Lecture 15

Edge Mediated Effects in Two Species Competition

I. We consider

(1) $$\frac{\partial u_1}{\partial t} = D_1 \Delta u_1 + [a_1 - u_1 - b_1 u_2]u_1$$
$$\frac{\partial u_2}{\partial t} = D_2 \Delta u_2 + [a_2 - b_2 u_1 - u_2]u_2 \qquad \text{in } \Omega \times (0,\infty)$$

(2) $$\alpha_i \nabla u_i \cdot \vec{n} + \beta u_i = 0 \qquad \text{on } \partial\Omega \times (0,\infty).$$

Here we think of β as a measure of the hostility of the matrix habitat exterior to Ω or of the likelihood that members of the species in question that leave Ω do not return. To this end, we can proceed along the lines of the classic paper (Ludwig et al, JMB 8(1979), 217-258) on the spruce budworm.

Consider a one-dimensional habitat, say

$\Omega = (a,b)$, viewing the infinite rays $(-\infty, a)$ and (b, ∞) as the surrounding matrix environment. Assume that in (a,b), the density u of a species is governed by a diffusive logistic growth law

(3) $$\frac{\partial u}{\partial t} = D_{in} \Delta u + r\left(1 - \frac{u}{K}\right)u \quad \text{in } (a,b) \times (0,\infty)$$

and that the density is governed in the matrix by the linear model

(4) $$\frac{\partial u}{\partial t} = D_{out} \Delta u - s u \quad \text{in } [(-\infty, a) \cup (b, \infty)] \times (0,\infty)$$

where $s > 0$ is the death rate of the species in the matrix environment. The diffusion rates in the habitat and in the matrix may possibly be different.

Matching densities and fluxes for an equilibrium to (3) with the unique bounded equilibrium to (4) leads to the equation

(5) $$\frac{D_{in}}{\sqrt{D_{out}}} \nabla u \cdot \vec{\eta} + \sqrt{s}\, u = 0$$

which is of the form (2) with $\alpha = \frac{D_{in}}{\sqrt{D_{out}}}$ and $\beta = \sqrt{s}$.

When two species are involved, their death rates in the matrix environment may differ but be proportional to some overall level of matrix mortality, induced, for example, via road density or pesticide contamination. In such a case, we could replace s in (4) by $c_i s$ for $i = 1, 2$, so that (5) becomes

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

(6) is of the form (2). When $\beta = 0$, we have

$$\nabla u \cdot \eta = 0.$$

In this case, the matrix environment has no impact on the habitat. We say that the habitat is closed and refer to the boundary condition as reflecting. Notice that this is a homogeneous Neumann condition and in this problem is a no-flux condition.

Since

$$\alpha \nabla u \cdot \eta + \beta u = 0$$

can be re-written

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

we may view $\beta = \infty$ as corresponding to an absorbing or completely lethal boundary (a homogeneous Dirichlet condition). Here we sometimes speak of the habitat as open.

Notice also that

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

can be expressed as

$$\left(1 - \frac{\beta}{\alpha+\beta}\right) \nabla u \cdot \eta + \frac{\beta}{\alpha+\beta} u = 0$$

which is of the form

(7) $$(1-\rho) \nabla u \cdot \eta + \rho u = 0$$

with $\rho \in [0,1]$. In (2), $\beta = 0$ refers to the Neumann case, and likewise $\rho = 0$ refers to the Neumann case in (7). But now the Dirichlet case refers to $\beta = \infty$ in (2) and $\rho = 1$ in (7). In the second half of the lecture, we will employ (7) in place of (2). Since (2) is used in both

JMB 37 (1998), 491-533 (the original paper w/Fagan) and in "Spatial Ecology via Reaction-Diffusion Equations",

I will follow the original formulation for the first part of the lecture.

Conditions for coexistence via compressivity (permanence) or for extinction at low densities follow as in the preceding lecture. We assume first that the principal eigenvalue σ_i is positive in the eigenvalue problem

(8) $$D_i \Delta \phi_i + a_i \phi_i = \sigma_i \phi_i \quad \text{in } \Omega$$

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

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

for $i = 1, 2$.

$\sigma_i > 0$ in (8) implies that the population model

(9) $$\frac{\partial u_i}{\partial t} = D_i \Delta u_i + (a_i - u_i) u_i \quad \text{in } \Omega \times (0, \infty)$$

(10) $$\alpha_i \nabla u_i \cdot \vec{\eta} + \beta u_i = 0 \qquad \text{in } \Omega \times (0,\infty),$$

$i = 1, 2$, admits a globally attracting equilibrium $\bar{u}_i = \bar{u}_i(\beta)$, which is positive in the habitat Ω.

The density $\bar{u}_i$ may be regarded as the carrying capacity for species i in Ω relative to the loss to the surrounding matrix reflected in (10) in the absence of competition from species j. Ecologically speaking, the bounded habitat Ω is large enough (has enough "core habitat") relative to the loss through the boundary to sustain the population. Here

(11) $$\sigma_i = a_i - D_i \lambda_i^{\beta/\alpha_i}(\Omega)$$

where $\lambda_i^{\gamma}(\Omega)$ is the principal eigenvalue in

(12) $$-\Delta \phi = \lambda \phi \qquad \text{in } \Omega$$

$$\nabla\phi\cdot\eta + \gamma\phi = 0 \qquad \text{on } \partial\Omega$$

and $\lambda_1^{\infty}(\Omega)$ is the Dirichlet eigenvalue.

So $\sigma_i > 0$ in (8) $\Longleftrightarrow$ $\dfrac{a_i}{D_i} > \lambda_1^{\beta/\alpha_i}(\Omega)$.

(Note: When $\beta = 0$, $\lambda_1^{\beta/\alpha_i}(\Omega) = 0$, the principal eigenvalue for $-\Delta$ + Neumann boundary conditions. In this case, $\sigma_i > 0$ independent of D_i)

Under the assumption $\sigma_i > 0$ in (8) for $i = 1, 2$, we consider the eigenvalue problems

(13) $$D_i \Delta \psi_i + (a_i - b_i \bar{u}_j)\psi_i = \tilde{\sigma}_i \psi_i \qquad \text{in } \Omega$$

(14) $$\alpha_i \nabla\psi_i \cdot \vec{\eta} + \beta\psi_i = 0 \qquad \text{on } \partial\Omega,$$

for $i = 1, 2$, where $j \neq i$ and $\bar{u}_j$ is the globally attracting positive equilibrium for (9)-(10).

If $\tilde{\sigma}_i > 0$ in (13)-(14), species i can invade Ω when species j is present at its carrying capacity. Consequently, species i is predicted to persist if it competes with species j in Ω. On the other hand, if $\tilde{\sigma}_i < 0$ in (13)-(14), species j will eliminate species i from the habitat patch if the density of species i is low. In particular, species i cannot invade Ω when species j is at carrying capacity.

Our objective regarding (1)-(2) is to examine how the predictions of the model depend on the level of hostility in the matrix surrounding the habitat patch, which we track via the parameter β in (2).

Is it possible to switch from a situation in which $\tilde{\sigma}_i > 0$ and $\tilde{\sigma}_j < 0$ (so that species i has a clear competitive advantage in Ω)

to a situation in which $\hat{\sigma}_i < 0$ and $\tilde{\sigma}_j > 0$ (so that species j has the advantage) by changing only the parameter β in (1)-(2)?

Note that $\hat{\sigma}_i = 0$ and $\tilde{\sigma}_j = 0$ represent the thresholds between different model predictions for species i and j, respectively. Geometrically, each of $\hat{\sigma}_i = 0$ and $\tilde{\sigma}_j = 0$ can be realized as a hypersurface in an appropriate Euclidean space. The value of $\hat{\sigma}_i$ depends on the parameters which appear explicitly in the equations, namely a_i, D_i, α_i, β and b_i, and on $\bar{u}_j$ as well. Observe that $\bar{u}_j$ depends on a_j, D_j, α_j and β, but not b_j. Likewise, the value of $\tilde{\sigma}_j$ depends on a_i, D_i, α_i, a_j, D_j, α_j, β and b_j but not on b_i.

So $\hat{\tilde{\sigma}}_i = 0$ and $\hat{\tilde{\sigma}}_j = 0$ may each be regarded as a hypersurface in $\mathbb{R}^8$, with seven of the eight coordinates common to both (i.e., $a_1, a_2, D_1, D_2, \alpha_1, \alpha_2$, and β).

We will not attempt a complete analysis of these hypersurfaces. Instead, we fix configurations of the parameters $a_1, a_2, D_1, D_1, \alpha_1$ and α_2 and examine the relationship between b_1 and β on the hypersurface $\hat{\sigma}_1 = 0$ and b_2 and β on the hypersurface $\tilde{\sigma}_2 = 0$.

