $r_2(s)$, we need to determine $u_1(s)$ in (2.7). Substituting (2.7) into (2.1) establishes that

$$\begin{aligned} &\Delta u_1(s) + (1-\theta_s)u_1(s) = \theta_s u_1(s) - g\theta_s \quad \text{in } \Omega \\ &(1-s)\nabla u_1(s)\cdot\eta + s u_1(s) = 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{2.12}$$

Next, substituting (2.7)–(2.9) into (2.4) yields

$$\begin{aligned} &\Delta\rho_2(s) + (1-\theta_s)\rho_2(s) = \frac{u_1\theta_s}{\|\theta_s\|_2} + \frac{r_2\theta_s^2}{\|\theta_s\|_2} \quad \text{in } \Omega \\ &(1-s)\nabla\rho_2(s)\cdot\eta + s\rho_2(s) = 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{2.13}$$

Multiplying (2.12) by $\theta_s/(\|\theta_s\|_2)$ and (2.13) by θ_s and subtracting yields that

$$\theta_s\Delta\left(\rho_2(s)-\frac{u_1(s)}{\|\theta_s\|_2}\right)+\theta_s(1-\theta_s)\left(\rho_2(s)-\frac{u_1(s)}{\|\theta_s\|_2}\right)=\frac{r_2(s)\theta_3^2+g\theta_s^2}{\|\theta_s\|_2} \quad \text{in } \Omega$$
$$(1-s)\nabla\left(\rho_2(s)-\frac{u_1(s)}{\|\theta_s\|_2}\right)\cdot\eta+s\left(\rho_2(s)-\frac{u_1(s)}{\|\theta_s\|_2}\right)=0 \quad \text{on } \partial\Omega. \tag{2.14}$$

Integrating (2.14) and employing the Divergence Theorem establishes that

$$r_2(s)=\frac{-\int_\Omega g\theta_s^2\,\mathrm{d}x}{\int_\Omega \theta_s^3\,\mathrm{d}x}. \tag{2.15}$$

It follows immediately from (2.11) and (2.15) that

$$\bar{b}_1(\varepsilon,s)=1+\varepsilon\frac{\int_\Omega g\theta_s^2\,\mathrm{d}x}{\int_\Omega \theta_s^3\mathrm{d}x}+0(\varepsilon^2)$$
$$\bar{b}_2(\varepsilon,s)=1-\varepsilon\frac{\int_\Omega g\theta_s^2\,\mathrm{d}x}{\int_\Omega \theta_s^3\,\mathrm{d}x}+0(\varepsilon^2). \tag{2.16}$$

From (2.16) we have

$$1<\bar{b}_1(\varepsilon,s), \qquad 1>\bar{b}_2(\varepsilon,s) \tag{2.17}$$

if $\int_\Omega g\theta_s^2\,\mathrm{d}x>0$ and $0<\varepsilon\ll 1$ and

$$1>\bar{b}_1(\varepsilon,s), \qquad 1<\bar{b}_2(\varepsilon,s) \tag{2.18}$$

if $\int_\Omega g\theta_s^2\,\mathrm{d}x<0$ and $0<\varepsilon\ll 1$. We now have established the following result.

Theorem 2.1. *Consider* (1.16) *for a fixed* $s\in[0,1]$.

(i) *If* $\int_\Omega g\theta_s^2\,\mathrm{d}x>0$ *and* $0<\varepsilon\ll 1$, (2.17) *holds and thus species* 1 *has a competitive advantage in* (1.16) *over species* 2 *in the sense that species* 1 *may invade* Ω *when species* 2*'s density is at the carrying capacity* θ_s *it obtains in the absence of species* 1, *while species* 2 *cannot invade* Ω *when species* 1*'s density is at the carrying capacity* $\tilde{u}_{\varepsilon,s}$ *it obtains in the absence of species* 2.

(ii) *If* $\int_\Omega g\theta_s^2\,\mathrm{d}x<0$ *and* $0<\varepsilon\ll 1$, (2.18) *holds and thus species* 2 *has a competitive advantage in* (1.16) *over species* 1 *in the sense that species* 2 *may invade* Ω *when species* 1*'s density is at the carrying capacity* $\tilde{u}_{\varepsilon,s}$ *it obtains in the absence of species* 2, *while species* 1 *cannot invade* Ω *when species* 2*'s density is at the carrying capacity* θ_s *it obtains in the absence of species* 1.

It is not too difficult to establish that for small enough ε that the conclusions of Theorem 2.1 may be strengthened to assert that species 1 competitively excludes species 2 in (1.16) when $\int_\Omega g\theta_s^2\,dx > 0$ and that species 2 competitively excludes species 1 in (1.16) when $\int_\Omega g\theta_s^2\,dx < 0$. To this end, we first need the following observation.

Proposition 2.2. *If (u,v) is a componentwise positive equilibrium solution to* (1.16), *then* $\int_\Omega guv = 0$.

Proof. Multiply the first equation in (1.16) by v and the second by u, integrate and employ Green's second identity.

Now define $G:[0,1]\to\mathbb{R}$ by

$$G(s) = \int_\Omega g\theta_s^2\,dx.$$

Theorem 3.1 of [4] tells us that θ_s is differentiable in s. Indeed, the argument in [4] may be modified to have θ_s differentiable in s to any desired order. Consequently, G is continuously differentiable. We have the following result.

Theorem 2.3. *Suppose $G(s)\neq 0$ for $s\in[a,b]$, where $0\leqslant a<b\leqslant 1$. Then*

(i) *There is an $\varepsilon_0>0$ so that if $0<\varepsilon<\varepsilon_0$ and $s\in[a,b]$,* (1.16) *admits no componentwise positive equilibrium.*

(ii) *If $G(s)>0$ for $s\in[a,b]$, then if $0<\varepsilon<\varepsilon_0$ and $s\in[a,b]$, all componentwise positive solutions to* (1.16) *converge over time in $C^1(\bar\Omega)\times C^1(\bar\Omega)$ to $(\bar u_{\varepsilon,s},0)$. Consequently,* (1.16) *predicts that species 1 competitively excludes species 2 in Ω in this case.*

(iii) *If $G(s)<0$ for $s\in[a,b]$, then if $0<\varepsilon<\varepsilon_0$ and $s\in[a,b]$, all componentwise positive solutions to* (1.16) *converge over time in $C^1(\bar\Omega)\times C^1(\bar\Omega)$ to $(0,\theta_s)$. Consequently,* (1.16) *predicts that species 2 competitively excludes species 1 in Ω in this case.*

Proof. Suppose (i) fails to hold. Then there is a sequence $(\varepsilon_n, s_n, u_n, v_n)$ so that

$$\begin{aligned}
&\Delta u_n + u_n[1+\varepsilon_n g - u_n - v_n] = 0 \\
&\qquad\qquad\qquad\qquad\qquad\qquad \text{in } \Omega, \\
&\Delta v_n + v_n[1-u_n-v_n] = 0 \qquad\qquad\qquad\qquad (2.19)\\
&(1-s_n)\nabla u_n\cdot\eta + s_n u_n = 0 = (1-s_n)\nabla v_n\cdot\eta + s_n v_n \quad \text{on } \partial\Omega,
\end{aligned}$$

where $u_n>0$ and $v_n>0$ in $\Omega, s_n\in[a,b]$ and $\varepsilon_n\to 0$ as $\eta\to\infty$. The Bolzano–Weierstrass Theorem guarantees that $s_n\to s^*$ for some subsequence (which we relabel if need be). The Maximum Principle guarantees the uniform boundedness of u_n and v_n for all n. For each n, so long as

$s_n \neq 0$, the Laplace operator Δ plus the relevant boundary condition in (2.19) is invertible with an inverse which is compact as an operator from $C^1(\bar{\Omega})$ into $C^1(\bar{\Omega})$. If $s_n = 0$, the same is true for $\Delta - \rho$ for any $\rho > 0$. Moreover, these compact inverses are continuous in s. Consequently, there is a further subsequence (which again we relabel if need be) so that $u_n \to u^*$, $v_n \to v^*$ with $u^* \geq 0$ and $v^* \geq 0$ satisfying

$$\begin{aligned} &\left.\begin{aligned}\Delta u^* + u^*[1 - u^* - v^*] = 0\\ \Delta v^* + v^*[1 - u^* - v^*] = 0\end{aligned}\right\} \quad \text{in } \Omega,\\ &(1 - s^*)\nabla u^* \cdot \eta + s^* u^* = 0 = (1 - s^*)\nabla v^* \cdot \eta + s^* v^* \quad \text{on } \partial\Omega. \end{aligned}$$

Hence it follows from (1.20) that there is a $\tau^* \in [0, 1]$ so that $(u^*, v^*) = (\tau^*\theta_{s^*}, (1 - \tau^*)\theta_{s^*})$. Proposition 2.2 implies that $\int_\Omega g u_n v_n \, dx = 0$ for all n. Consequently, we have that

$$\tau^*(1 - \tau^*) \int_\Omega g\theta_{s^*}^2 \, dx = 0.$$

Since $\int_\Omega g\theta_{s^*}^2 \, dx \neq 0$, it must be the case that $\tau^* = 0$ or $\tau^* = 1$, meaning that $(u^*, v^*) = (\theta_{s^*}, 0)$ or $(0, \theta_{s^*})$.

So to establish (i), we need to rule out the possibility that u_n may converge to 0 or v_n may converge to 0 as $n \to \infty$. Suppose, for instance, that $u_n \to 0$. Then

$$\left.\begin{aligned}\Delta\left(\frac{u_n}{\|u_n\|_\infty}\right) + \frac{u_n}{\|u_n\|_\infty}[1 + \varepsilon_n g - u_n - v_n] = 0\\ \Delta v_n + v_n[1 - u_n - v_n] = 0\end{aligned}\right\} \quad \text{in } \Omega,$$

with

$$(1 - s_n)\nabla\left(\frac{u_n}{\|u_n\|_\infty}\right) \cdot \eta + s_n \frac{u_n}{\|u_n\|_\infty} = 0 = (1 - s_n)\nabla v_n \cdot \eta + s_n v_n \quad \text{on } \partial\Omega.$$

Again, there is a subsequence which we relable if need be so that $u_n/(\|u_n\|_\infty) \to u^{**}$, $v_n \to \theta_{s^*}$ with

$$\begin{aligned} &\Delta u^{**} + u^{**}[1 - \theta_{s^*}] = 0 \quad \text{in } \Omega\\ &(1 - s^*)\nabla u^{**} \cdot \eta + s^* u^{**} = 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{2.20}$$

Since $\|u_n/(\|u_n\|_\infty)\|_\infty = 1$, $u^{**} \neq 0$. Consequently, it follows from (2.20) that $u^{**} = \alpha\theta_{s^*}, \alpha \neq 0$. Now for all n, since $\int_\Omega g u_n v_n \, dx = 0$, $\int_\Omega g(u_n/(\|u_n\|_\infty))v_n \, dx = 0$. So we have $\alpha \int_\Omega g\theta_{s^*}^2 \, dx = 0$, a contradiction. So it is not possible for $u_n \to 0$ as $n \to \infty$. A similar argument rules out the possibility of

$v_n \to 0$ as $n \to \infty$. Thus (i) is established. Parts (ii) and (iii) of the result now follow from part (i), Theorem 2.1 and Lemma 3.3 of [9].

As a corollary to Theorem 2.3, we have the following.

