Lecture 17

Applications of Persistence Theory

I. Predator-prey models.

We consider two Lotka-Volterra models: (A) with a generalist predator and (B) with a specialist predator. The models are:

$$(1)\quad \begin{cases} \dfrac{\partial u_1}{\partial t} = \Delta u_1 + u_1(a_1 - u_1 - b_1 u_2) & \text{in } \Omega \times (0,\infty) \\ \dfrac{\partial u_2}{\partial t} = d\Delta u_2 + u_2(a_2 + b_2 u_1 - u_2) & \\ u_1 = 0 = u_2 & \text{on } \partial\Omega \times (0,\infty) \end{cases}$$

$$(2)\quad \begin{cases} \dfrac{\partial u_1}{\partial t} = \Delta u_1 + u_1(a_1 - u_1 - b_1 u_2) & \text{in } \Omega \times (0,\infty) \\ \dfrac{\partial u_2}{\partial t} = d\Delta u_2 + u_2(a_2 + b_2 u_1) & \\ u_1 = 0 = u_2 & \text{on } \partial\Omega \times (0,\infty) \end{cases}$$

In both (1) and (2) the dispersal and demographic parameters are constants. In (1) all of the parameters are positive ; in (2) , $a_2 < 0$ while the remaining parameters are positive. In both (1) and (2), u_1 denotes the density of the prey species in question, while u_2 denotes the density of its predator.

We employ the Average Lyapunov Function Approach to establish conditions for the permanence of (1) and (2). From the preceding lecture, we know that we must be able to recast (1) and (2) as semi-dynamical systems. Here we let

$$\pi((u_1^0, u_2^0), t)$$

denote the unique solution to (1) or (2) $(u_1(x,t), u_2(x,t))$ which is such that

$$(u_1(x,0), u_2(x,0)) \equiv (u_1^0(x), u_2^0(x)).$$

Then π may be regarded as a map from $Y \times [0,\infty) \to Y$, where Y is the cone K of componentwise nonnegative functions in space $C_0^1(\bar{\Omega}) \times C_0^1(\bar{\Omega})$, so that Y is a complete metric space.

In this context, dissipativity of Π and the compactness of $\Pi(\cdot, t): Y \to Y$ follow from the theory of reaction-diffusion systems provided we establish that there are positive constants c_1 and c_2 so that for any $(u_1^0, u_2^0) \in Y$, there $\exists$ a $t_0(u_1^0, u_2^0)$ so that

$$u_1(x,t) \le c_1$$

$$u_2(x,t) \le c_2$$

for $t \ge t_0(u_1^0, u_2^0)$.

For either (1) or (2), c_1 can be taken as $a_1 + 1$, since

(3) $$\frac{\partial u_1}{\partial t} \le \Delta u_1 + u_1(a_1 - u_1) \qquad \text{in } \Omega \times (0, \infty)$$

$$u_1 = 0 \qquad \text{on } \partial\Omega \times (0, \infty)$$

and the dynamics of

(4)
$$\frac{\partial u_1}{\partial t} = \Delta u_1 + u_1(a_1 - u_1) \qquad \text{in } \Omega \times (0,\infty)$$
$$u_1 = 0 \qquad \text{on } \partial\Omega \times (0,\infty)$$

are well-understood. (Namely, if $a_1 > \lambda_0^1(\Omega)$, the principal eigenvalue of $-\Delta$ on Ω subject to homogeneous Dirichlet boundary conditions, all nonnegative nontrivial solutions to (4) converge over time in $C_0^1(\bar{\Omega})$ to a positive equilibrium $\bar{u}_1$ of (4). The maximum principle guarantees $\bar{u}_1 < a_1$ on $\bar{\Omega}$. If $a_1 \leq \lambda_0^1(\Omega)$, all solutions converge in $C_0^1(\bar{\Omega})$ to zero. In either case, given $\varepsilon > 0$, there is a $t^* = t^*(u_1^0)$ so that $u_1(x,t) \leq a_1 + \varepsilon$ for $t \geq t^*$.)