Theorem 1. Consider (1)-(2). Assume that for $i = 1, 2$, a_i, D_i, and α_i are fixed with

$$\frac{a_i}{D_i} > \lambda_1^{\infty}(\Omega).$$

Then for each $\beta \in [0, \infty]$, there are unique values of the competition coefficients b_1 and b_2, denoted $\bar{b}_1(\beta)$ and $\bar{b}_2(\beta)$, respectively, with the following properties:

(i) For $i = 1, 2$, and $j \neq i$, if $b_i < \bar{b}_i(\beta)$, species i can invade the habitat Ω when species j is at its carrying capacity density in the absence of competition (i.e., $\bar{u}_j = \bar{u}_j(\beta)$) If $b_i > \bar{b}_i(\beta)$, species j eliminates species i from Ω when species i is at low densities. In particular, species i cannot invade Ω when species j is at its carrying capacity in the absence of competition.

(ii) For $i = 1, 2$, $\bar{b}_i(\beta)$ is a differentiable function from $[0, \infty]$ into $(0, \infty)$.

Proof: We will show that for all $\beta \in [0,\infty]$ there is a unique $b_i(\beta) > 0$ so that $\tilde{\sigma}_i > 0$ for $b_i < b_i(\beta)$, $\tilde{\sigma}_i = 0$ where $b_i = b_i(\beta)$ and $\tilde{\sigma}_i < 0$ when $b_i > b_i(\beta)$. We establish these facts by showing that $\tilde{\sigma}_i$ decreases as b_i increases, $\tilde{\sigma}_i > 0$ when $b_i = 0$ and $\tilde{\sigma}_i < 0$ for b_i large enough.

Now fix a $\beta \in [0,\infty]$. Let $0 \le b_i < b_i'$ and let $\tilde{\sigma}_i$, $\tilde{\sigma}_i'$, ψ_i, ψ_i' denote the corresponding principal eigenvalues and eigenfunctions in (13)-(14), so that

$$(15)\quad \begin{cases} D_i \Delta \psi_i + (a_i - b_i \bar{u}_j)\psi_i = \tilde{\sigma}_i \psi_i & \text{in } \Omega \\ \alpha_i \nabla \psi_i \cdot \eta + \beta \psi_i = 0 & \text{on } \partial\Omega \end{cases}$$

and

$$(16)\quad \begin{cases} D_i \Delta \psi_i' + (a_i - b_i' \bar{u}_j)\psi_i' = \tilde{\sigma}_i' \psi_i' & \text{in } \Omega \\ \alpha_i \nabla \psi_i' \cdot \eta + \beta \psi_i' = 0 & \text{on } \partial\Omega. \end{cases}$$

Multiplying the first equation in (15) by ψ_i' and the first equation in (16) by ψ_i, integrating over Ω, and employing Green's Second Identity tells us

(17) $$(b_i' - b_i)\int_\Omega \bar{u}_j \psi_i \psi_i' = (\hat{\sigma}_i - \hat{\sigma}_i')\int_\Omega \psi_i \psi_i'$$

From (17), $b_i < b_i' \Rightarrow \hat{\sigma}_i > \hat{\sigma}_i'$, so that $\hat{\sigma}_i$ decreases as b_i increases.

Observe that if $b_i = 0$, $\hat{\sigma}_i = \sigma_i > 0$.

To see that $\hat{\sigma}_i < 0$ for b_i large, we separate our argument into the cases $0 \leq \beta < \infty$ and $\beta = \infty$.

Suppose first that $0 \leq \beta < \infty$.

Then $\bar{u}_j = \bar{u}_j(\beta) > 0$ on $\bar{\Omega}$. Multiply (15) by ψ_i and integrate. Then

(18) $$D_i \int_\Omega \psi_i \Delta \psi_i \, dx + \int_\Omega (a_i - b_i \bar{u}_j)\psi_i^2 dx = \hat{\sigma}_i \int_\Omega \psi_i^2 dx$$

Divergence Theorem $\Rightarrow$ $D_i \int_\Omega \psi_i \Delta \psi_i \, dx = D_i \int_\Omega [\mathrm{div}(\psi_i \nabla \psi_i) - |\nabla \psi_i|^2]$

$$= -D_i \int_\Omega |\nabla \psi_i|^2 + D_i \int_{\partial\Omega} \psi_i (\nabla \psi_i \cdot \eta)$$

$$= -D_i \int_\Omega |\nabla \psi_i|^2 - \frac{\beta D_i}{\alpha_i} \int_{\partial\Omega} \psi_i^2 \, dS,$$

so that (18) can be re-written as

(19) $$-D_i \int_\Omega |\nabla \psi_i| dx - \frac{\beta D_i}{\alpha_i} \int_{\partial\Omega} \psi_i^2 dS - b_i \int_\Omega \bar{u}_j \psi_i^2 dx$$

$$= (\hat{\sigma}_i - a_i) \int_\Omega \psi_i^2 dx$$

So $\hat{\sigma}_i < a_i - b_i (\min_{\bar{\Omega}} \bar{u}_j)$. $\therefore \hat{\sigma}_i < 0$

for sufficiently large b_i.

If $\beta = \infty$, $\min_{\bar{\Omega}} \bar{u}_j = 0$, so the preceding argument does not hold. So we proceed as follows.

The principal eigenvalue σ in

(20) $$D_i \Delta \phi + m(x) \phi = \sigma \phi \quad \text{in } \Omega$$
$$\phi = 0 \quad \text{on } \partial\Omega$$

depends continuously on $m \in L^\infty(\Omega)$

thought of as a subspace of $L^p(\Omega)$ for p large. Consequently, there is an open subset Ω' of Ω with $\overline{\Omega'} \subseteq \Omega$ so that if

$$m_{\Omega'}(x) = \begin{cases} a_i & \text{in } \Omega \setminus \Omega' \\ -1 & \text{in } \Omega' \end{cases}$$

the principal eigenvalue in (20) is negative.

Now $\min_{\overline{\Omega'}} \bar{u}_j > 0$. So $a_i - b_i \bar{u}_j < m_{\Omega'}$ for b_i sufficiently large. Since σ in (20) increases with m, $\hat{\sigma}_i < 0$ for b_i sufficiently large.

To establish Part (ii) of Theorem 1, we first employ the Implicit Function Theorem to establish that $\beta \to \bar{u}_i(\beta)$ is differentiable from $[0, \infty]$ into $C^{2+\alpha}(\bar{\Omega})$. (Since I will be employing the Implicit Function Theorem in an analogous fashion to show that $b_i(\beta)$ is differentiable, I will leave the argument to the class.)

Next normalize $\psi_i(\beta)$ in (13)-(14) by $\int_\Omega \psi_i^2\,dx = 1$. Define a differentiable map

$$\rho: C^{2+\alpha}(\bar{\Omega}) \times [0,\infty) \times [0,\infty) \to C^{\alpha}(\bar{\Omega}) \times \mathbb{R} \times C^{1+\alpha}(\partial\Omega)$$

by

(21) $$\rho(\psi, b, \beta) = \Big(D_i \Delta\psi + (a_i - b\bar{u}_j(\beta))\psi,\ \int_\Omega \psi^2 dx - 1,\ \alpha_i \nabla\psi \cdot \vec{\eta} + \beta\psi\Big)$$

One may calculate that

(22) $$\left[\frac{\partial\rho}{\partial(\psi,b)}(\psi, b, \beta)\right](z,c)$$

$$= \Big(D_i \Delta z + (a_i - b\bar{u}_j(\beta))z - c\,\bar{u}_j(\beta)\psi,\ 2\int_\Omega (\psi z)\,dx,\ \alpha_i \nabla z \cdot \vec{\eta} + \beta z\Big)$$

$$\rho(\psi_i(\beta), \bar{b}_i(\beta), \beta) = (0,0,0)$$

Let $(\psi, b, \beta) = (\psi_i(\beta), \bar{b}_i(\beta), \beta)$.

Suppose now

$$\left[\frac{\partial \rho}{\partial(\psi, b)}(\psi, b, \beta)\right](z, c) = (0, 0, 0)$$

Then

$$D_i \Delta z + (a_i - \bar{b}_i'(\beta)\bar{u}_j(\beta))z - c\bar{u}_j(\beta)\psi_i = 0 \quad \text{in } \Omega$$

(23) $$\int_\Omega z\psi_i = 0$$

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

The Fredholm Alternative guarantees that there can be a $z \in C^{2+\alpha}(\bar{\Omega})$ solving the first and third equations in (23) $\Leftrightarrow$ $c\int_\Omega \bar{u}_j(\beta)\psi_i^2 = 0$

$\Leftrightarrow c = 0$. So $z = k\psi_i$ for some constant k. The second equation in (23) $\Rightarrow$

$$k\int_\Omega \psi_i^2 = 0 \quad \Rightarrow k = 0.$$

So $\left[\frac{\partial \rho}{\partial(\psi, b)}(\psi, b, \beta)\right]$ is injective.