Theorem 2.4. *Suppose that G changes sign n times on* [0,1]. *Then there is an $\varepsilon_0 > 0$ so that if $0 < \varepsilon < \varepsilon_0$,* (1.16) *exhibits at least $n-1$ changes of competitive advantage in which the species holding the competitive advantage excludes the other from Ω over time.*

Clearly G may change sign only when there is an $\bar{s} \in (0,1)$ with $G(\bar{s}) = 0$. If we impose the additional condition $G'(\bar{s}) \neq 0$, we can show that the regions in $\varepsilon - s$ parameter space in which the prediction of (1.16) is that one species competitively excludes the other ae bordered by regions in which coexistence is predicted by (1.16). In fact, we have the following result.

Theorem 2.5. *If $G(\bar{s}) = 0$ and $G'(\bar{s}) \neq 0$ for some $\bar{s} \in (0,1)$, then there are $\varepsilon_0 > 0$ and $\delta_0 > 0$ so that for every $\varepsilon \in (0, \varepsilon_0)$, there are $s_*(\varepsilon) < s^*(\varepsilon)$ with $\lim_{\varepsilon \to 0} s_*(\varepsilon) = \lim_{\varepsilon \to 0} s^*(\varepsilon) = \bar{s}$ so that* (1.16) *admits a coexistence state for $s \in [\bar{s} - \delta_0, \bar{s} + \delta_0]$ if and only if $s \in (s_*(\varepsilon), s^*(\varepsilon))$. Moreover, such a coexistence state is unique for every $s \in (s^*(\varepsilon), s^*(\varepsilon))$ and is globally asymptotically stable.*

The proof of Theorem 2.5 amounts to a very careful unfolding of the equilibria (u, v, s, ε) to (1.16) in a neighborhood of

$$\gamma_{\bar{s}} = \{(\tau\theta_{\bar{s}}, (1-\tau)\theta_{\bar{s}}, \bar{s}, 0) : \tau \in [0,1]\} \tag{2.21}$$

and requires several preliminary results. We begin with the following.

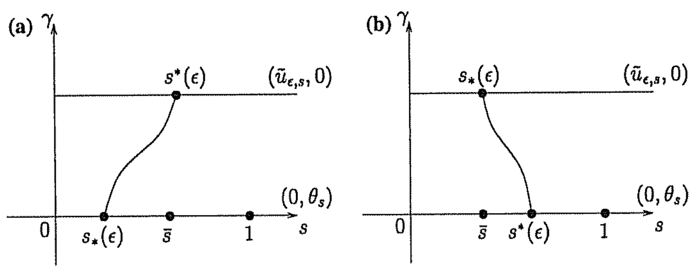

Figure 1. This provides a schematic illustration of Theorem 2.5. Both (a) and (b) illustrate the componentwise nonnegative equilibria for (1.16) for some fixed $\varepsilon \in (0, \varepsilon_0)$ where ε_0 is as in Theorem 2.5 and s near $\bar{s}$. In (a), a branch of coexistence states bifurcates (in the parameters) from the semitrivial solutions $(0, \theta_s)$ at $s = s_*(\varepsilon)$ and meets the semitrivial solutions $(\tilde{u}_{\varepsilon,s}, 0)$ at $s = s^*(\varepsilon)$. In (b), the branch of coexistence states meets $(\tilde{u}_{\varepsilon,s}, 0)$ at $s = s_*(\varepsilon)$ and $(0, \theta_s)$ at $s = s^*(\varepsilon)$. The vertical axis is $\gamma = \|u\|_2/(\|u\|_2 + \|v\|_2)$.

Proposition 2.6. *Let* $X = C^{2+\alpha}(\bar{\Omega}) \times C^{2+\alpha}(\bar{\Omega})$. *Then there are an* $\varepsilon_0 > 0$ *and a neighborhood* U *of* $\gamma_{\bar{s}}$ *in* $X \times (0,1) \times (-\varepsilon_0, \varepsilon_0)$ *so that for every* $\varepsilon \in (0, \varepsilon_0)$, *the set of equilibrium solutions to* (1.16) *in* U *consist of the semitrival solutions and of those accounted for by the set* $\Gamma_\varepsilon \cap U$, *where* Γ_ε *is a smooth curve in* $X \times (0,1)$ *given by*

$$\Gamma_s = \{(u(\cdot, \varepsilon, \tau), v(\cdot, \varepsilon, \tau), s(\varepsilon, \tau)) : -\varepsilon_0 \le \tau \le 1 + \varepsilon_0\} \tag{2.22}$$

and u, v, s *satisfy*

$$(u(\cdot, \varepsilon, 0), v(\cdot, \varepsilon, 0)) = (0, \theta_{s(\varepsilon,0)}), \tag{2.23}$$

$$(u(\cdot, \varepsilon, 1), v(\cdot, \varepsilon, 1)) = (\tilde{u}(\cdot)_{\varepsilon, s(\varepsilon,1)}, 0), \tag{2.24}$$

$$(u(\cdot, 0, \tau), v(\cdot, 0, \tau), s(0, \tau)) = (\tau\theta_{\bar{s}}, (1-\tau)\theta_{\bar{s}}, \bar{s}). \tag{2.25}$$

Proof. Let $X_1 = \{(y, z) \in X : \int_\Omega (y - z)\theta_{\bar{s}} \, dx = 0\}$. For any $s \in [0,1]$, any $(u, v) \in X$ may be uniquely expressed as

$$\begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} \tau\theta_s \\ (1-\tau)\theta_s \end{pmatrix} + \begin{pmatrix} y \\ z \end{pmatrix}, \tag{2.26}$$

where $\tau \in \mathbb{R}$ and $\begin{pmatrix} y \\ z \end{pmatrix} \in X_1$. Moreover, if (u, v, s) is close to $\gamma_{\bar{s}}$, then $\tau \in (-\delta, 1+\delta)$ for some $\delta > 0$ and small. We shall seek solutions to (1.16) in the form of (2.26). To this end, let $Y = C^\alpha(\bar{\Omega}) \times C^\alpha(\bar{\Omega}) \times C^{1+\alpha}(\partial\Omega) \times C^{1+\alpha}(\partial\Omega)$. Then for $\delta \in (0, \min(\bar{s}, 1-\bar{s}))$, define a map

$$H : X_1 \times (-\delta, \delta) \times (-\delta, 1+\delta) \times (\bar{s} - \delta, \bar{s} + \delta) \to Y$$

by

$$H(y, z, \varepsilon, \tau, s) = \begin{pmatrix} \Delta y - (y+z)\tau\theta_s + (1-\theta_s)y - (y+z)y + \varepsilon g\tau\theta_s + \varepsilon g y \\ \Delta z - (y+z)(1-\tau)\theta_s + (1-\theta_s)z - (y+z)z \\ (1-s)\nabla y \cdot \eta + sy \\ (1-s)\nabla z \cdot \eta + sz \end{pmatrix}.$$

Then (u, v, ε, s) with (u, v) as in (2.26) solves (1.16) if and only if $H(y, z, \varepsilon, \tau, s) = 0$.

It is easy to see that

$$H(0, 0, 0, \tau, s) = 0 \tag{2.27}$$

for all $\tau \in (-\delta, 1+\delta)$ and $s \in (\bar{s} - \delta, \bar{s} + \delta)$. As we are looking for solutions to $H(y, z, \varepsilon, \tau, s) = 0$ for (y, z) in X_1 close to (0,0) and $0 < \varepsilon \ll 1$, it is natural to consider the linear operator $L(\tau, s) = D_{(y,z)} H(0, 0, 0, \tau, s)$ which is given by

$$L(\tau, s)\begin{pmatrix}\varphi\\ \psi\end{pmatrix}=\begin{pmatrix}\Delta\varphi-(\varphi+\psi)\tau\theta_s+(1-\theta_s)\varphi\\ \Delta\psi-(\varphi+\psi)(1-\tau)\theta_s+(1-\theta_s)\psi\\ (1-s)\nabla\varphi\cdot\eta+s\varphi\\ (1-s)\nabla\psi\cdot\eta+s\psi\end{pmatrix}. \tag{2.28}$$

$L(\tau, s)$ is a bounded linear operator from X to Y which is smooth in the parameters τ, s. It follows from (2.28) that for any $\tau\in(-\delta, 1+\delta)$ and $s\in(\bar{s}-\delta, \bar{s}+\delta)$

$$\ker L(\tau, s)=\left\langle\begin{pmatrix}\theta_s\\ -\theta_s\end{pmatrix}\right\rangle. \tag{2.29}$$

Notice that X_1 is the kernel of the bounded linear functional $f: X\to\mathbb{R}$ given by

$$f\begin{pmatrix}u\\ v\end{pmatrix}=\int_\Omega (u-v)\theta_{\bar{s}}\,\mathrm{d}x.$$

X may be expressed as

$$X=\left\langle\begin{pmatrix}u_0\\ v_0\end{pmatrix}\right\rangle\oplus X_1$$

for any

$$\begin{pmatrix}u_0\\ v_0\end{pmatrix}\in X$$

for which

$$f\begin{pmatrix}u_0\\ v_0\end{pmatrix}\neq 0.$$

Since for any $s\in[0, 1], \theta_s>0$ in Ω and

$$f\begin{pmatrix}\theta_s\\ -\theta_s\end{pmatrix}=\int_\Omega 2\theta_s\theta_{\bar{s}}\,\mathrm{d}x>0,$$

we have from (2.29) that for any $s\in(\bar{s}-\delta, \bar{s}+\delta)$ and $\tau\in(-\delta, 1+\delta)$

$$X=\ker L(\tau, s)\oplus X_1.$$

In particular, $L(\tau, s): X_1\to Y$ is injective.

Now define the operator $P(\tau, s): Y \to \ker L(\tau, s) \times \{0, 0\} \subseteq Y$ by

$$P(\tau, s)\begin{pmatrix} y \\ z \\ p \\ q \end{pmatrix} = \begin{pmatrix} \left[\dfrac{\int_\Omega \theta_s[(1-\tau)y - \tau z]\mathrm{d}x - \int_{\partial\Omega} \theta_s\left[\frac{(1-\tau)}{(1-s)}p - \frac{\tau}{1-s}q\right]\mathrm{d}s}{\int_\Omega \theta_s^2 \mathrm{d}x}\right]\theta_s \\ -\left[\dfrac{\int_\Omega \theta_s[(1-\tau)y - \tau z]\mathrm{d}x - \int_{\partial\Omega} \theta_s\left[\frac{(1-\tau)}{(1-s)}p - \frac{\tau}{1-s}q\right]\mathrm{d}s}{\int_\Omega \theta_s^2 \mathrm{d}x}\right]\theta_s \\ 0 \\ 0 \end{pmatrix}. \tag{2.30}$$

One may check fairly readily from (2.30) that for any $s \in (\bar{s} - \delta, \bar{s} + \delta)$ and $\tau \in (-\delta, 1 + \delta)$ that $P^2(\tau, s) = P(\tau, s)$ (i.e., $P(\tau, s)$ is a projection operator) and that $P(\tau, s)L(\tau, s) = 0$, the latter following from an integration by parts argument. A slightly more involved calculation will show that

$$R(I - P(\tau, s)) = R(L(\tau, s)) = R((I - P(\tau, s))L(\tau, s)) \tag{2.31}$$

for any $s \in (\bar{s} - \delta, \bar{s} + \delta)$ and $\tau \in (-\delta, 1 + \delta)$. As a consequence of (2.31), we have that $L(\tau, s)$ is a linear homeomorphism from X_1 onto $R(I - P(\tau, s))$, which is smooth in τ and s for $\tau \in (-\delta, 1 + \delta)$ and $s \in (\bar{s} - \delta, s - \delta)$. It is an exercise in functional analysis to conclude that $L(\tau, s)^{-1}$ is a linear homeomorphism from $R(I - P(\tau, s))$ into X_1 which is smooth in τ and s as well.

We may consider the Lyapunov–Schmidt decomposition for $H(y, z, \varepsilon, \tau, s) = 0$ given by

$$P(\tau, s)H(y, z, \varepsilon, \tau, s) = 0, \tag{2.32a}$$

$$(I - P(\tau, s))H(y, z, \varepsilon, \tau, s) = 0. \tag{2.32b}$$

Since

$$\begin{aligned} &D_{(y,z)}((I - P(\tau, s))H(0, 0, 0, \tau, s)) \\ &\quad = (I - P(\tau, s))L(\tau, s) \\ &\quad = L(\tau, s) \end{aligned}$$

for all $s \in (\bar{s} - \delta, \bar{s} + \delta)$ and $\tau \in (-\delta, 1 + \delta)$, it follows from the Implicit Function Theorem as in [1] that we can solve (2.32b) for (y, z) in terms of (ε, τ, s) to find that there are a $\delta_1 \in (0, \delta)$ and neighborhood

V of (0,0) in X_1 and smooth functions $(y_1(\varepsilon,\tau,s), z_1(\varepsilon,\tau,s)) : (-\delta_1,\delta_1) \times (-\delta_1, 1+\delta_1) \times (\bar{s}-\delta_1, \bar{s}+\delta_1) \to X_1$ so that $(y_1(0,\tau,s), z_1(0,\tau,s)) = (0,0)$ and $(y,z,\varepsilon,\tau,s) \in V \times (-\delta_1, 1+\delta_1) \times (-\delta_1, 1+\delta_1) \times (\bar{s}-\delta_1, \bar{s}+\delta_1)$ satisfies $H(y,z,\varepsilon,\tau,s)=0$ if and only if

$$(y,z) = (y_1(\varepsilon,\tau,s), z_1(\varepsilon,\tau,s)) \tag{2.33}$$

and (ε,τ,s) satisfies

$$P(\tau,s)H(y_1(\varepsilon,\tau,s), z_1(\varepsilon,\tau,s), \varepsilon,\tau,s) = 0. \tag{2.34}$$

Here the fact that $L(\tau,s)$ is a linear homeomorphism from X_1 onto $R(I - P(\tau,s))$ plays a crucial role.

From the definition of $P(\tau,s)$ we have that

$$P(\tau,s)H(y_1(\varepsilon,\tau,s), z_1(\varepsilon,\tau,s), \varepsilon,\tau,s) = \begin{pmatrix} C(\varepsilon,\tau,s)\theta_s \\ -C(\varepsilon,\tau,s)\theta_s \\ 0 \\ 0 \end{pmatrix}$$

for some real valued function $C(\varepsilon,\tau,s)$. Hence (2.33) and (2.34) are equivalent to

$$C(\varepsilon,\tau,s) = 0. \tag{2.35}$$

Since $(y_1(0,\tau,s), z_1(0,\tau,s)) = (0,0)$, it follows from (2.27) that

$$C(0,\tau,s) = 0 \tag{2.36}$$

for all $\tau \in (-\delta, 1+\delta_1)$ and $s \in (\bar{s}-\delta_1, \bar{s}+\delta_1)$. One may readily check that $H(0,0,\varepsilon,0,s) = 0$ for all $\in (-\delta_1,\delta_1)$ and $s \in (\bar{s}-\delta_1, \bar{s}+\delta_1)$. It follows that $(y_1(\varepsilon,0,s), z_1(\varepsilon,0,s)) = (0,0)$ and hence that

$$C(\varepsilon,0,s) = 0 \tag{2.37}$$

for all $\varepsilon \in (-\delta_1,\delta_1)$ and $s \in (\bar{s}-\delta_1, \bar{s}+\delta_1)$.

Now consider the semi-trival equilibria $(\tilde{u}_{\varepsilon,s}, 0)$ to (1.16). It must be the case that when

$$\begin{pmatrix} \tilde{u}_{\varepsilon,s} \\ 0 \end{pmatrix}$$

is written in the form

$$\begin{pmatrix} \tilde{u}_{\varepsilon,s} \\ 0 \end{pmatrix} = \begin{pmatrix} \tau_0(\varepsilon,s)\theta_s \\ (1-\tau_0(\varepsilon,s))\theta_s \end{pmatrix} + \begin{pmatrix} y_0(\cdot,\varepsilon,s) \\ z_0(\cdot,\varepsilon,s) \end{pmatrix}$$

as in (2.26),

$$H(y_0(\cdot,\varepsilon,s), z_0(\cdot,\varepsilon,s), \varepsilon, \tau_0(\varepsilon,s), s) = 0$$

so that $y_0(\cdot,\varepsilon,s) = y_1(\cdot,\varepsilon,\tau_0(\varepsilon,s),s), z_0(\cdot,\varepsilon,s) = z_1(\cdot,\varepsilon,\tau_0(\varepsilon,s),s)$, with $\tau_0(0,s)=1$ and $(y_0(\cdot,0,s), z_0(\cdot,0,s)) = (0,0)$. Indeed, one may calculate that

$$\tau_0(\varepsilon,s) = \frac{1}{2}\left[\frac{\int_\Omega \tilde{u}_{\varepsilon,s}\theta_{\bar{s}}\,\mathrm{d}x}{\int_\Omega \theta_s\theta_{\bar{s}}\,\mathrm{d}x} + 1\right]$$

guaranteeing that $\tau_0(\varepsilon,s)$ is smooth in ε and s. Consequently, it must be the case that

$$C(\varepsilon, \tau_0(\varepsilon,s), s) = 0 \tag{2.38}$$

for all $\varepsilon \in (-\delta_1, \delta_1)$ and $s \in (\bar{s}-\delta_1, \bar{s}+\delta_1)$.

Combining (2.36)–(2.38), we have that

$$C(\varepsilon,\tau,s) = \varepsilon\tau[\tau_0(\varepsilon,s) - \tau]C_1(\varepsilon,\tau,s), \tag{2.39}$$

so that (2.35) is reduced to solving $C_1(\varepsilon,\tau,s)=0$. We see from (2.39) and the fact that $\tau_0(0,s)=1$ that

$$\frac{\partial C}{\partial \varepsilon}(0,\tau,s) = \tau(1-\tau)C_1(0,\tau,s). \tag{2.40}$$

On the other hand, since

$$C(\varepsilon,\tau,s)\begin{pmatrix}\theta_s\\ -\theta_s\\ 0\\ 0\end{pmatrix} = P(\tau,s)H(y_1(\varepsilon,\tau,s), z_1(\varepsilon,\tau,s), \varepsilon,\tau,s),$$

$$\begin{aligned}\frac{\partial C}{\partial \varepsilon}(0,\tau,s)\begin{pmatrix}\theta_s\\ -\theta_s\\ 0\\ 0\end{pmatrix} &= \frac{\partial}{\partial\varepsilon}[P(\tau,s)H(y_1(\varepsilon,\tau,s), z_1(\varepsilon,\tau,s),\varepsilon,\tau,s)]|_{\varepsilon=0}\\ &= P(\tau,s)H_\varepsilon(0,0,0,\tau,s) + P(\tau,s)L(\tau,s)\begin{pmatrix}\frac{\partial y_1}{\partial\varepsilon}\\ \frac{\partial z_1}{\partial\varepsilon}\end{pmatrix}\\ &= P(\tau,s)H_\varepsilon(0,0,0,\tau,s)\end{aligned} \tag{2.41}$$

$$= P(\tau, s)\begin{pmatrix}\tau g\theta_s \\ 0 \\ 0 \\ 0\end{pmatrix}$$

$$= \frac{\tau(1-\tau)\int_\Omega g\theta_s^2\,\mathrm{d}x}{\int_\Omega \theta_s^2\,\mathrm{d}x}\begin{pmatrix}\theta_s \\ -\theta_s \\ 0 \\ 0\end{pmatrix}.$$

So by (2.40) and (2.41), we have that

$$C_1(0, \tau, s) = \frac{G(s)}{\int_\Omega \theta_s^2\,\mathrm{d}x}. \tag{2.42}$$

Since $C_1(0, \tau, \bar{s}) = G(\bar{s})/\int_\Omega \theta_s^2\,\mathrm{d}x = 0$ and $(\partial C_1/\partial s)(0, \tau, \bar{s}) = G'(\bar{s})/\int_\Omega \theta_{\bar{s}}^2\,\mathrm{d}x \neq 0$, the Implicit Function Theorem guarantees that there is a $\delta_2 \in (0, \delta_1)$ so that all solutions of $C_1(\varepsilon, \tau, s) = 0$ in the domain $(-\delta_2, \delta_2) \times (-\delta_2, 1+\delta_2) \times (\bar{s}-\delta_2, \bar{s}+\delta_2)$ are given by

$$s = h(\varepsilon, \tau)$$

for $\varepsilon \in (-\delta_2, \delta_2)$ and $\tau \in (-\delta_2, 1+\delta_2)$ with

$$\bar{s} = h(0, \tau).$$

Thus all solutions of $C(\varepsilon, \tau, s) = 0$ for $\varepsilon \in [0, \delta_2), \tau \in (-\delta_2, 1+\delta_2)$ and $s \in (\bar{s}-\delta_2, \bar{s}+\delta_2)$ fall into three families

(i) $\Gamma_1 = \{(\varepsilon, 0, s) : \varepsilon \in [0, \delta_2), s \in (\bar{s}-\delta_2, \bar{s}+\delta_2)\}$, corresponding to the semi-trivial equilibria $(0, \theta_s)$ of (1.16);
(ii) $\Gamma_2 = \{(\varepsilon, \tau_0(\varepsilon, s), s) : \varepsilon \in [0, \delta_2), s \in (\bar{s}-\delta_2, \bar{s}+\delta_2)\}$, corresponding to the semi-trivial equilibria $(\tilde{u}_{\varepsilon,s}, 0)$, of (1.16);
(iii) $\Gamma_3 = \{(\varepsilon, \tau, h(\varepsilon, \tau)) : \varepsilon \in [0, \delta_2), \tau \in (-\delta_2, 1+\delta_s)\}$, accounting for all coexistence states to (1.16) near $\gamma_{\bar{s}}$.