Consider the system

$$D_i \Delta z + (a_i - b_i(\beta)\bar{u}_j(\beta))z - c\bar{u}_j(\beta)\psi_i = f \qquad \text{in } \Omega$$

(24) $$\int_\Omega z\psi_i \, dx = g$$

$$\alpha_i \nabla z \cdot \eta + \beta z = h \qquad \text{on } \partial\Omega,$$

with $f \in C^\alpha(\Omega)$, $g \in \mathbb{R}$ and $h \in C^{1+\alpha}(\partial\Omega)$.

The Fredholm Alternative implies that there is a z solving the first and third equations of (24) $\iff$

(25) $$\int_\Omega (f + c\bar{u}_j\psi_i)\psi_i \, dx = \frac{D_i}{\alpha_i}\int_{\partial\Omega} h\psi_i \, ds$$

which is equivalent to

(26) $$c = \frac{-\int_\Omega f\psi_i \, dx + \frac{D_i}{\alpha_i}\int_{\partial\Omega} h\psi_i \, ds}{\int_\Omega \bar{u}_j \psi_i^2 \, dx}$$

Since $\bar{u}_j$ and ψ_i are positive in Ω, c is well-defined in (26). Choose c as in (26) and let z_0 be some solution to the first and third equations in (24). Notice that

$$z_0 + k\varphi_1$$

is also a solution for any choice of $k \in \mathbb{R}$.

To satisfy the second equation in (24), we need

$$\int_\Omega (z_0 + k\varphi_1)\varphi_1 \, dx = g$$

$$\Leftrightarrow \quad k = g - \int_\Omega z_0 \varphi_1 \, dx.$$

So $\left[\frac{\partial \rho}{\partial(\varphi, b)}(\varphi, b, \beta)\right]$ is surjective.

$\therefore$ $\left[\frac{\partial \rho}{\partial(\varphi, b)}(\varphi, b, \beta)\right]$ is a linear homeomorphism.

So part (ii) of Theorem 1 follows from the Implicit Function Theorem for $\beta < \infty$. To extend the result to $\beta = \infty$, we rewrite the boundary condition on Ω as as

$$d_i \gamma \nabla u \cdot \vec{\eta} + u = 0$$

with $\gamma = \frac{1}{\beta}$ and argue as before.

Remark: Since $\lambda_1^{\beta/d_i}(\Omega)$ can be determined variationally, it follows that $\lambda_1^{\beta/d_i}(\Omega)$ is an increasing function of β on $[0, \infty]$. So the condition

$$\frac{a_i}{D_i} > \lambda_1^{\infty}(\Omega)$$

means that we require both species to persist in Ω in the absence of competition whatever the level of matrix hostility.

When $b_i = 0$, $\tilde{\sigma}_i = \sigma_i > 0$. The proof of Theorem 1 shows for any β that $\tilde{\sigma}_i$ is a strictly decreasing function of b_i on $[0, \infty)$ which becomes negative for large enough b_i.

Suppose now for some habitat Ω and some fixed configuration of the six parameters $a_1, a_2, D_1, D_2, \alpha_1$ and α_2 we can establish

(27) $$\bar{b}_1(0) > 1 > \bar{b}_2(0)$$

but

(28) $$\bar{b}_1(\infty) < 1 < \bar{b}_2(\infty)$$

Then we can choose competition coefficients b_1 and b_2 so that species 1 has a competitive advantage when the degree of matrix hostility as represented by β is low, but loses the competitive advantage to species 2 when the degree of matrix hosility is very high.

Why? If (27) and (28) hold, part (ii) of Theorem 1 $\Rightarrow$

$$\bar{b}_1(\beta) > 1 < \bar{b}_2(\beta)$$

for small β, while

$$\bar{b}_1(\beta) < 1 < \bar{b}_2(\beta)$$

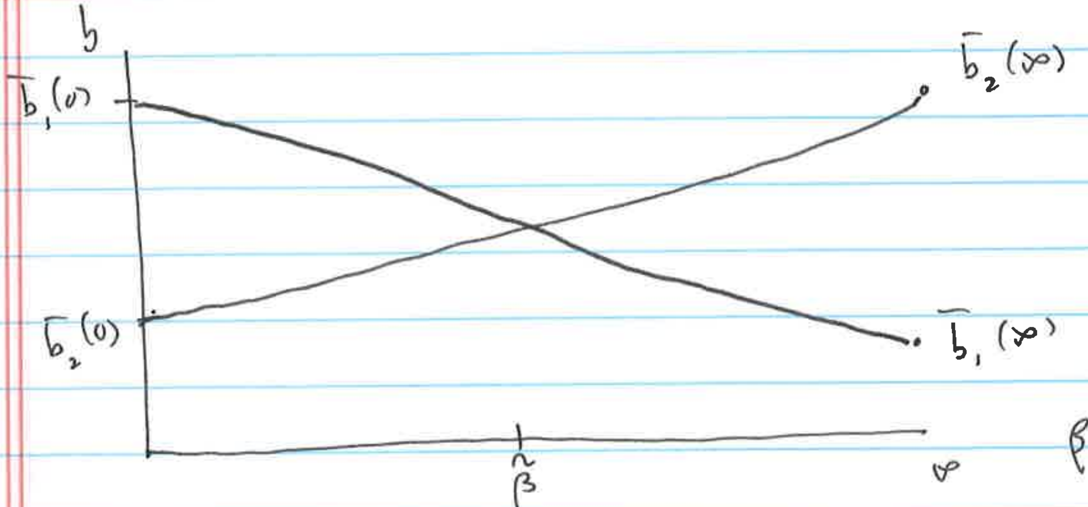
for large β. So we may choose competition coefficients b_1, b_2 so that

$$b_1 < \bar{b}_1(\beta) \quad \text{for small } \beta$$

$$b_1 > \bar{b}_1(\beta) \quad \text{for large } \beta$$

$$b_2 > \bar{b}_2(\beta) \quad \text{for small } \beta$$

$$b_2 < \bar{b}_2(\beta) \quad \text{for large } \beta$$



Degradation of the area surrounding the habitat patch can lead to a profound change in the outcome of an ecological process inside the patch.

Our objective is met if we can identify a habitat Ω and a configuration of the parameters $a_1, a_2, D_1, D_2, \alpha_1$ and α_2 so that (27) and (28) hold. To this end, note that the definition of $\bar{b}_i$ yields that

$$D_i \Delta \psi_i + (a_i - \bar{b}_i(\beta)\bar{u}_j(\beta))\psi_i = 0 \qquad \text{in } \Omega$$

$$\nabla \psi_i \cdot \eta + \frac{\beta}{\alpha_i}\psi_i = 0 \qquad \text{on } \partial\Omega$$

$\Rightarrow$

$$-\Delta \psi_i + \frac{\bar{b}_i(\beta)\bar{u}_j(\beta)}{D_i}\psi_i = \frac{a_i}{D_i}\psi_i \qquad \text{in } \Omega$$

$$\nabla \psi_i \cdot \vec{\eta} + \frac{\beta}{\alpha_i}\psi_i = 0 \qquad \text{on } \partial\Omega$$

So if we let $\mu_1^{\beta/\alpha_i}(m)$ denote the principal eigenvalue for the problem

$$-\Delta \phi + m\phi = \mu\phi \qquad \text{in } \Omega$$

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

we have

$$\mu_1^{\beta/\alpha_i}\left(\frac{\bar{b}_i(\beta)\,\bar{u}_j(\beta)}{D_i}\right) = \frac{a_i}{D_i} \tag{29}$$

We aim to exploit (29) to obtain (27) and (28) for an appropriate selection of Ω and parameters $a_1, a_2, D_1, D_2, \alpha_1$ and α_2. To do so, we express $\bar{u}_i(\beta)$, $i = 1, 2$, in a form that highlights its dependence on a_i, D_i, and α_i. Note that $\bar{u}_i(\beta)$ satisfies

$$-D_i \Delta \bar{u}_i = (a_i - \bar{u}_i)\bar{u}_i \quad \text{in } \Omega$$

$$\nabla \bar{u}_i \cdot \eta + \frac{\beta}{\alpha_i}\bar{u}_i = 0 \quad \text{on } \partial\Omega$$

so that

$$-\Delta\left(\frac{\bar{u}_i}{D_i}\right) = \left(\frac{a_i}{D_i} - \frac{\bar{u}_i}{D_i}\right)\frac{\bar{u}_i}{D_i} \quad \text{in } \Omega$$

$$\nabla\left(\frac{\bar{u}_i}{D_i}\right)\cdot\vec{\eta} + \frac{\beta}{\alpha_i}\left(\frac{\bar{u}_i}{D_i}\right) \quad \text{on } \partial\Omega$$

So if we let $a > \lambda_1^\gamma(\Omega)$ and let θ_a^γ

represent the unique positive solution to

$$-\Delta\theta = (a-\theta)\theta \quad \text{in } \Omega$$

(30)

$$\nabla\theta \cdot \eta + \gamma\phi = 0 \quad \text{on } \partial\Omega,$$

we get that

(31) $$\bar{u}_i(\beta) = D_i\, \theta_{a_i/D_i}^{\beta/d_i}$$

Estimates on the quantity $\mu_1^{\gamma_2}(e\theta_a^\gamma)$ are the key to analyzing (29) closely enough to get the estimates we need on $\bar{b}_1$ and $\bar{b}_2$ in (27) and (28). The kind of estimates we need were first derived in

* Cantrell and Cosner, Houston J. Math 13 (1987), 337-352

for the Dirichlet case $(\gamma_1 = \gamma_2 = \infty)$ and were extended in

** Cantrell, Cosner and Fagan, JMB 37 (1998), 491–533.
in general.

Theorem 2. Suppose that $0 \le \gamma_1 \le \gamma_2$ and that $a > \lambda_1^{\gamma_2}(\Omega)$.

(i) For $0 < e < 1$, $\mu_1^{\gamma_2}(e\theta_a^{\gamma_1})$ satisfies

(32) $$ae + \lambda_1^{\gamma_2}(\Omega)(1-e) < \mu_1^{\gamma_2}(e\theta_a^{\gamma_1}) \le \lambda_1^{\gamma_2}(\Omega) + ae$$

while for $e > 1$,

$\mu_1^{\gamma_2}(e\theta_a^{\gamma_1})$

satisfies

(33) $$a < \mu_1^{\gamma_1}(e\theta_a^{\gamma_1}) \le \lambda_1^{\gamma_2}(\Omega) + ae.$$

(ii) For $0 < e < 1$, $\mu_1^{\gamma_1}(e\theta_a^{\gamma_2})$ satisfies

(34) $$\lambda_1^{\gamma_1}(\Omega) < \mu_1^{\gamma_1}(e\theta_a^{\gamma_2}) < a$$

while for $e > 1$,

$\mu_1^{\gamma_1}(e\theta_a^{\gamma_2})$ satisfies

(35) $$\mu_1^{\gamma_1}(e\theta_a^{\gamma_2}) \le ae + (1-e)\lambda_1^{\gamma_1}(\Omega)$$

Proof: We begin with the equations defining $\mu_1^{\gamma_2}(e\theta_a^{\gamma_1})$, where $0 \le \gamma_1 \le \gamma_2$ and $a > \lambda_1^{\gamma_2}(\Omega)$, namely

(36) $$-\Delta\psi_e + e\theta_a^{\gamma_1}\psi_e = \mu_1^{\gamma_2}(e\theta_a^{\gamma_1})\psi_e \quad \text{in } \Omega$$

(37) $$\nabla\psi_e \cdot \eta + \gamma_2\psi_e = 0 \quad \text{on } \partial\Omega$$

with $\psi_e > 0$. If we normalize ψ_e by the requirement

$$\int_\Omega \psi_e^2 \, dx = 1$$

an Implicit Function Theorem argument akin to that for part (ii) of Theorem 1 $\Rightarrow$ ψ_e is a differentiable function of e.

Choose $e_1, e_2 \ge 0$ with $e_1 \ne e_2$. Employ Green's Second Identity to obtain

(38) $$\left[\mu_1^{\gamma_2}(e_1\theta_a^{\gamma_1}) - \mu_1^{\gamma_2}(e_2\theta_a^{\gamma_1})\right] \int_\Omega \psi_{e_1}\psi_{e_2} \, dx$$
$$= (e_1 - e_2)\int_\Omega \theta_a^{\gamma_1}\psi_{e_1}\psi_{e_2} \, dx$$

Now set $e_1 = e$ and $e_2 = 0$ in (38).

Since $\theta_\omega^{\gamma_1} \le a$ in $\bar{\Omega}$ by the maximum principle,

and $\mu_1^{\gamma_2}(0) = \lambda_1^{\gamma_2}(\Omega)$, we get

$$\mu_1^{\gamma_2}(e\theta_\omega^{\gamma_1}) \le ae + \lambda_1^{\gamma_2}(\Omega),$$

which establishes the RHS of both (32) and (33).

Now return to (38). Suppose $\gamma_2 = \gamma_1 = \gamma$.

Divide by $(e_1 - e_2)\int_\Omega \psi_{e_1}\psi_{e_2}\,dx$ to obtain

(39) $$\frac{[\mu_1^\gamma(e_1\theta_\omega^\gamma) - \mu_1^\gamma(e_2\theta_\omega^\gamma)]}{e_1 - e_2} = \frac{\int_\Omega \theta_\omega^\gamma \psi_{e_1}\psi_{e_2}\,dx}{\int_\Omega \psi_{e_1}\psi_{e_2}\,dx}$$

Let $e_1 \to e_1$ in (39) to obtain

(40) $$\frac{d}{de_1}[\mu_1^\gamma(e_1\theta_\omega^\gamma)] = \int_\Omega \theta_\omega^\gamma \psi_{e_1}^2\,dx.$$

Now re-write (36) as

$$\theta_\omega^\gamma \psi_e = \frac{1}{e}[\Delta\psi_e + \mu_1^\gamma(e\theta_\omega^\gamma)\psi_e] \text{ in } \Omega$$

Multiply by ψ_e and integrate. Green's First Identity,

and (40) $\Rightarrow$

$$\frac{d}{de}\left\{\mu_1^\gamma(e\theta_a^\gamma)\right\} = \frac{1}{e}\left[\mu_1^\gamma(e\theta_a^\gamma) - \gamma\int_{\partial\Omega}\psi_e^2\,dS - \int_\Omega |\nabla\psi_e|^2 dx\right]$$

Now $\int_\Omega |\nabla\psi_e|^2 dx + \gamma\int_{\partial\Omega}\psi_e^2\,dS \geq \lambda_1^\gamma(\Omega) \Rightarrow$

$$\frac{e\frac{d}{de}\left(\mu_1^\gamma(e\theta_a^\gamma)\right) - \mu_1^\gamma(e\theta_a^\gamma)}{e^2} \leq -\frac{\lambda_1^\gamma(\Omega)}{e^2}$$

(41) $\Leftrightarrow$ $$\frac{d}{de}\left\{\frac{\mu_1^\gamma(e\theta_a^\gamma)}{e}\right\} \leq -\frac{\lambda_1^\gamma(\Omega)}{e^2}$$

for all $e > 0$.

Now think of fixing $e \in (0,1)$ and integrate (41) between e and 1 and use the fact that $\mu_1^\gamma(\theta_a^\gamma) = a$ to obtain

(42) $$ae + (1-e)\lambda_1^\gamma(\Omega) \leq \mu_1^\gamma(e\theta_a^\gamma).$$

If now $\gamma_1 \leq \gamma_2$, the method of upper and lower solutions

$$\Rightarrow \quad \theta_a^{\gamma_2} \le \theta_a^{\gamma_1}.$$

So (41) $\Rightarrow$

$$ae + (1-e)\lambda_1^{\gamma_2}(\Omega) \le \mu_1^{\gamma_2}(e\theta_a^{\gamma_2})$$
$$\le \mu_1^{\gamma_2}(e\theta_a^{\gamma_1})$$

which establishes the LHS of (32) and hence part (i) of Theorem 2. To finish the proof of Theorem 2, we need to establish (35).

Fix an $e > 1$, and integrate (41) between 1 and e. Again, using the fact that $\mu_1^{\gamma}(\theta_a^{\gamma}) = a$, we get

$$\mu_1^{\gamma}(e\theta_a^{\gamma}) \le ae + (1-e)\lambda_1^{\gamma}(\Omega)$$

so that

$$\mu_1^{\gamma_1}(e\theta_a^{\gamma_2}) \le \mu_1^{\gamma_1}(e\theta_a^{\gamma_1})$$
$$\le ae + (1-e)\lambda_1^{\gamma_1}(\Omega),$$

which gives (35).

We may now establish a result which enables us to identify conditions on Ω and configurations of $a_1, a_2, D_1, D_2, \alpha_1$ and α_2 so that (27) and (28) hold.

Theorem 3. Suppose that $\frac{a_2}{D_2} > \frac{a_1}{D_1} > \lambda_1^\infty(\Omega)$

and that $a_1 > a_2$.

Then

$$\bar{b}_1(0) > 1 > \bar{b}_2(0)$$

while

$$\bar{b}_1(\infty) \leq \frac{a_1 - D_1 \lambda_1^\infty(\Omega)}{a_2 - D_2 \lambda_1^\infty(\Omega)}$$

$$\bar{b}_2(\infty) \geq \frac{a_2 - D_2 \lambda_1^\infty(\Omega)}{a_1 - D_1 \lambda_1^\infty(\Omega)}$$

Proof: When $\beta = 0$, $\sigma_i = a_i$ and $\bar{u}_i = a_i$, so that $\tilde{\sigma}_i = a_i - b_i a_j$.

It follows that $\bar{b}_i(0) = a_i / a_j$.

So $\bar{b}_1(0) = \frac{a_1}{a_2} > 1 > \frac{a_2}{a_1} = \bar{b}_2(0)$.