Clearly $\Gamma_1 \cap \Gamma_2 = \phi$ and $\Gamma_1 \cap \Gamma_3 = \{(\varepsilon, 0, h(\varepsilon, 0)) : \varepsilon \in [0, \delta_2)\}$. As for $\Gamma_2 \cap \Gamma_3$, observe that $(\varepsilon, \tau_0(\varepsilon, s), s) = (\varepsilon, \tau, h(\varepsilon, \tau))$ if and only if $\tau = \tau_0(\varepsilon, h(\varepsilon, \tau))$. Set $F(\varepsilon, \tau) = \tau - \tau_0(\varepsilon, h(\varepsilon, \tau))$. Then

$$\frac{\partial F}{\partial \tau}(\varepsilon, \tau) = 1 - \frac{\partial \tau_0}{\partial s}(\varepsilon, h(\varepsilon, \tau)) \cdot \frac{\partial h}{\partial \tau}(\varepsilon, \tau).$$

Hence

$$\frac{\partial F}{\partial \tau}(0, 1) = 1 - \frac{\partial \tau_0}{\partial s}(0, \bar{s})\frac{\partial h}{\partial \tau}(0, 1).$$

Now $C_1(\varepsilon, \tau, h(\varepsilon, \tau)) = 0$, so that for any fixed ε

$$\frac{\partial C_1}{\partial \tau}(\varepsilon, \tau, h(\varepsilon, \tau)) + \frac{\partial C_1}{\partial s}(\varepsilon, \tau, h(\varepsilon, \tau)) \frac{\partial h}{\partial \tau}(\varepsilon, \tau) \equiv 0$$

in τ. In particular,

$$\frac{\partial C_1}{\partial \tau}(0, 1, \bar{s}) + \frac{\partial C_1}{\partial s}(0, 1, \bar{s}) \frac{\partial h}{\partial \tau}(0, 1) = 0.$$

Now $\frac{\partial C_1}{\partial s}(0, 1, \bar{s}) = G'(\bar{s}) / \int_\Omega \theta_{\bar{s}}^2 \, dx \neq 0$, so that

$$\frac{\partial h}{\partial \tau}(0, 1) = -\frac{\partial C_1}{\partial \tau}(0, 1, \bar{s}) \Big/ \frac{\partial C_1}{\partial s}(0, 1, \bar{s}).$$

For $\tau^* \in (-\delta_2, 1 + \delta_2)$ and ε and s fixed, we have

$$C_1(\varepsilon, \tau, s) = C_1(\varepsilon, \tau^*, s) + (\tau - \tau^*) \frac{\partial C_1}{\partial \tau}(\varepsilon, \tau^*, s) + (\tau - \tau^*)^2 \tilde{C}(\varepsilon, \tau, s).$$

In particular,

$$\begin{aligned} C_1(0, \tau, s) &= C_1(0, \tau^*, s) + (\tau - \tau^*) \frac{\partial C_1}{\partial \tau}(0, \tau^*, s) \\ &\quad + (\tau - \tau^*)^2 \tilde{C}(0, \tau, s). \end{aligned}$$

But now $C_1(0, \tau, s) = G(s) / \int_\Omega \theta_s^2 \, dx$ for any $\tau \in (-\delta_2, 1 + \delta_2)$. So $(\partial C_1 / \partial \tau)(0, \tau^*, s) + (\tau - \tau^*) \tilde{C}(0, \tau, s) = 0$, implying $\partial C / \partial \tau (0, \tau^*, s) = 0$ for any τ^* and s. It follows that $(\partial h / \partial \tau)(0, 1) = 0$ and thus that $(\partial F / \partial \tau)(0, 1) = 1$. Since $F(0, 1) = 1 - \tau_0(0, h(0, 1)) = 1 - \tau_0(0, \bar{s}) = 1 - 1 = 0$, the Implicit Function Theorem guarantees that

$$\tau = \tau_0(\varepsilon, h(\varepsilon, \tau))$$

has a unique solution $\tau = \bar{\tau}(\varepsilon)$ for all $\varepsilon \in [0, \delta_3)$ for some $\delta_3 \leqslant \delta_2$ with $\bar{\tau}(0) = 1$. Thus $\Gamma_2 \cap \Gamma_3 = \{(\varepsilon, \bar{\tau}(\varepsilon), h(\varepsilon, \bar{\tau}(\varepsilon)) : \varepsilon \in [0, \delta_3)\}$.

Now for $\varepsilon \in [0, \delta_3)$ and $\tau \in (-\delta_3, 1 + \delta_3)$, define

$$u(\cdot, \varepsilon, \tau) = \tau \bar{\tau}(\varepsilon) \theta_{h(\varepsilon, \tau\bar{\tau}(\varepsilon))} + y_1(\varepsilon, \tau\bar{\tau}(\varepsilon), h(\varepsilon, \tau\bar{\tau}(\varepsilon))), \tag{2.43}$$

$$v(\cdot, \varepsilon, \tau) = (1 - \tau\bar{\tau}(\varepsilon)) \theta_{h(\varepsilon, \tau\bar{\tau}(\varepsilon))} + z_1(\varepsilon, \tau\bar{\tau}(\varepsilon), h(\varepsilon, \tau\bar{\tau}(\varepsilon))), \tag{2.44}$$

$$s(\varepsilon, \tau) = h(\varepsilon, \tau\bar{\tau}(\varepsilon)). \tag{2.45}$$

This construction yields the branch of equilibrium solutions to (1.16) Γ_ε given in (2.22). The preceding discussion shows that Γ_ε and the semi-trivial equilibrium solutions constitute all equilibrium solutions to (1.16) in a neighborhood of $\gamma_{\bar{s}}$ for ε fixed provided ε is sufficiently small. Moreover, (2.23)–(2.25) follow from the preceding constructions, completing the proof of Proposition 2.6.

We now turn to the question of stability of coexistence states to (1.16) when $\varepsilon > 0$ is sufficiently small. We have the following proposition.

Proposition 2.7. *Suppose that* $G(\bar{s}) = 0$ *and* $G'(\bar{s}) \neq 0$ *for some* $\bar{s} \in (0, 1)$. *Then if* U *is as in Proposition* 2.6, *there is an* $\varepsilon_1 > 0$ *such that for* $0 < \varepsilon < \varepsilon_1$ *all coexistence states for* (1.16) *in* U *are linearly stable.*

Proof. In light of Proposition 2.6, all coexistence states for (1.16) near $\gamma_{\bar{s}}$ may be parameterized in terms of ε and τ and for fixed ε are contained in Γ_ε. (To ensure that one has componentwise positive equilibrium solutions to (1.16), one must require that $\tau \in (0, 1)$.) It follows from (2.23) to (2.25) that we have the expansions

$$u(\cdot, \varepsilon, \tau) = \tau[\theta_{\bar{s}} + \varepsilon u_1(\tau) + 0(\varepsilon^2)], \tag{2.46}$$

$$v(\cdot, \varepsilon, \tau) = (1-\tau)[\theta_{\bar{s}} + \varepsilon v_1(\tau) + 0(\varepsilon^2)], \tag{2.47}$$

$$s(\varepsilon, \tau) = \bar{s} + \varepsilon s_1(\tau) + 0(\varepsilon^2), \tag{2.48}$$

where $0(\varepsilon^2)$ denotes functions which are bounded by $C\varepsilon^2$, with C independent of ε for $0 < \varepsilon \ll 1$ and $\tau \in [0, 1]$.

Our next step is to be identify $u_1(\tau)$ in (2.46) and $v_1(\tau)$ in (2.47). To this end we have the following result.

Lemma 2.8. *There is a* $\gamma = \gamma(\tau) \in \mathbb{R}$ *so that*

$$u_1(\tau) = -[A + \tau B + (1-\tau)C] + (1-\tau)\gamma\theta_{\bar{s}},$$

$$v_1(\tau) = -[A + \tau B - \tau C] - \tau\gamma\theta_{\bar{s}},$$

where the functions A, B and C are uniquely determined by:

$$\begin{aligned} &\Delta A + (1 - 2\theta_{\bar{s}})A = 0 \quad \text{in } \Omega \\ &(1-\bar{s})\nabla A \cdot \eta + \bar{s}A = \frac{s_1(\tau)}{1-\bar{s}}\theta_{\bar{s}} \quad \text{on } \partial\Omega, \end{aligned} \tag{2.49}$$

with $s_1(\tau)$ as in (2.48);

$$\begin{aligned} &\Delta B+(1-2\theta_{\bar{s}})B=g\theta_{\bar{s}} \quad \text{in } \Omega \\ &(1-\bar{s})\nabla B\cdot\eta+\bar{s}B=0 \quad \text{on } \partial\Omega; \end{aligned} \tag{2.50}$$

$$\begin{aligned} &\Delta C+(1-\theta_{\bar{s}})C=g\theta_{\bar{s}} \quad \text{in } \Omega \\ &(1-\bar{s})\nabla C\cdot\eta+\bar{s}C=0 \quad \text{on } \partial\Omega, \\ &\int_\Omega C\theta_{\bar{s}}\,\mathrm{d}x=0. \end{aligned} \tag{2.51}$$

Proof of Lemma 2.8. Direct calculation reveals that $u_1=u_1(\tau)$ and $v_1=v_1(\tau)$ satisfy

$$\Delta u_1+(1-\theta_{\bar{s}})u_1+\theta_{\bar{s}}[g-\tau u_1-(1-\tau)v_1]=0 \quad \text{in } \Omega \tag{2.52}$$

$$\Delta v_1+(1-\theta_{\bar{s}})v_1+\theta_{\bar{s}}(-\tau u_1-(1-\tau)v_1)=0 \quad \text{in } \Omega, \tag{2.53}$$

with

$$(1-\bar{s})\nabla u_1\cdot\eta+\bar{s}u_1=(1-\bar{s})\nabla v_1\cdot\eta+\bar{s}v_1=\frac{-s_1(\tau)}{1-\bar{s}}\theta_{\bar{s}} \quad \text{on} \quad \partial\Omega. \tag{2.54}$$

It follows from (2.52) to (2.54) that

$$\begin{aligned} &\Delta(u_1-v_1)+(1-\theta_{\bar{s}})(u_1-v_1)+g\theta_{\bar{s}}=0 \quad \text{in } \Omega \\ &(1-\bar{s})\nabla(u_1-v_1)\cdot\eta+\bar{s}(u_1-v_1)=0 \quad \text{on } \partial\Omega. \end{aligned} \tag{2.55}$$

We have from (2.51) and (2.55) that

$$\begin{aligned} &\Delta(u_1-v_1+C)+(1-\theta_{\bar{s}})(u_1-v_1+C)=0 \quad \text{in } \Omega \\ &(1-\bar{s})\nabla(u_1-v_1+C)+\bar{s}(u_1-v_1+C)=0 \quad \text{on } \partial\Omega. \end{aligned}$$

from which it follows that there is a $\gamma\in\mathbb{R}$ so that

$$u_1-v_1=-C+\gamma\theta_{\bar{s}}. \tag{2.56}$$

Multiplying (2.52) by τ and (2.53) by $1-\tau$ and adding the result tells us that

$$\begin{aligned} &[\Delta+(1-2\theta_{\bar{s}})](\tau u_1+(1-\tau)v_1)+\tau g\theta_{\bar{s}}=0 \quad \text{in } \Omega \\ &(1-\bar{s})\nabla(\tau u_1+(1-\tau)v_1)\cdot\eta+\bar{s}(\tau u_1+(1-\tau)v_1)=\frac{-s_1(\tau)}{1-\bar{s}}\theta_{\bar{s}} \quad \text{on } \partial\Omega. \end{aligned} \tag{2.57}$$

It follows from (2.49), (2.50) and (2.57) that

$$\tau u_1+(1-\tau)v_1=-A-\tau B. \tag{2.58}$$

Multiplying (2.56) by $1-\tau$ and adding to (2.58) gives $u_1(\tau)$ as claimed. Similarly, multiplying (2.56) by $-\tau$ and adding to (2.58) gives $v_1(\tau)$, completing the proof of Lemma 2.8.