Now $\bar{u}_i(\infty) = D_i \theta^\infty_{a_i/D_i}$

and hence $$\frac{a_1}{D_1} = \mu_1^\infty\left(\frac{\bar{b}_1(\infty)\,\bar{u}_2(\infty)}{D_1}\right)$$

$$= \mu_1^\infty\left(\frac{\bar{b}_1(\infty)}{D_1} D_2\,\theta^\infty_{\frac{a_2}{D_2}}\right)$$

Suppose $\bar{b}_1(\infty)\frac{D_2}{D_1} \geq 1$.

Then $$\bar{b}_1(\infty)\frac{D_2}{D_1}\theta^\infty_{\frac{a_2}{D_2}} \geq \theta^\infty_{a_2/D_2}$$

$$\Rightarrow \frac{a_1}{D_1} = \mu_1^\infty\left(\bar{b}_1(\infty)\frac{D_2}{D_1}\theta^\infty_{\frac{a_2}{D_2}}\right)$$

$$\geq \mu_1^\infty\left(\theta^\infty_{\frac{a_2}{D_2}}\right)$$

$$= \frac{a_2}{D_2} \qquad \times$$

$\therefore \bar{b}_1(\infty)\frac{D_2}{D_1} < 1$.

So $$\frac{a_1}{D_1} = \mu_1^\infty\left(\bar{b}_1(\infty)\frac{D_2}{D_1}\theta^\infty_{\frac{a_2}{D_2}}\right)$$

$$\geq \frac{a_2}{D_2}\left(\bar{b}_1(\infty)\frac{D_2}{D_1}\right) + \lambda_1^\infty(\Omega)\left(1 - \bar{b}_1(\infty)\frac{D_2}{D_1}\right)$$

by (32), which implies

$$\left(a_1 - D_1\lambda_1^\infty(\Omega)\right) \geq \bar{b}_1(\infty)\left(a_2 - D_2\lambda_1^\infty(\Omega)\right)$$

$$\Leftrightarrow \qquad \bar{b}_1(\infty) \leq \frac{a_1 - D_1\lambda_1^\infty(\Omega)}{a_2 - D_2\lambda_1^\infty(\Omega)}$$

Similarly, $\dfrac{a_2}{D_2} = \mu_1^\infty\left(\dfrac{\bar{b}_2(\infty)\bar{u}_1(\infty)}{D_2}\right)$

$$= \mu_1^\infty\left(\frac{\bar{b}_2(\infty)}{D_2} D_1 \theta^\infty_{a_1/D_1}\right)$$

$$= \mu_1^\infty\left(\bar{b}_2(\infty)\frac{D_1}{D_2}\theta^\infty_{\frac{a_1}{a_1}}\right)$$

Now, if $\bar{b}_2(\infty)\dfrac{D_1}{D_2} \leq 1$,

$$\frac{a_2}{D_2} = \mu_1^\infty\left(\bar{b}_2(\infty)\frac{D_1}{D_2}\theta^\infty_{\frac{a_1}{D_1}}\right) \leq \mu_1^\infty\left(\theta^\infty_{\frac{a_1}{D_1}}\right) = \frac{a_1}{D_1} \quad \otimes$$

$$\therefore \quad \bar{b}_2(\infty)\frac{D_1}{D_2} > 1$$

So from (35) we have

$$\frac{a_2}{D_2} = \mu_1^\infty\left(\bar{b}_2(\infty)\frac{D_1}{D_2}\theta^\infty_{\frac{a_1}{D_1}}\right)$$

$$\leq \left(\frac{a_1}{D_1}\right)\left(\bar{b}_2(\infty)\frac{D_1}{D_2}\right) + \left(1 - \bar{b}_2(\infty)\frac{D_1}{D_2}\right)\lambda_1^\infty(\Omega)$$

which implies

$$a_2 - D_2\lambda_1^\infty(\Omega) \leq \bar{b}_2(\infty)\left(a_1 - D_1\lambda_1^\infty(\Omega)\right)$$

or

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

Theorem 4. Suppose the conditions of Theorem 3 hold and that the habitat patch Ω is such that

$$\lambda_1^\infty(\Omega) > \frac{a_1 - a_2}{D_1 - D_2}$$

Then $\bar{b}_1(\infty) < 1 < \bar{b}_2(\infty)$.

Consequently, species 1 has a competitive advantage when the hostility in the matrix environment surrounding the habitat patch Ω is low but loses the advantage to species 2 when the hostility in the matrix environment is high.

Proof: $\frac{a_2}{D_2} > \frac{a_1}{D_1} \Rightarrow D_1 > \left(\frac{a_1}{a_2}\right) D_2$.

$a_1 > a_2 \Rightarrow D_1 > D_2 \therefore \frac{a_1 - a_2}{D_1 - D_2} > 0$.

From Theorem 3,

$$\bar{b}_1(\infty) \le \frac{a_1 - D_1 \lambda_1^\infty(\Omega)}{a_2 - D_2 \lambda_1^\infty(\Omega)}$$

$$\bar{b}_2(\infty) \ge \frac{a_2 - D_2 \lambda_1^\infty(\Omega)}{a_1 - D_1 \lambda_1^\infty(\Omega)}$$

So $\bar{b}_1(\infty) < 1 < \bar{b}_2(\infty)$, provided

$$\frac{a_2 - D_2 \lambda_1^\infty(\Omega)}{a_1 - D_1 \lambda_1^\infty(\Omega)} > 1$$

$$\Leftrightarrow \quad a_2 - D_2 \lambda_1^\infty(\Omega) > a_1 - D_1 \lambda_1^\infty(\Omega)$$

$$\Leftrightarrow \quad (D_1 - D_2)\lambda_1^\infty(\Omega) > a_1 - a_2$$

$$\Leftrightarrow \quad \lambda_1^\infty(\Omega) > \frac{a_1 - a_2}{D_1 - D_2}$$

Note: If $\Omega_1 \subseteq \Omega_2$, $\lambda_1^\infty(\Omega_1) \geq \lambda_1^\infty(\Omega_2)$, so that the less "core habitat" the larger the loss through the boundary. So as the core habitat shrinks the more likely is a reversal in competitive advantage due to changes in the exterior of the focal patch.

II. Follow-up: Multiple Reversals of Competitive Dominance in Ecological Reserves via External Habitat Degradation

(43)
$$\frac{\partial u}{\partial t} = \Delta u + u[1+\varepsilon g - u - v]$$
$$\frac{\partial v}{\partial t} = \Delta v + v[1 - u - v] \qquad \text{in } \Omega \times (0,\infty)$$

(44)
$$(1-s)\nabla u \cdot \eta + su = 0 = (1-s)\nabla v \cdot \eta + sv \qquad \text{on } \partial\Omega \times (0,\infty),$$

$s \in [0,1]$, $g \in C^{\alpha}(\bar{\Omega})$.

When $\varepsilon = 0$, we have

(45)
$$\frac{\partial u}{\partial t} = \Delta u + u(1-u-v)$$
$$\frac{\partial v}{\partial t} = \Delta v + v(1-u-v) \qquad \text{in } \Omega \times (0,\infty)$$

(46)
$$(1-s)\nabla u \cdot \eta + su = 0 = (1-s)\nabla v \cdot \eta + sv \qquad \text{on } \partial\Omega \times (0,\infty)$$

For $s \in [0,1]$, let $\lambda_1(\Omega, s)$ denote the principal eigenvalue for

$$-\Delta \phi = \lambda \phi \qquad \text{in } \Omega \tag{47}$$

$$(1-s)\nabla\phi \cdot \eta + s\phi = 0 \qquad \text{on } \partial\Omega .$$

Then $\lambda_1(\Omega, s) = \lambda_1^{\frac{s}{1-s}}(\Omega)$ from the first part of the lecture with the convention $\lambda_1(\Omega, 1) = \lambda_1^{\infty}(\Omega)$.

When $1 > \lambda_1(\Omega, s)$, the diffusive logistic problem

$$\frac{\partial z}{\partial t} = \Delta z + z(1-z) \qquad \text{in } \Omega \times (0,\infty) \tag{48}$$

$$(1-s)\nabla z \cdot \eta + sz = 0 \qquad \text{on } \partial\Omega \times (0,\infty)$$

admits a globally attracting positive equilibrium which we denote by θ_s.

$\lambda_1(\Omega, s)$ is increasing in s on $[0,1]$, so that when $1 > \lambda_1(\Omega, 1)$, $\theta_s > 0$ exists for all $s \in [0,1]$. Since θ_s satisfies

(49) $$\Delta w + w(1-\theta_s) = \sigma w \quad \text{in } \Omega$$

$$(1-s)\nabla w \cdot \vec{\eta} + s w = 0 \quad \text{on } \partial\Omega$$

we have that

(50) $$\bar{b}_1(s) \equiv 1, \quad \bar{b}_2(s) \equiv 1$$

So in the system (45)-(46) neither species ever holds a competitive advantage of the sort we discussed in the first part of the lecture.

Indeed, suppose (u,v) is a nontrivial, componentwise nonnegative equilibrium solution to (45)-(46) for some $s \in [0,1]$. Then $w = u+v$ satisfies

$$0 = \Delta w + w(1-w) \quad \text{in } \Omega$$

$$(1-s)\nabla w \cdot \eta + s w = 0 \quad \text{on } \partial\Omega$$

so that $w = \theta_s$. Since then

$$\Delta u + u(1-\theta_s) = 0$$

$$\Delta v + v(1-\theta_s) = 0,$$

u and v must be multiples of Θ_s. Hence

$$u = \tau \Theta_s, \quad v = (1-\tau)\Theta_s$$

for some $\tau \in [0,1]$. Consequently, for each $s \in [0,1]$ (45)-(46) has the one parameter family

(51) $$\{(\tau\Theta_s, (1-\tau)\Theta_s) : \tau \in [0,1]\}$$

of componentwise-nonnegative equilibria, so long as $1 > \lambda_1(\Omega, 1)$.

Now consider the perturbed system (43)-(44).

Make as a standing assumption

$$1 > \lambda_1(\Omega, 1).$$

When $\varepsilon \neq 0$, $(0, \Theta_s)$ remains an equilibrium solution to (43)-(44) for any ε and all $s \in [0,1]$. However, the remainder of the one parameter family (51) are NOT equilibria to (43)-(44).

Notice that when $v = 0$, (43)-(44)

reduces to

$$(52)\quad \frac{\partial u}{\partial t} = \Delta u + (1+\varepsilon g - u)u \qquad \text{in } \Omega$$

$$(1-s)\nabla u\cdot\eta + s u = 0 \qquad \text{on } \partial\Omega$$

The dynamics of (52) are the same as those of (48).

Namely, if the principal eigenvalue σ is positive

in

$$(53)\quad \Delta\phi + (1+\varepsilon g)\phi = \sigma\phi \qquad \text{in } \Omega$$

$$(1-s)\nabla\phi\cdot\eta + s\phi = 0 \qquad \text{on } \partial\Omega,$$

all solutions to (52) with $u(x,0) \gneq 0$ in Ω

converge over time in $C^1(\bar{\Omega})$ to a unique positive

equilibrium solution, which we denote

$$\tilde{u}_{\varepsilon,s};$$

if $\sigma \le 0$ in (53), all nonnegative solutions to (52)

converge over time in $C^1(\bar{\Omega})$ to 0.

Now $g \in C^{\alpha}(\bar{\Omega}) \Rightarrow \varepsilon g \geq -|\varepsilon| \|g\|_\infty$ so

(54) $$\sigma \geq 1 - |\varepsilon| \|g\|_\infty - \lambda_1(\Omega, s)$$
$$\geq 1 - |\varepsilon| \|g\|_\infty - \lambda_1(\Omega, 1)$$
$$> 0$$

provided that $|\varepsilon|$ is sufficiently small.

We assume $|\varepsilon|$ to be small enough so that $\tilde{u}_{\varepsilon,s}$ exists and is the globally attracting positive equilibrium for (52) for all $s \in [0, 1]$.

For the general competition problem

(55) $$\frac{\partial u}{\partial t} = \Delta u + u[1 + \varepsilon g - u - b_1 v]$$
$$\frac{\partial v}{\partial t} = \Delta v + v[1 - b_2 u - v] \quad \text{in } \Omega \times (0, \infty)$$

$$(1-s)\nabla u \cdot \eta + s u = 0 = (1-s)\nabla v \cdot \eta + s v \quad \text{on } \partial\Omega \times (0, \infty)$$

we have $\bar{b}_1 = \bar{b}_1(\varepsilon, s)$ and $\bar{b}_2 = \bar{b}_2(\varepsilon, s)$ with the same meanings as before. Namely,

$\bar{b}_1(\varepsilon, s)$ and $\bar{b}_2(\varepsilon, s)$ are the unique positive values for which the principal eigenvalues $\sigma_1(\varepsilon, s)$ and $\sigma_2(\varepsilon, s)$ in the problems

$$(56) \quad \Delta\phi_{\varepsilon,s} + (1 + \varepsilon g - \bar{b}_1(\varepsilon, s)\Theta_s)\phi_{\varepsilon,s} = \sigma_1(\varepsilon, s)\phi_{\varepsilon,s} \quad \text{in } \Omega$$

$$(1-s)\nabla\phi_{\varepsilon,s} \cdot \vec{\eta} + s\phi_{\varepsilon,s} = 0 \quad \text{on } \partial\Omega$$

and

$$(57) \quad \Delta\psi_{\varepsilon,s} + (1 - \bar{b}_2(\varepsilon, s)\hat{u}_{\varepsilon,s})\psi_{\varepsilon,s} = \sigma_2(\varepsilon, s)\psi_{\varepsilon,s} \quad \text{in } \Omega$$

$$(1-s)\nabla\psi_{\varepsilon,s} \cdot \vec{\eta} + s\psi_{\varepsilon,s} = 0 \quad \text{on } \partial\Omega$$

are both zero.

We need to estimate $\bar{b}_1(\varepsilon, s)$ and $\bar{b}_2(\varepsilon, s)$ for ε small and s fixed. The Implicit Function Theorem can be employed as before to show that $\hat{u}_{\varepsilon,s}$, $\bar{b}_1(\varepsilon, s)$, $\bar{b}_2(\varepsilon, s)$

are differentiable in ε for $|\varepsilon|$ small and that $\phi_{\varepsilon,s}$ and $\psi_{\varepsilon,s}$ are as well provided we normalize them by requiring them to be positive in Ω with

$$\int_\Omega \phi^2_{\varepsilon,s}\, dx = 1$$

$$\int_\Omega \psi^2_{\varepsilon,s}\, dx = 1.$$

Moreover, we can modify the earlier arguments so as to have these functions differentiable in ε for $|\varepsilon|$ small to any desired order.

So we have the following expansions:

(58) $$\bar{b}_1(\varepsilon, s) = 1 + \varepsilon r_1(s) + O(\varepsilon^2)$$

$$\phi_{\varepsilon,s} = \frac{\Theta_s}{\|\Theta_s\|_2} + \varepsilon \rho_1(s) + O(\varepsilon^2)$$

$$\tilde{u}_{\varepsilon,s} = \Theta_s + \varepsilon u_1(s) + O(\varepsilon^2)$$

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

$$\psi_{\varepsilon,s} = \frac{\Theta_s}{\|\Theta_s\|_2} + \varepsilon \rho_2(s) + O(\varepsilon^2)$$

We need to determine $r_1(s)$ and $r_2(s)$ in (58).

To find $r_1(s)$, substitute the expansions of $\overline{b}_1(\varepsilon, s)$ and $\phi_{\varepsilon, s}$ into (56). After simplification, we get that $\rho_1(s)$ satisfies

(59) $$\Delta \rho_1(s) + (1-\theta_s)\rho_1(s) = \frac{(r_1(s)\theta_s - g)\theta_s}{\|\theta_s\|_2} \quad \text{in } \Omega$$

$$(1-s)\nabla\rho_1(s)\cdot\vec{\eta} + s\,\rho_1(s) = 0 \quad \text{on } \partial\Omega$$

So $$\theta_s \Delta\rho_1(s) + \theta_s(1-\theta_s)\rho_1(s) = \frac{r_1(s)\theta_s^3 - g\,\theta_s^2}{\|\theta_s\|_2}$$

Integrating and applying Green's Second Identity yields

$$0 = r_1(s)\int_\Omega \theta_s^3\,dx - \int_\Omega g\,\theta_s^2\,dx$$

so that

(60) $$r_1(s) = \frac{\int_\Omega g\,\theta_s^2\,dx}{\int_\Omega \theta_s^3\,dx}$$

In order to find $r_2(s)$, we need $u_1(s)$.