To study the stability of coexistence states of (1.16), it suffices to consider the linear eigenvalue problem

$$\begin{aligned} &\Delta\varphi+(1+\varepsilon g-2u-v)\varphi+(-u)\psi=-\lambda\varphi \quad \text{in } \Omega \\ &\Delta\psi+(-v)\varphi+(1-u-2v)\psi=-\lambda\psi \quad \text{in } \Omega \\ &(1-s)\nabla\varphi\cdot\eta+s\varphi=0=(1-s)\nabla\psi\cdot\eta+s\psi \quad \text{on } \partial\Omega. \end{aligned} \tag{2.59}$$

When $\varepsilon=0$, we have $(u,v)=(\tau\theta_s,(1-\tau)\theta_s)$ for some $\tau\in[0,1]$ and for such (u,v) (2.59) has eigenvalue $\lambda=0$ with corresponding eigenfunction $(\theta_s,-\theta_s)$. Since $\theta_s>0$ and (1.16) is monotonic in the skew order $(u_1,v_1)\le(u_2,v_2)\Leftrightarrow u_1\le u_2$ and $v_1\ge v_2, \lambda=0$ is the principal eigenvalue for (2.59). Moreover, it is algebraically simple and all other eigenvalues λ of (2.59) have positive real parts. The spectral perturbation theory for compact operators [12] guarantees that for $0<\varepsilon\ll 1$, if (u,v) is a coexistence state for (1.16) with (u,v,s,ε) near $\gamma_{\bar{s}}$, where $\gamma_{\bar{s}}$ is as in (2.21), then (2.59) have a unique principal eigenvalue, denoted $\lambda(\varepsilon,\tau)$, with corresponding eigenfunction $(\varphi(\varepsilon,\tau),\psi(\varepsilon,\tau))$ with $\varphi>0$ in Ω and $\psi<0$ in Ω, so that $\lim_{\varepsilon\to o^+}\lambda(\varepsilon,\tau)=0$. All other eigenvalues of (2.59) have positive real parts which are uniformly bounded away from zero for all $\tau\in[0,1]$ and $0<\varepsilon\ll 1$. Consequently, the coexistence states (u,v) with (u,v,s,ε) near $\gamma_{\bar{s}}$ are linearly stable provided $\lambda(\varepsilon,\tau)>0$ for $\tau\in[0,1]$ and $0<\varepsilon\ll 1$. We now obtain a formula for $\lambda(\varepsilon,\tau)$.

Lemma 2.9. *Suppose that $G(\bar{s})=0$ and $G'(\bar{s})\neq 0$ for some $\bar{s}\in(0,1)$. Let $(u(\cdot,\varepsilon,\tau),v(\cdot,\varepsilon,\tau),s(\varepsilon,\tau))$ denote the coexistence states and corresponding boundary parameters on Γ_ε given by Proposition* 2.6. *Then for $0<\tau<1$ and $0<\varepsilon\ll 1$, the principal eigenvalue $\lambda(\varepsilon,\tau)$ satisfies*

$$\lambda(\varepsilon,\tau)=2\tau(1-\tau)\varepsilon^2\left[\frac{\int_\Omega g\theta_{\bar{s}}(B-C)\,\mathrm{d}x}{\int_\Omega\theta_{\bar{s}}^2\,\mathrm{d}x}+C_1(\varepsilon_1,\tau)\varepsilon\right], \tag{2.60}$$

where $C_1(\varepsilon_1,\tau)\in\mathbb{R}$ is uniformly bounded for $0<\tau<1$ and $0<\varepsilon\ll 1$.

Proof of Lemma 2.9. Let $u=u(\cdot,\varepsilon,\tau), v=v(\cdot,\varepsilon,\tau)$ be a coexistence state associated to $s=s(\varepsilon,\tau)$ and $\varphi=\varphi(\cdot,\varepsilon,\tau), \psi=\psi(\cdot,\varepsilon,\tau)$ the eigenfunction corresponding to $\lambda=\lambda(\varepsilon,\tau)$. We have

$$\begin{aligned} &\Delta u+u[1+\varepsilon g-u-v]=0 \\ & \qquad\qquad\qquad\qquad\qquad \text{in } \Omega \\ &\Delta v+v[1-u-v]=0 \\ &(1-s)\nabla u\cdot\eta+su=0=(1-s)\nabla v\cdot\eta+sv \qquad \text{on } \partial\Omega. \end{aligned} \tag{2.61}$$

If we multiply the top equation in (2.59) by v, integrate over Ω and employ the second equation in (2.61) we get

$$\begin{aligned} -\lambda\int_\Omega \varphi v\,\mathrm{d}x &= \int_\Omega [v\Delta\varphi+v(1-u-v)\varphi]\mathrm{d}x+\varepsilon\int_\Omega g\varphi v\,\mathrm{d}x \\ &\quad -\int_\Omega (uv\varphi+uv\psi)\,\mathrm{d}x \\ &= \varepsilon\int_\Omega g\varphi v\,\mathrm{d}x-\int_\Omega uv(\varphi+\psi)\,\mathrm{d}x. \end{aligned} \tag{2.62}$$

Likewise, if we multiply the second equation in (2.59) by u, integrate over Ω and employ the top equation in (2.61) we get

$$-\lambda\int_\Omega u\psi\,\mathrm{d}x=-\int_\Omega uv(\varphi+\psi)\,\mathrm{d}x-\varepsilon\int_\Omega gu\psi\,\mathrm{d}x. \tag{2.63}$$

Subtracting (2.63) from (2.62) yields

$$\lambda\int_\Omega (u\psi-v\varphi)\,\mathrm{d}x=\varepsilon\int_\Omega g(u\psi+v\varphi)\,\mathrm{d}x. \tag{2.64}$$

Now we recall that we have expansions (2.46)–(2.48) for u, v and s. For φ and ψ we have

$$\varphi=\theta_{\bar{s}}+\varepsilon\varphi_1(\tau)+0(\varepsilon^2) \tag{2.65}$$

and

$$\psi=-\theta_{\bar{s}}+\varepsilon\psi_1(\tau)+0(\varepsilon^2). \tag{2.66}$$

From (2.46), (2.47), (2.65) and (2.66) we may conclude that $\int_\Omega(u\psi-v\varphi)\,\mathrm{d}x\neq 0$ for any $\tau\in(0,1)$ and $0<\varepsilon\ll 1$, so that (2.64) yields

$$\lambda=-\varepsilon\int_\Omega g(u\psi+v\varphi)\,\mathrm{d}x\Big/\int_\Omega (u\psi-v\varphi)\,\mathrm{d}x. \tag{2.67}$$

Notice that (2.67) implies that $(\partial\lambda/\partial\varepsilon)(0,\tau)=0$ for all $\tau\in(0,1)$. Consquently, if we differentiate (2.59) with respect to ε at $\varepsilon=0$ and employ the expansions for φ, ψ, u, v and s we obtain

$$\left.\begin{aligned}&\Delta\varphi_1+(1-\theta_{\bar s})\varphi_1-\tau\theta_{\bar s}(\varphi_1+\psi_1)+\theta_{\bar s}(g-\tau u_1-(1-\tau)v_1)=0\\&\Delta\psi_1+(1-\theta_{\bar s})\psi_1-(1-\tau)\theta_{\bar s}(\varphi_1+\psi_1)+\theta_{\bar s}(\tau u_1+(1-\tau)v_1)=0\end{aligned}\right\}\quad \text{in } \Omega,$$

$$\left.\begin{aligned}&(1-\bar s)\nabla\varphi_1\cdot\eta+\bar s\varphi_1=\frac{-s_1}{1-\bar s}\theta_{\bar s}\\&(1-\bar s)\nabla\psi_1\cdot\eta+\bar s\psi_1=\frac{s_1}{1-\bar s}\theta_{\bar s}\end{aligned}\right\}\quad\text{on } \Omega. \tag{2.68}$$

It follows from (2.68) that $\varphi_1+\psi_1$ satisfies

$$\begin{aligned}&\Delta(\varphi_1+\psi_1)+(1-2\theta_{\bar s})(\varphi_1+\psi_1)=-g\theta_{\bar s} &&\text{in } \Omega\\&(1-\bar s)\nabla(\varphi_1+\psi_1)\cdot\eta+\bar s(\varphi_1+\psi_1)=0 &&\text{on } \partial\Omega,\end{aligned}$$

so that (2.50) implies that

$$\varphi_1+\psi_1=-B. \tag{2.69}$$

Employing (2.69), (2.58), (2.49), (2.50) and (2.51), we obtain that there is $\gamma_2=\gamma_2(\tau)$ so that

$$\varphi_1+A+2\tau B-(2\tau-1)C=\gamma_2\theta_{\bar s}. \tag{2.70}$$

Hence we have that

$$\varphi_1=\varphi_1(\tau)=-A-2\tau B+(2\tau-1)C+\gamma_2\theta_{\bar s}. \tag{2.71}$$

Consequently, by (2.69),

$$\psi_1=\psi_1(\tau)=A+(2\tau-1)B-(2\tau-1)C-\gamma_2\theta_{\bar s}. \tag{2.72}$$

Proposition 2.2 guarantees that $\int_\Omega guv\,dx=0$. Substituting the expansions (2.46) and (2.47) for u and v, respectively, into $\int_\Omega guv\,dx$ and employing Lemma 2.8 yields

$$0=\tau(1-\tau)\left[\int_\Omega g\theta_{\bar s}^2\,dx-\varepsilon\int_\Omega g\theta_{\bar s}[2A+2\tau B+(1-2\tau)C]dx+0(\varepsilon^2)\right].$$

Since $G(\bar s)=0$, we have

$$\int_\Omega g\theta_{\bar s}[2A+2\tau B+(1-2\tau)C]dx=0. \tag{2.73}$$

We may now establish (2.60). We have $\lambda(\varepsilon,\tau)$ given in (2.67). It is straight-forward to see that

$$\int_\Omega (v\varphi - u\psi)\,\mathrm{d}x = \int_\Omega \theta_{\bar{s}}^2\,\mathrm{d}x + 0(\varepsilon). \tag{2.74}$$

Substituting for u, v, φ and ψ in $\int_\Omega g(v\varphi + u\psi)\,\mathrm{d}x$, we have

$$\begin{aligned}
&\int_\Omega g(v\varphi+u\psi)\,\mathrm{d}x \\
&= (1-2\tau)\int_\Omega g\theta_{\bar{s}}^2\,\mathrm{d}x \\
&\quad +\varepsilon\int_\Omega g\theta_{\bar{s}}[(1-\tau)v_1 - \tau u_1 + (1-\tau)\varphi_1 + \tau\psi_1] + 0(\varepsilon^2) \\
&= \varepsilon\int_\Omega g\theta_{\bar{s}}[(4\tau-2)A + (6\tau^2-4\tau)B + (-1+6\tau-6\tau^2)C] + 0(\varepsilon^2) \\
&= 2\varepsilon\tau(1-\tau)\left[\int_\Omega g\theta_{\bar{s}}(C-B) + 0(\varepsilon)\right].
\end{aligned} \tag{2.75}$$

Substituting (2.74) and (2.75) into (2.67) establishes (2.60) and completes proof of Lemma 2.9.

By Lemma 2.9, we will have that $\lambda(\varepsilon,\tau) > 0$ for $\tau \in (0,1)$ and $0 < \varepsilon \ll 1$ provided that

$$\int_\Omega g\theta_{\bar{s}}(B-C) > 0. \tag{2.76}$$

This result may be argued along the lines of Lemma 4.15 in [11] and thus we refer the interested reader to [11]. Now having $\lambda(\varepsilon,\tau) > 0$ guarantees the linear stability of (u, v) and completes the proof of Proposition 2.7.

We are now ready to prove Theorem 2.5.

Proof of Theorem 2.5. By choosing $\varepsilon_0 > 0$ small enough, we have that all componentwise nonnegative equilibria to (1.16) in a neighborhood of $\gamma_{\bar{s}}$ are as described by Proposition 2.6. Hence, for any $\varepsilon \in (0, \varepsilon_0)$ it suffices to consider Γ_ε as given in Proposition 2.6. By (2.48), we have that

$$s(\varepsilon,\tau) = \bar{s} + \varepsilon s_1(\tau) + 0(\varepsilon^2).$$

We show that $s_1(\tau)$ is a nonconstant affine function of τ. To this end, let $A_0(x) = (\partial\theta_s/\partial s)|_{s=\bar{s}}$. Then A_0 satisfies

$$\begin{aligned}
&\Delta A_0 + (1-2\theta_{\bar{s}})A_0 = 0 \quad \text{in } \Omega \\
&(1-\bar{s})\nabla A_0\cdot\eta + \bar{s}A_0 = \frac{-1}{1-\bar{s}}\theta_{\bar{s}} \quad \text{on } \partial\Omega.
\end{aligned} \tag{2.77}$$

It follows from (2.49) and (2.77) that

$$A = -s_1(\tau)A_0. \tag{2.78}$$

Combining (2.73) and (2.78) we have

$$2s_1(\tau)\int_\Omega g\theta_{\bar{s}}A_0\,\mathrm{d}x = \int_\Omega g\theta_{\bar{s}}[2\tau B + (1-2\tau)C]\mathrm{d}x. \tag{2.79}$$

Now $G'(\bar{s}) = 2\int_\Omega g\theta_{\bar{s}}\frac{\partial\theta_s}{\partial s}\big|_{s=\bar{s}}\,\mathrm{d}x = 2\int_\Omega g\theta_{\bar{s}}A_0$. So $\int_\Omega g\theta_{\bar{s}}A_0\,\mathrm{d}x \neq 0$ and (2.79) implies that

$$s_1(\tau) = \left[\frac{\int_\Omega g\theta_{\bar{s}}(B-C)\,\mathrm{d}x}{\int_\Omega g\theta_{\bar{s}}A_0\,\mathrm{d}x}\right]\tau + \frac{1}{2}\left[\frac{\int_\Omega g\theta_{\bar{s}}C\,\mathrm{d}x}{\int_\Omega g\theta_{\bar{s}}A_0\,\mathrm{d}x}\right]. \tag{2.80}$$

That $s_1(\tau)$ is as indicated follows from (2.76). So, for $0 < \varepsilon \ll 1, s(\varepsilon,\tau)$ is strictly monotonic in τ.

Consequently, we may define

$$s_*(\varepsilon) = \min_{0\leq\tau\leq 1} s(\varepsilon,\tau), \qquad s^*(\varepsilon) = \max_{0\leq\tau\leq 1} s(\varepsilon,\tau). \tag{2.81}$$

Proposition 2.6 guarantees that (1.16) has a coexistence state for s in a neighborhood of $\bar{s}$ if and only if $s \in (s_*(\varepsilon), s^*(\varepsilon))$. The monotonicity of $s(\varepsilon,\tau)$ in τ guarantees that any such coexistence state, if it exists, is unique. Propositoin 2.7 guarantees the local stability of the coexistence state. Since (1.16) is a monotonic system, the coexistence state must in fact be globally asymptotically stable and the proof of Theorem 2.5 is complete.

As a corollary to Theorem 2.5, we have the following.

Theorem 2.10. Suppose that $G(s)$ changes sign at $\bar{s}_1 < \bar{s}_2 < \cdots < \bar{s}_n$ in (0,1) with $G'(\bar{s}_i) \neq 0$ for $i = 1,\ldots,n$. Then for any sufficient small $\varepsilon > 0$, (1.16) exhibits $n-1$ changes of competitive advantage in which the species holding the competitive advantage excludes the other from Ω over time. Moreover, there is an $\varepsilon_0 > 0$ so that for each $i \in \{1,\ldots,n\}$ and each $\varepsilon \in (0,\varepsilon_0)$, there are $s_{*i}(\varepsilon)$ and $s_i^*(\varepsilon)$ with $\lim_{\varepsilon\to 0} s_{*i}(\varepsilon) = \bar{s}_i = \lim_{\varepsilon\to 0} s_i^*(\varepsilon)$ so that (1.16) admits a coexistence state for s near $\bar{s}_i$ if and only if s lies between $s_{*i}(\varepsilon)$ and $s_i^*(\varepsilon)$ (See Fig. 1). Moreover, such a coexistence state to (1.16) is unique and globally asymptotically stable.

3. GUARANTEEING THE EXISTENCE OF SUITABLE PERTURBATIONS

The results of the preceding section are predicated upon having a perturbation (1.16) of (1.17) so that the conditions of Theorem 2.4 or Theorem 2.10 are met. Specifically, the function g which determines (1.16) must be such that the corresponding function $G:[0,1]\rightarrow \mathbb{R}$ changes sign more than once (in order for Theorem 2.4 to hold) and with only simple zeros (in order for the stronger Theorem 2.10 to hold.) In this section, we show first that such g can be constructed provided for some $n \geqslant 3$, $\{\theta_{s_1}^2,\ldots,\theta_{s_n}^2\}$ is linearly indepedent in $L^2(\Omega)$, where $s_i\in[0,1]$ and (without loss of generality) $s_1<s_2<\cdots<s_n$. We then examine the question of linear indepedence. We show that for any domain Ω, 4 such θ's always exist and that in the special case in which Ω is an interval, such sets exist for any $n\geqslant 3$.

To these ends, as before, for each $s\in[0,1]$, let θ_s denote the unique positive solution of

$$\begin{aligned} -\Delta y &= y(1-y) \quad \text{in } \Omega \\ (1-s)\nabla y\cdot\eta+sy &= 0 \quad \text{on } \partial\Omega. \end{aligned}$$

The existence of θ_s is guaranteed for all $s\in[0,1]$ provided that Ω is such that $\lambda^1(\Omega,1)<1$, where $\lambda=\lambda^1(\Omega,1)$ is the principal eigenvalue in the problem

$$\begin{aligned} -\Delta\phi &= \lambda\phi \quad \text{in } \Omega \\ \phi &= 0 \quad \text{on } \partial\Omega. \end{aligned}$$

In this case, $\theta_s\in C^{2+\alpha}(\overline{\Omega})$ and the map $s\rightarrow\theta_s$ is a differentiable map from [0,1] into $C^{2+\alpha}(\overline{\Omega})$[4]. Hence $s\rightarrow\theta_s^2$ can be viewed as a diferentiable map from [0,1] into $L^2(\Omega)$ and if Λ is any bounded linear functional on $L^2(\Omega)$, then the map

$$s\rightarrow\Lambda(\theta_s^2)$$

is a differentiable map from [0,1] into $\mathbb{R}$.

Suppose now that $0\leqslant s_1<s_2<\cdots<s_n\leqslant 1$ are such that the collection $\{\theta_{s_1}^2,\ldots,\theta_{s_n}^2\}$ is linearly independent. Then a basic result of functional analysis (e.g., [14, Lemma 4.14]) tells us that there are bounded linear functionals $\{\Lambda_1,\ldots,\Lambda_n\}$ on $L^2(\Omega)$ so that

$$\Lambda_i(\theta_{s_j}^2)=\delta_{ij},$$

where δ_{ij} is the Kronecker delta. The Riesz Representation Theorem implies that there are elements $\{h_1, \ldots, h_n\} \subseteq L^2(\Omega)$ so that $\Lambda_i : L^2(\Omega) \to \mathbb{R}$ is given by

$$\Lambda_i(f) = \int_\Omega h_i f \, \mathrm{d}x.$$

For $i = 1, \ldots, n, h_i$ can be approximated in $L^2(\Omega)$ by functions in $C^\alpha(\bar{\Omega})$. So, for each $i \in \{1, \ldots, n\}$, choose a sequence $\{\tilde{h}_{ik}\}_{k=1}^\infty$ of functions in $C^\alpha(\bar{\Omega})$ so that $\|\tilde{h}_{ik} - h_i\|_2 \to 0$ as $k \to \infty$. Let $0 < \varepsilon \ll 1$ be given. Since

$$\left| \int_\Omega \tilde{h}_{ik} \theta_{s_j}^2 \, \mathrm{d}x - \int_\Omega h_i \theta_{s_j}^2 \, \mathrm{d}x \right| \leqslant \|\tilde{h}_{ik} - h_i\|_2 \|\theta_{s_j}^2\|_2$$

for all $i, j \in \{1, \ldots, n\}, k \in \mathscr{Z}^+$, it follows that for each $i \in \{1, \ldots, n\}$ we may choose a $k(i)$ so that

$$\int_\Omega \tilde{h}_{ik(i)} \theta_{s_j}^2 \, \mathrm{d}x > 1 - \frac{\varepsilon}{n}$$

if $i = j$ and

$$\left| \int_\Omega \tilde{h}_{ik(i)} \theta_{s_j}^2 \, \mathrm{d}x \right| < \frac{\varepsilon}{n}$$

if $i \neq j$.

Now define a map $V: \mathbb{R}^n \to C^\alpha(\bar{\Omega})$ by

$$V(c_1, \ldots, c_n) = \sum_{i=1}^n c_i \tilde{h}_{ik(i)}.$$

Then if $c_i^0 = (-1)^{i+1}$, we get that

$$\int_\Omega V(c_1^0, \ldots, c_n^0) \theta_{s_j}^2 \, \mathrm{d}x = \sum_{i=1}^n (-1)^{i+1} \int_\Omega \tilde{h}_{ik(i)} \theta_{s_j}^2 \, \mathrm{d}x > 1 - \varepsilon$$

if j is odd, and

$$< -1 + \varepsilon$$

if j is even. Consequently, if we define $G: \mathbb{R}^n \times [0, 1] \to \mathbb{R}$ by

$$G(c_1, \ldots, c_n, s) = \int_\Omega V(c_1, \ldots, c_n) \theta_s^2 \, \mathrm{d}x,$$

then $G(c_1^0, \ldots, c_n^0, s)$ changes sign at least $n-1$ times on [0,1]. There will be a $\delta > 0$ so that if $|(c_1, \ldots, c_n) - (c_1^0, \ldots, c_n^0)| < \delta$,

$$G(c_1, \ldots, c_n, s_j) > 1 - 2\varepsilon,$$

when j is odd and

$$G(c_1, \ldots, c_n, s_j) < -1 + 2\varepsilon,$$

when j is even. The Transversality Theorem [10, p. 68] guarantees for some $(\bar{c}_1, \ldots, \bar{c}_n)$ with $|(\bar{c}_1, \ldots, \bar{c}_n) - (c_1^0, \ldots, c_n^0)| < \delta$, $G(\bar{c}_1, \ldots, \bar{c}_n, s)$ has only simple zeros. Theorem 2.4 holds for any $(c_1, \ldots, c_n)$ with $|(c_1, \ldots, c_n) - (c_1^0, \ldots, c_n^0)| < \delta$ and the stronger Theorem 2.10 holds for $(\bar{c}_1, \ldots, \bar{c}_n)$ or any other $(c_1, \ldots, c_n)$ with $|(c_1, \ldots, c_n) - (c_1^0, \ldots, c_n^0)| < \delta$ such that $G(c_1, \ldots, c_n, s)$ has only simple zeros on [0,1].