If we substitute the third equation in (58) into (52), we get

(61) $$\Delta u_1(s) + (1-\theta_s)u_1(s) = \theta_s u_1(s) - g\theta_s \quad \text{in } \Omega$$
$$(1-s)\nabla u_1(s)\cdot\vec{\eta} + s\,u_1(s) = 0 \quad \text{on } \partial\Omega,$$

so that substituting the last three equations in (58) into (57) yields

(62) $$\Delta \rho_2(s) + (1-\theta_s)\rho_2(s) = \frac{u_1\theta_s}{\|\theta_s\|_2} + \frac{r_2\theta_s^2}{\|\theta_s\|_2} \quad \text{in } \Omega$$
$$(1-s)\nabla \rho_2(s)\cdot\vec{\eta} + s\rho_2(s) = 0 \quad \text{on } \partial\Omega$$

Multiply (61) by $\theta_s/\|\theta_s\|_2$ and (62) by θ_s and subtract to obtain

(63) $$\theta_s\Delta\left(\rho_2(s) - \frac{u_1(s)}{\|\theta_s\|_2}\right) + \theta_s(1-\theta_s)\left(\rho_2(s) - \frac{u_1(s)}{\|\theta_s\|_2}\right)$$
$$= \frac{r_2(s)\theta_s^3 + g\theta_s^2}{\|\theta_s\|_2} \quad \text{in } \Omega$$

$$(1-s)\nabla\left(\rho_2(s) - \frac{u_1(s)}{\|\theta_s\|_2}\right)\cdot\vec{\eta} + s\left(\rho_2(s) - \frac{u_1(s)}{\|\theta_s\|_2}\right) = 0$$

on $\partial\Omega$

Integrating (63) and employing Green's Second Identity yields

$$0 = r_2(s)\int_\Omega \theta_s^3\,dx + \int_\Omega g\,\theta_s^2\,dx$$

so that

(64) $$r_2(s) = -\frac{\int_\Omega g\,\theta_s^2\,dx}{\int_\Omega \theta_s^3\,dx}$$

So

(65) $$\bar{b}_1(\varepsilon, s) = 1 + \varepsilon\frac{\int_\Omega g\,\theta_s^2\,dx}{\int_\Omega \theta_s^3\,dx} + O(\varepsilon^2)$$

$$\bar{b}_2(\varepsilon, s) = 1 - \varepsilon\frac{\int_\Omega g\,\theta_s^2\,dx}{\int_\Omega \theta_s^3\,dx} + O(\varepsilon^2)$$

So we have

(66) $1 < \bar{b}_1(\varepsilon, s)$, $1 > \bar{b}_2(\varepsilon, s)$

when $\int_\Omega g\,\theta_s^2\,dx > 0$

and

(67) $1 > \bar{b}_1(\varepsilon, s)$, $1 < \bar{b}_2(\varepsilon, s)$

when $\int_\Omega g\,\theta_s^2\,dx < 0$

We now have :

Theorem 5. Consider (43)-(44) for a fixed $s \in [0,1]$

(i) If $\int_\Omega g\,\theta_s^2\,dx > 0$ and $0 < \varepsilon \ll 1$, (66) holds and thus species 1 has a competitive advantage in (43)-(44) over species 2 in the sense that species 1 may invade ~~&~~ when the density of species 2 is at the carrying capacity θ_s it obtains in the absence of species 1, while species 2 cannot invade

Ω when the density of species 1 is at the carrying capacity $\hat{u}_{\varepsilon,s}$ it obtains in the absence of species 2.

(ii) If $\int_\Omega g\,\Theta_s^2\,dx < 0$ and $0 < \varepsilon \ll 1$, (67) holds and thus species 2 has a competitive advantage in (43)-(44) over species 1 in the sense that species 2 may invade Ω when the density of species 1 is at the carrying capacity $\hat{u}_{\varepsilon,s}$ it obtains in the absence of species 2, while species 1 cannot invade Ω when the density of species 2 is at the carrying capacity Θ_s it obtains in the absence of species 1.

<u>Observation 6</u>. If (u,v) is a componentwise positive equilibrium solution

to (43)-(44), then $\int_\Omega g u v \, dx = 0$

Proof: Multiply the first equation in (43)-(44) by v and the second by u, integrate and employ Green's Second Identity.

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

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

We have from the first part of the talk that θ_s is differentiable in s. Moreover, we could modify the argument to have θ_s differentiable in s to any desired order. Consequently, G is continuously differentiable.

Theorem 7. Suppose $G(s) \neq 0$ for $s \in [a,b]$, where $0 \leq a < b \leq 1$. Then:

(i) There is an $\varepsilon_0 > 0$ so that if $0 < \varepsilon < \varepsilon_0$ and $s \in [a, b]$, (43)-(44) 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 (43)-(43) converge over time in $C^1(\bar{\Omega}) \times C^1(\bar{\Omega})$ to $(\hat{u}_{\varepsilon,s}, 0)$.

Consequently (43)-(44) 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 (43)-(44) converge over time in $C^1(\bar{\Omega}) \times C^1(\bar{\Omega})$ to

$(0, \theta_s)$. Consequently, (43)-(44) predicts that species 2 competitively excludes species 1 in this case.

Proof: In light of Theorem 5, we will only prove (i). Suppose (i) fails to hold. Then there is a sequence $(\varepsilon_n, s_n, u_n, v_n)$ so that

$$\left.\begin{aligned} \Delta u_n + u_n[1 + \varepsilon_n g - u_n - v_n] &= 0 \\ \Delta v_n + v_n[1 - u_n - v_n] &= 0 \end{aligned}\right\} \text{ in } \Omega$$

$$(1-s_n)\nabla u_n \cdot \eta + s_n u_n = 0 = (1-s_n)\nabla v_n \cdot \eta + s_n v_n$$

$$\text{on } \partial\Omega,$$

where $u_n > 0$ and $v_n > 0$ in Ω, $s_n \in [a, b]$, and $\varepsilon_n \to 0$ as $n \to \infty$. By passing to a subsequence, if need be, $s_n \to s^* \in [a, b]$.

The Maximum Principle $\Rightarrow$ u_n, v_n are uniformly bounded for all n.

For each n, so long as $s_n \neq 0$, the Laplace operator Δ plus the relevant boundary condition is invertible with an inverse which is compact as an operator from $C'(\bar{\Omega})$ to $C'(\bar{\Omega})$. If $s_n = 0$, the same is true fo $\Delta - \rho$ for any $\rho > 0$. Moreover, these compact inverses are continuous in s.

So by passing to a further subsequence if need be we have that $u_n \to u^*$, $v_n \to v^*$, with $u^* \geq 0$, $v^* \geq 0$ where u^* and v^* satisfy

$$\begin{aligned} \Delta u^* + u^*[1 - u^* - v^*] &= 0 \\ \Delta v^* + v^*[1 - u^* - v^*] &= 0 \end{aligned} \quad \text{in } \Omega$$

$$(1-s^*)\nabla u^* \cdot \vec{\eta} + s^* u^* = 0 = (1-s^*)\nabla v^* \cdot \eta + s^* v^* \quad \text{on } \partial\Omega$$

Since $1 > \lambda_1(\Omega, 1)$, $(u^*, v^*) \neq (0,0)$.

So there is a $\tau^* \in [0,1]$ so that

$$(u^*, v^*) = (\tau^* \theta_{s^*}, (1-\tau^*)\theta_{s^*}).$$

Now $\int_\Omega g u_n v_n \, dx = 0 \quad \forall n$

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

Since $\int_\Omega g \theta_{s^*}^2 \, dx \neq 0$, $\tau^* = 0$ or $\tau^* = 1$.

So $(u^*, v^*) = (\theta_{s^*}, 0)$ or $(0, \theta_{s^*})$

So we need to rule out the possibility that $u_n \to 0$ or $v_n \to 0$ as $n \to \infty$. Suppose for instance that $u_n \to 0$. Then

$$\Delta\left(\frac{u_n}{\|u_n\|_\infty}\right) + \frac{u_n}{\|u_n\|_\infty}\left[1 + \varepsilon_n g_n - u_n - v_n\right] = 0$$

$$\Delta v_n + v_n[1 - u_n - v_n] = 0$$

in Ω

$$(1-s_n)\nabla\left(\frac{u_n}{\|u_n\|_\infty}\right)\cdot \eta + s_n \frac{u_n}{\|u_n\|_\infty} = 0 = (1-s_n)\nabla v_n \cdot \eta + s_n v_n$$

on $\partial\Omega$

So there is a subsequence which we relabel if need be so that $\frac{u_n}{\|u_n\|_\infty} \to u^{**}$, $v_n \to \theta_{s^*}$

with

$$\Delta u^{**} + u^{*}[1 - \theta_{s^*}] = 0 \quad \text{in } \Omega$$

(69)

$$(1-s^*)\nabla u^{**}\cdot\vec{\eta} + s^* u^{**} = 0 \quad \text{on } \partial\Omega$$

$\left\| u_n / \|u_n\|_\infty \right\|_\infty = 1 \quad \forall n \Rightarrow u^{**} \neq 0.$

It follows from (69) that $u^{**} = \alpha\,\theta_{s^*}$, $\alpha \neq 0$.

Now $0 = \int_\Omega g u_n v_n \, dx = \int_\Omega g \frac{u_n}{\|u_n\|_\infty} v_n \, dx$

$\Rightarrow 0 = \alpha \int_\Omega g\, \theta_{s^*}^2 \, dx \Rightarrow \int_\Omega g\, \theta_{s^*}^2 \, dx = 0$

(x).

<u>Theorem 8</u>. Suppose that G changes sign n times on $[0,1]$. Then there is an $\varepsilon_0 > 0$ so that if $0 < \varepsilon < \varepsilon_0$, (43)–(44)

exhibits at least $n-1$ changes of competitive advantage in which the species holding the competitive advantage excludes the other from Ω over time.