The preceding discussion shows that there is a perturbation of (1.17) so that the perturbed system (1.16) exhibits at least n reversals of competitive advantage between the two species as matrix hostility increases as described in Theorems 2.4 and 2.10 so long as there are $n+1$ values of s, $0 \leqslant s_0 \leqslant s_1 < \cdots < s_n \leqslant 1$ so that $\{\theta_{s_0}^2, \theta_{s_1}^2, \ldots, \theta_{s_n}^2\}$ are linearly independent. Consequently we are led to the question of linear independence of such sets. We have the following result.

Theorem 3.1. (i) *For any domain* Ω *satisfying the hypotheses of Section* 1, *there are* s_1 *and* s_2 *with* $0 < s_1 < s_2 < 1$ *so that* $\{1, \theta_{s_1}^2, \theta_{s_2}^2, \theta_1^2\}$ *is linearly independent. Consequently, there are always perturbations of* (1.17) *so that the perturbed system* (1.16) *predicts at least* 3 *reversals of competitive advantage as matrix hostility increases as described in Theorems* 2.4 *and* 2.10.
(ii) *If* $\Omega = [a, b]$ *and* n *is any positive integer, there are* $s_0, s_1, \ldots, s_n$ *with* $0 \leqslant s_0 < s_1 < \cdots < s_n \leqslant 1$ *so that* $\{\theta_{s_0}^2, \theta_{s_1}^2, \ldots, \theta_{s_n}^2\}$ *is linearly independent. Consequently, in one space dimension there can be an arbitrary number of reversals of competitive advantage as matrix hostility increases as described in Theorems* 2.4 *and* 2.10.

Proof. (i) It is not difficult to see that $\{\theta_0^2, \theta_s^2, \theta_1^2\} = \{1, \theta_s^2, \theta_1^2\}$ is linearly indepedent for any $s \in (0, 1)$. For, if

$$c_0 + c_s\theta_s^2 + c_1\theta_1^2 = 0$$

in Ω, then

$$2c_s\theta_s(\theta_s)_{x_i} + 2c_1\theta_1(\theta_1)_{x_i} = 0$$

in Ω for $i=1,\ldots,k$. It follows that

$$c_s\theta_s\nabla\theta_s\cdot\eta=0$$

on $\partial\Omega$. Hence, $c_s(s/(1-s))\theta_s^2=0$ on $\partial\Omega$, so that $c_s=0$. Since θ_1^2 is non-constant,

$$c_0+c_1\theta_1^2=0$$

in Ω implies that $c_0=0=c_1$.

So now consider $\{1,\theta_{s_1}^2,\theta_{s_2}^2,\theta_1^2\}$, where $0<s_1<s_2<1$, and suppose

$$c_0+c_{s_1}\theta_{s_1}^2+c_{s_2}\theta_{s_2}^2+c_1\theta_1^2=0$$

in Ω. Then

$$c_{s_1}\theta_{s_1}(\theta_{s_1})_{x_i}+c_{s_2}\theta_{s_2}(\theta_{s_2})_{x_i}+c_1\theta_1(\theta_1)_{x_i}=0$$

in Ω for $i=1,\ldots,n$. It follows that on $\partial\Omega$

$$\begin{pmatrix} c_{s_1} & c_{s_2} \\ c_{s_1}\left(\frac{s_1}{1-s_1}\right) & c_{s_2}\left(\frac{s_2}{1-s_2}\right)\end{pmatrix}\begin{pmatrix}\theta_{s_1}^2\\ \theta_{s_2}^2\end{pmatrix}=\begin{pmatrix}-c_0\\ 0\end{pmatrix}.$$

Since

$$\begin{vmatrix} c_{s_1} & c_{s_2} \\ c_{s_1}\left(\frac{s_1}{1-s_1}\right) & c_{s_2}\left(\frac{s_2}{1-s_2}\right)\end{vmatrix}=c_{s_1}c_{s_2}\left(\frac{s_2}{1-s_2}-\frac{s_1}{1-s_1}\right),$$

if $c_{s_1}\neq 0$ and $c_{s_2}\neq 0,\theta_{s_1}^2$ and $\theta_{s_2}^2$ are constant on $\partial\Omega$. Consequently, θ_{s_1} and $\nabla\theta_{s_1}\cdot\eta$ and θ_{s_2} and $\nabla\theta_{s_2}\cdot\eta$ are constant on $\partial\Omega$. It follows from [15] that Ω is a ball. Consequently, unless Ω is a ball, at least one of c_{s_1} and c_{s_2} must be zero. If such is the case, the linear independence of $\{1,\theta_{s_1}^2,\theta_{s_2}^2,\theta_1^2\}$ follows from the linear independence of $\{1,\theta_s^2,\theta_1^2\}$ for any $s\in(0,1)$.

So long as Ω is not a ball, $\{1,\theta_{s_1}^2,\theta_{s_2}^2,\theta_1^2\}$ is linearly independent for any choice of $s_1,s_2\in(0,1)$ with $s_1<s_2$. In the case when Ω is a ball, our result is not quite as general. Namely, we can show that for any $s_1\in(0,1)$ there is an $\bar{s}_2>s_1$ so that $\{1,\theta_{s_1}^2,\theta_{s_2}^2,\theta_1^2\}$ is linearly independent for $s_2>\bar{s}_2$.

Without loss of generality, assume that Ω is the unit ball in $\mathbb{R}^N$, $N > 1$. Since for any $s \in [0, 1]$,

$$\Delta\theta + \theta - \theta^2 = 0 \quad \text{in } \Omega,$$
$$(1-s)\nabla\theta \cdot \eta + s\theta = 0 \quad \text{on } \partial\Omega$$

can have at most one positive solution, it follows that for all $s \in [0, 1]$, θ_s satisfies

$$\begin{aligned} &(\theta_s)_{rr} + \frac{N-1}{r}(\theta_s)_r + \theta_s - \theta_s^2 = 0 \quad \text{on} \quad (0,1), \\ &(\theta_s)_r(0) = 0, \\ &(1-s)(\theta_s)_r(1) + s\theta_s(1) = 0. \end{aligned} \tag{3.1}$$

Now suppose that

$$c_0 + c_{s_1}\theta_{s_1}^2 + c_{s_2}\theta_{s_2}^2 + c_1\theta_1^2 = 0 \tag{3.2}$$

in (0,1). Differentiation with respect to r yields

$$c_{s_1}\theta_{s_1}(\theta_{s_1})_r + c_{s_2}\theta_{s_2}(\theta_{s_2})_r + c_1\theta_1(\theta_1)_r = 0 \tag{3.3}$$

in (0,1), so that

$$\begin{aligned} &c_{s_1}(\theta_{s_1})_r^2 + c_{s_1}\theta_{s_1}(\theta_{s_1})_{rr} + c_{s_2}(\theta_{s_2})_r^2 + c_{s_2}\theta_{s_2}(\theta_{s_2})_{rr} + c_1(\theta_1)_r^2 \\ &\quad + c_1\theta_1(\theta_1)_{rr} = 0 \end{aligned} \tag{3.4}$$

in (0,1). We obtain from (3.1) that

$$\begin{aligned} &c_{s_1}(\theta_{s_1})_r^2 + c_{s_1}\theta_{s_1}\left[\theta_{s_1}^2 - \theta_{s_1} - \frac{N-1}{r}(\theta_{s_1})_r\right] + c_{s_2}(\theta_{s_2})_r^2 \\ &\quad + c_{s_2}\theta_{s_2}\left[\theta_{s_2}^2 - \theta_{s_2} - \frac{N-1}{r}(\theta_{s_2})_r\right] + c_1(\theta_1)_r^2 \\ &\quad + c_1\theta_1\left[\theta_1^2 - \theta_1 - \frac{N-1}{r}(\theta_1)_r\right] \\ &= 0 \end{aligned} \tag{3.5}$$

in (0,1). Using (3.2) and (3.3) we may reduce (3.5) to

$$c_{s_1}(\theta_{s_1})_r^2 + c_{s_1}\theta_{s_1}^3 + c_{s_2}(\theta_{s_2})_r^2 + c_{s_2}\theta_{s_2}^3 + c_1(\theta_1)_r^2 + c_1\theta_1^3 + c_0 = 0. \tag{3.6}$$

Differentiating (3.6) yields

$$\begin{aligned} &2c_{s_1}(\theta_{s_1})_r(\theta_{s_1})_{rr} + 3c_{s_1}\theta_{s_1}^2(\theta_{s_1})_r + 2c_{s_2}(\theta_{s_2})_r(\theta_{s_2})_{rr} + 3c_{s_2}\theta_{s_2}^2(\theta_{s_2})_r \\ &\quad + 2c_1(\theta_1)_r(\theta_1)_{rr} + 3c_1\theta_1^2(\theta_1)_r = 0 \end{aligned} \tag{3.7}$$

in (0,1). Substituting via (3.1) yields

$$\begin{aligned}
&2c_{s_1}(\theta_{s_1})_r\left[-\frac{(N-1)}{r}(\theta_{s_1})_r-\theta_{s_1}+\theta_{s_1}^2\right]+3c_{s_1}\theta_{s_1}^2(\theta_{s_1}^2)_r\\
&\quad+2c_{s_2}(\theta_{s_2})_r\left[-\frac{(N-1)}{r}(\theta_{s_2})_r-\theta_{s_2}+\theta_{s_2}^2\right]+3c_{s_2}\theta_{s_2}^2(\theta_{s_2}^2)_r\\
&\quad+2c_1(\theta_1)_r\left[-\frac{(N-1)}{r}(\theta_1)_r-\theta_1+\theta_1^2\right]+3c_1\theta_1^2(\theta_1)_r\\
&=0
\end{aligned}\tag{3.8}$$

in (0,1). Employing (3.3) we may rewrite (3.8) as

$$\begin{aligned}
&-2\frac{(N-1)}{r}\left[c_{s_1}(\theta_{s_1})_r^2+c_{s_2}(\theta_{s_2})_r^2+c_1(\theta_1)_r^2\right]\\
&\quad+5\left[c_{s_1}\theta_{s_1}^2(\theta_{s_1})_r+c_{s_2}\theta_{s_2}^2(\theta_{s_2})_r+c_1\theta_1^2(\theta_1)_r\right]\\
&=0
\end{aligned}\tag{3.9}$$

in (0,1). Using (3.4), we may express (3.9) as

$$\begin{aligned}
&2\frac{(N-1)}{r}\left[c_{s_1}\theta_{s_1}(\theta_{s_1})_{rr}+c_{s_2}\theta_{s_2}(\theta_{s_2})_{rr}+c_1\theta_1(\theta_1)_{rr}\right]\\
&\quad+5\left[c_{s_1}\theta_{s_1}^2(\theta_{s_1})_r+c_{s_2}\theta_{s_2}^2(\theta_{s_2})_r+c_1\theta_1^2(\theta_1)_r\right]\\
&=0
\end{aligned}\tag{3.10}$$

in (0,1). Now using (3.1) to substitute for $(\theta_{s_1})_{rr}$ and $(\theta_{s_2})_{rr}$ in (3.10), we obtain

$$\begin{aligned}
&\frac{2(N-1)}{r}\left[-c_{s_1}\frac{(N-1)}{r}\theta_{s_1}(\theta_{s_1})_r-c_{s_1}\theta_{s_1}^2+c_{s_1}\theta_{s_1}^3\right]\\
&\quad+\frac{2(N-1)}{r}\left[-c_{s_2}\frac{(N-1)}{r}\theta_{s_2}(\theta_{s_2})_r-c_{s_2}\theta_{s_2}^2+c_{s_2}\theta_{s_2}^3\right]\\
&\quad+\frac{2(N-1)}{r}c_1\theta_1(\theta_1)_{rr}+5\left[c_{s_1}\theta_{s_1}^2(\theta_{s_1})_r+c_{s_2}\theta_{s_2}^2(\theta_{s_2})_r+c_1\theta_1^2(\theta_1)_r\right]\\
&=0
\end{aligned}\tag{3.11}$$

in (0,1). Now set $r=1$ in (3.3) and (3.11) to get

$$c_{s_1}\frac{s_1}{1-s_1}\theta_{s_1}^2(1)+c_{s_2}\frac{s_2}{1-s_2}\theta_{s_2}^2(1)=0 \tag{3.12}$$

and

$$\begin{aligned} &c_{s_1}\theta_{s_1}^2(1)\left[2(N-1)^2\frac{s_1}{1-s_1}-2(N-1)+\theta_{s_1}(1)(2(N-1)-\frac{5s_1}{1-s_1})\right] \\ &+c_{s_2}\theta_{s_2}^2(1)\left[2(N-1)^2\frac{s_2}{1-s_2}-2(N-1)+\theta_{s_2}(1)(2(N-1)-\frac{5s_2}{1-s_2})\right] \\ &=0. \end{aligned} \tag{3.13}$$

The equations (3.12) and (3.13) can be written as

$$A\begin{bmatrix} c_{s_1}\theta_{s_1}^2(1) \\ c_{s_2}\theta_{s_2}^2(1) \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \end{bmatrix}, \tag{3.14}$$

where

$$A=\begin{bmatrix} \frac{s_1}{1-s_1} & \frac{s_2}{1-s_2} \\ 2(N-1)^2\frac{s_1}{1-s_1}-2(N-1) & 2(N-1)^2\frac{s_2}{1-s_2}-2(N-1) \\ +\theta_{s_1}(1)(2(N-1)-5(\frac{s_1}{1-s_1})) & +\theta_{s_2}(1)(2(N-1)-5(\frac{s_2}{1-s_2})) \end{bmatrix}. \tag{3.15}$$

From (3.15) it is straightforward to calculate that

$$\begin{aligned} |A| = {} & 2(N-1)(\frac{s_2}{1-s_2})(1-\theta_{s_1}(1)) \\ & +2(N-1)(\frac{s_1}{1-s_1})(\theta_{s_2}(1)-1) \\ & +5(\frac{s_1}{1-s_1})(\frac{s_2}{1-s_2})(\theta_{s_1}(1)-\theta_{s_2}(1)). \end{aligned} \tag{3.16}$$

The first and third terms in the expression for $|A|$ increase in s_2 on the interval $[s_1, 1]$, while the second decreases. Consequently, it is not immediate that $|A|$ increases as s_2 increases on $[s_1, 1]$. (Since $|A|=0$ when $s_2=s_1$, knowing that $|A|$ increases with s_2 on [0,1] would have guaranteed that $|A|\neq 0$ for all $s_2 \in (s_1, 1)$.) However, since $\lim_{s_2 \nearrow 1}(s_2/(1-s_2))=+\infty$ and $\lim_{s_2\nearrow 1}\theta_{s_2}(1)=0$, it follows from (3.16) that:

$$\lim_{s_2\nearrow 1}|A|=+\infty. \tag{3.17}$$

Consequently, there is $\bar{s}_2>s_1$ so that $|A|>0$ for $s_2 \geqslant \bar{s}_2$. From (3.14) we obtain that if $s_2 \geqslant \bar{s}_2$,

$$c_{s_1}\theta_{s_1}^2(1)=0=c_{s_2}\theta_{s_2}^2(1) \tag{3.18}$$

and hence

$$c_{s_1} = 0 = c_{s_2}. \tag{3.19}$$

It now follows that $\{1, \theta_{s_1}^2, \theta_{s_2}^2, \theta_1^2\}$ is lineraly independent so long as $s_2 \geqslant \bar{s}_2$.

(ii) In the case of one space dimension, we consider the equation

$$\theta'' + \theta(1-\theta) = 0. \tag{3.20}$$

Any solution to (3.20) is analytic on its domain of definition. Ludwig, Aronson and Weinberger [13] made a systematic analysis of solutions to (3.20), exploiting the fact that (3.20) may be recast in the system form

$$\begin{aligned} \theta' &= -\rho \\ \rho' &= \theta(1-\theta) \end{aligned}$$

so that phase plane analysis may be brought to bear on the problem. From these results, one may conclude that for any $\theta_0 \in (0, 1)$, the solution $\theta(x, \theta_0)$ to (3.20) satisfying

$$\begin{aligned} \theta(0) &= \theta_0 \\ \theta'(0) &= 0 \end{aligned} \tag{3.21}$$

exists on $(-\infty, \infty)$, is positive and symmetric on $(-\ell(\theta_0), \ell(\theta_0))$ with $\theta(\ell(\theta_0), \theta_0) = 0$ and $\theta'(x, \theta_0) < 0$ on $(0, \ell(\theta_0))$, and is periodic with minimal period $P(\theta_0)$. Here $\ell(\theta_0)$ and $P(\theta_0)$ are continuous increasing functions of $\theta_0 \in (0, 1)$, with

$$\lim_{\theta_0 \to 0} \ell(\theta_0) = \pi/2, \qquad \lim_{\theta_0 \to 1} \ell(\theta_0) = +\infty, \tag{3.22}$$

$$\lim_{\theta_0 \to 0} P(\theta_0) = 2\pi, \qquad \lim_{\theta_0 \to 1} P(\theta_0) = +\infty. \tag{3.23}$$

Notice, that due to the periodicity of $\theta(x, \theta_0), \theta'(kP(\theta_0), \theta_0) = 0$ for any positive integer k.

Let us now construct a sequence $\{\tilde{\theta}_1, \ldots, \tilde{\theta}_n\}$ of solutions to (3.20) as follows. First, choose $\tilde{\theta}_1(x) = \theta(x, \theta_{01})$, where $\theta_{01} \in (0, 1)$ is such that $((b-a)/2) < \ell(\theta_{01})$. Then, for $i = 2, \ldots, n$, take $\tilde{\theta}_i(x) = \theta(x, \theta_{0i})$, where $\theta_{0i} \in (\theta_{0i-1}, 1)$ is such that

$$\ell(\theta_{0i}) > P(\theta_{0i-1}) \tag{3.24}$$

and

$$P(\theta_{0i}) = k_i P(\theta_{0i-1}) \tag{3.25}$$

for some positive integer k_i. Observe that (3.25) implies that if $1 \leqslant i < j \leqslant n$.

$$P(\theta_{0j}) = k_j \dots k_{i+1} P(\theta_{0i}). \tag{3.26}$$

Suppose now that

$$\sum_{j=1}^{n} c_j \tilde{\theta}_j^2(x) = 0 \quad \text{on } (-L, L), \tag{3.27}$$

where $L = (b-a)/2$. Since each $\tilde{\theta}_j$ is analytic on $(-\infty, \infty)$, so is $\sum_{j=1}^{n} c_j \tilde{\theta}_j^2(x)$. Consequently, (3.27) implies

$$\sum_{j=1}^{n} c_j \tilde{\theta}_j^2(x) = 0 \quad \text{on } (-\infty, \infty),$$

so that

$$\sum_{j=1}^{n} c_j \tilde{\theta}_j(x) \tilde{\theta}_j'(x) = 0 \quad \text{on } (-\infty, \infty). \tag{3.28}$$

Since $\theta'(kP(\theta_0), \theta_0) = 0$ for all $\theta_0 \in (0,1)$ and all positive integers k, it follows from (3.26) that the value of the left hand side of (3.28) at $x_n = P(\theta_{0n-1})$ is

$$c_n \theta(P(\theta_{0n-1}), \theta_{0n}) \theta'(P(\theta_{0n-1}), \theta_{0n}). \tag{3.29}$$

Since $P(\theta_{0n-1}) < \ell(\theta_{0n})$ by (3.24), (3.28) and (3.29) imply that $c_n = 0$. So

$$\sum_{j=1}^{n-1} c_j \tilde{\theta}_j^2 = 0$$

on $(-\infty, \infty)$. Repeating the argument, we may conclude that $\{\tilde{\theta}_1^2, \dots, \tilde{\theta}_n^2\}$ is a linearly independent set on $[-L, L]$.

Since $L < \ell(\theta_{0j})$ for $j = 1, \dots, n$, we have that $\tilde{\theta}_j(L) > 0$ and $\tilde{\theta}_j'(L) < 0$. Consequently, there is an $s_j \in (0,1)$ so that

$$\nabla \tilde{\theta}_j \cdot \eta + \frac{s_j}{1 - s_j} \tilde{\theta}_j = 0$$

at $\pm L$. Consequently, $\{\tilde{\theta}_1, \dots, \tilde{\theta}_n\} = \{\theta_{s_1}, \theta_{s_2} \dots, \theta_{s_n}\}$ and we have produced the desired linearly independent set $\{\theta_{s_1}^2, \dots, \theta_{s_n}^2\}$.

4. BIOLOGICAL RAMIFICATIONS

It was shown in [4] that increasing the hostility of the "matrix" habitat surrounding a focal patch of habitat (such as a nature preserve) could prompt a reversal of dominance between two species competing inside the focal patch. The current results build upon the observations in [4]. Indeed, the current results show that it is conceivable that the dynamics of two-species competition within the focal patch are very sensitive to the degree of hostility in the "matrix" environment, with multiple reversals of competitive exclusion as the parameter measuring the level of exterior hostility increases, punctuated by narrow opportunities for coexistence.

The current results are based upon a slight perturbation in the local *per capita* growth rate of one of two previously identical competitors. The results of [4] do not apply to the competitive system analyzed here. Indeed, in [4], when there was a reversal of competitive advantage between the two competitors, one species held the advantage in the focal habitat patch when the level of hostility in the surrounding "matrix" habitat was low, while the other species held the advantage in the focal patch when the hostility in the surrounding "matrix" habitat was high. In the current situation, whether there is an ultimate "reversal of fortune" depends upon how the local *per capita* growth rate of one of the species is perturbed. Moreover, not all perturbations of (1.17) of the form (1.16) exhibit such shifts in their predictions as the hostility of the "matrix" habitat surrounding the focal habitat patch increases. For instance, if g in (1.16) is a constant or more generally, simply stays of one sign throughout the habitat patch, one species is necessarily dominant and excludes the other in the focal habitat patch whatever the level of hostility in the surrounding "matrix" habitat. Indeed, in the example we have considered, spatial heterogeneity inside the focal habitat patch in the form of a perturbation g which changes sign in the focal habitat patch is a prerequisite for such sensitivity of the model predictions to the level of exterior hostility. The changes in the predictions of (1.16) are due to increasing the parameters, but will not occur if g fails to change sign in Ω.

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