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 (43)-(44) is that one species competitively excludes the other are bordered by regions in which (43)-(44) predicts coexistence. We have:

Theorem 9. 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 $\lim_{\varepsilon \to 0} s_*(\varepsilon) = \bar{s}$ $= \lim_{\varepsilon \to 0} s^*(\varepsilon)$ so that (43)-(44) admits a coexistence state for $s \in [\bar{s} - \delta_0, \bar{s} + \delta_0]$ $\Longleftrightarrow$ $s \in (s_*(\varepsilon), s^*(\varepsilon))$. Moreover, such a coexistence state is unique for every $s \in (s_*(\varepsilon), s^*(\varepsilon))$ and is globally asymptotically stable.

Remark: The proof of Theorem 9 can be found in Cantrell, Cosner and Lou, J. Dynamics and Differential Equations 16 (2004), 973-1010.

All results in this part of the talk are based on this paper. The proof amounts to a very careful unfolding of the equilibria (u, v, s, ε) of (43)-(44) in a nbd of $\{(\tau\theta_{\bar{s}}, (1-\tau)\theta_{\bar{s}}, \bar{s}, 0) \mid \tau \in [0,1]\}$

Theorem 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 sufficiently small $\varepsilon > 0$, (43)-(44) 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 (43)-(44) admits a coexistence state for s near $\bar{s}_i$ $\Leftrightarrow$ s lies in $(s_{*i}(\varepsilon), s_i^*(\varepsilon))$. Moreover, such a coexistence state to (43)-(44) is unique and globally asymptotically stable.

In order for us to exhibit a model with multiple reversals of competitive dominance we need to find a function g so that $G : [0,1] \to \mathbb{R}$ changes sign more than once. We will first show that such a g can be constructed provided that for some $n \geq 3$, $\{ \Theta^2_{s_1}, \ldots, \Theta^2_{s_n} \}$ is linearly independent in $L^2(\Omega)$, where $s_i \in [0,1]$ and $s_1 < s_2 < \cdots < s_n$.

(We then examine the question of linear independence of $\{\Theta^2_{s_1}, \ldots, \Theta^2_{s_n}\}$.)

The map $s \to \Theta_s^2$ can be viewed as a differentiable map $[0,1]$ into $L^2(\Omega)$. If Λ is a bounded linear functional on $L^2(\Omega)$, the map $s \to \Lambda(\Theta_s^2)$ is a differentiable map from $[0,1]$ into $\mathbb{R}$.

Suppose $0 \le s_1 < s_2 < \cdots < s_n \le 1$ are such that $\{\theta_{s_1}^2, \ldots, \theta_{s_n}^2\}$ is a linear independent set. Then a basic result of functional analysis (e.g. Schechter's <u>Principles of Functional Analysis</u>, AMS (2002), Lemma 4.14) $\Rightarrow$ 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.

Riesz Representation Theorem $\Rightarrow \exists \{h_1, \ldots, h_n\} \subseteq L^2(\Omega)$ so that

$$\Lambda_i : L^2(\Omega) \to \mathbb{R}$$

is given by

$$\Lambda_i(f) = \int_\Omega h_i f \, dx$$

For $i = 1, \dots, n$, h_i can be approximated in $L^2(\Omega)$ by functions in $C^\alpha(\bar{\Omega})$. So for each $i \in \{1, \dots, n\}$, choose a sequence $\{\hat{h}_{i_k}\}_{k=1}^\infty$ of functions in $C^\alpha(\bar{\Omega})$ so that

$$\| \hat{h}_{i_k} - h_i \|_2 \to 0$$

as $k \to \infty$. Let $0 < \varepsilon << 1$ be given.

Since

$$\left| \int_\Omega \hat{h}_{i_k} \theta_{s_j}^2 \, dx - \int_\Omega h_i \theta_{s_j}^2 \, dx \right|$$

$$\leq \| \hat{h}_{i_k} - h_i \|_2 \, \| \theta_{s_j}^2 \|_2$$

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

$$\int_\Omega \hat{h}_{ik(i)} \theta_{s_j}^2 \, dx > 1 - \frac{\varepsilon}{n}$$

if $i = j$ and

$$\left| \int_\Omega \hat{h}_{ik(i)} \theta_{s_j}^2 \right| < \frac{\varepsilon}{n}$$

if $i \neq j$.

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

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

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

$$\int_\Omega V(c_1^0, \ldots, c_n^0) \theta_{s_j}^2 \, dx$$

$$= \sum_{i=1}^n (-1)^{i+1} \int_\Omega \hat{h}_{ik(i)} \theta_{s_j}^2 \, dx > 1 - \varepsilon$$

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

$$G(c_1, \dots, c_n, s) = \int_\Omega V(c_1, \dots, c_n)\, \theta_s^\epsilon \, dx,$$

then $G(c_1^0, \dots, c_n^0, s)$ changes sign at least $n-1$ times on $[0,1]$.

There will be a $\delta > 0$ so that if

$$|(c_1, \dots, c_n) - (c_1^0, \dots, c_n^0)| < \delta,$$

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

when j is odd and

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

when j is even. The Transversality Theorem (Guillemin and Pollack, Differential Toplogy, Prentice Hall (1974), p. 68) guarantees for some $(\bar{c}_1, \dots, \bar{c}_n)$ with $|(\bar{c}_1, \dots, \bar{c}_n) - (c_1^0, \dots, c_n^0)| < \delta$, $G(\bar{c}_1, \dots, \bar{c}_n, s)$ has only simple zeros.

Theorem 11. (i) For any bounded domain Ω with sufficiently smooth boundary, 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 perturbations of (45)-(46) so that the perturbed system (43)-(44) predicts at least 3 reversals of competitive advantage as matrix hostility increases.

(ii) If $\Omega = [a, b]$ and n is any positive integer, there are $s_0, s_1, \dots, s_n$ with $0 \leq s_0 < s_1 < \cdots < s_n \leq 1$ so that $\{\theta_{s_0}^2, \theta_{s_1}^2, \dots, \theta_{s_n}^2\}$ is linearly independent. Consequently, in one space dimension there can be an arbitrary number of reversals of competitive advantage as matrix hostility increases.

Remarks:

(i) Establishing a result comparable to that of part (ii) for a general domain in higher dimensions is an open and possibly challenging problem.

(ii) I will give the proof of part (i) in the case that Ω is not a ball. In this case, we can show that $\{\theta_0^2, \theta_{s_1}^2, \theta_{s_2}^2, \theta_1^2\}$ is linearly independent for any s_1, s_2 with $0 < s_1 < s_2 < 1$.

The proofs of part (i) in the case Ω is a ball and of part (ii) are found in Cantrell, Cosner and Lou, J. Dyn. Diff. Eq. 16 (2004), 973 – 1010.

Proof: Claim: $\{\theta_0^2, \theta_s^2, \theta_1^2\} = \{1, \theta_s^2, \theta_1^2\}$ is linearly independant for any $s \in (0,1)$.

To this end, suppose that

$$c_0 + c_s\theta_s^2 + c_1\theta_1^2 \equiv 0 \quad \text{in } \Omega$$

Then for $i = 1, \dots, n$,

$$2c_s\theta_s(\theta_s)_{x_i} + 2c_1\theta_1(\theta_1)_{x_i} \equiv 0 \quad \text{in } \Omega.$$

$$\therefore \quad c_s\theta_s\nabla\theta_s \cdot \eta = 0 \quad \text{on } \partial\Omega.$$

Hence $\quad c_s\left(\frac{s}{1-s}\right)\theta_s^2 = 0 \quad$ on $\partial\Omega$

$\Rightarrow \quad c_s = 0.$ Since θ_1^2 is nonconstant,

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

$\Rightarrow \quad c_0 = 0 = c_1.$

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

Suppose

$$c_0 + c_{s_1}\theta_{s_1}^2 + c_{s_2}\theta_{s_2}^2 + c_1\theta_1^2 \equiv 0 \qquad \text{on } \Omega$$

Then

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

on Ω for $i = 1, \dots, n$. $\therefore$

$$c_{s_1}\theta_{s_1}\nabla\theta_{s_1}\cdot\eta + c_{s_2}\theta_{s_2}\nabla\theta_{s_2}\cdot\eta = 0$$

on $\partial\Omega$, $\Rightarrow$

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

on $\partial\Omega$.

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

on $\partial\Omega$.

Now

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

So 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 θ_{s_2} are constant on $\partial\Omega$. $\therefore$ $\nabla\theta_{s_1} \cdot \eta$ and $\nabla\theta_{s_2} \cdot \eta$ are constant on $\partial\Omega$. A classic result of Serrin (Arch. Rational Mech. Anal. 43 (1971), 304-318) $\Rightarrow$ Ω is a ball.

So assuming Ω is not a ball

at least one of c_{s_1} and c_{s_2} must be zero.
Wlog assume $c_{s_1} = 0$.
↑ So we reduce to having

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

The first part of the proof $\Rightarrow$ $(c_0, c_{s_2}, c_1) = (0,0,0)$.

Remark: Another interesting question here concerns optimal control through boundary habit hostility. Lenhart et al [Mathematical Methods in the Applied Sciences 22 (1999), 1061-1077] treats the problem in the predator-prey case. To the best of our knowledge, the competition case remains open.