Now consider (1). In this case,

(5)
$$\frac{\partial u_2}{\partial t} \leq d\Delta u_2 + u_2(a_2 + b_2(a_2+\varepsilon) - u_2)$$

on $\Omega \times (t^*, \infty)$ and we may take

$$c_2 = a_2 + b_2 a_1 + 1.$$

Let us turn to (2). In this case we first obtain a bound on the total predator population $\int_\Omega u_2(x,t)\,dx$ from which we can obtain a bound on $u_2(x,t)$. Choose $\alpha, \beta > 0$ so that

$$\beta b_2 - \alpha b_1 < 0$$

and $\gamma > 0$ with

$$a_2 + \gamma < 0.$$

Then

$$\alpha u_1 (a_1 - u_1 - b_1 u_2 + \gamma) + \beta u_2 (a_2 + b_2 u_1 + \gamma)$$

$$\leq \alpha u_1 (a_1 + \gamma - u_1)$$

so long as $u_1 \geq 0$ and $u_2 \geq 0$. Suppose now that $(u_1(x,t), u_2(x,t))$ is a solution to (2) with $u_1(x,0) \overset{>}{\not\equiv} 0$, $u_2(x,0) \overset{>}{\not\equiv} 0$.

Let $G : [0,\infty) \to (0,\infty)$ be given by

$$G(t) = \int_\Omega \left[\alpha u_1(x,t) + \beta u_2(x,t)\right] dx$$

Then

$$G'(t) = \int_\Omega \left(\alpha \frac{\partial u_1}{\partial t} + \beta \frac{\partial u_2}{\partial t}\right) dx$$

$$= \int_\Omega (\alpha \Delta u_1 + \beta \Delta u_2)\, dx$$

$$+ \int_\Omega \left[\alpha u_1(a_1 - u_1 - b_1 u_2 + \gamma) + \beta u_2(a_2 + b_2 + \gamma)\right] dx$$

$$- \gamma \int_\Omega (\alpha u_1 + \beta u_2)\, dx$$

Now $\int_\Omega \Delta u_i\, dx = \int_\Omega \nabla \cdot (\nabla u_i)\, dx = \int_{\partial\Omega} \nabla u_i \eta\, dS \leq 0$

$$\Rightarrow \quad G'(t) \leq \int_\Omega \alpha u_1 (a_1 + \gamma - u_1)\, dx - \gamma G(t)$$

$$\alpha u_1 (a_1 + \gamma - u_1) \leq \frac{\alpha (a_1 + \gamma)^2}{4} \text{ for all } u_1 \geq 0.$$

$$\Rightarrow \quad G'(t) \leq \frac{\alpha (a_1 + \gamma)^2}{4} |\Omega| - \gamma G(t)$$

$$= G_0 - \gamma G(t)$$

$$\Rightarrow \quad G(t) \leq G(0) e^{-\gamma t} + \frac{G_0}{\gamma}(1 - e^{-\gamma t})$$

$\exists\ t_* = t_*(G(0))$ so that if $t \geq t_*$,

$$G(t) \leq \frac{G_0}{\gamma} + 1$$

Consequently, it follows that for $t \geq t_*(G(0))$

$= t_*(u_1(x,0), u_2(x,0))$, $\|u_2\|_1 \leq \frac{1}{b_1}\left(\frac{G_0}{\gamma} + 1\right)$.

So we have that

(6) $$\frac{\partial u_2}{\partial t} \leq d\Delta u_2 + u_2(a_2 + b_2(a_1+1))$$

on $\Omega \times (\hat{t}, \infty)$

$$u_2 = 0$$ on $\partial\Omega \times (\hat{t}, \infty)$

and

(7) $$\|u_2(x,t)\|_1 \leq \frac{1}{b_1}\left(\frac{G_0}{\gamma} + 1\right)$$

for $t \geq \tilde{t}$,

where $\tilde{t} = \max\{t^*, t_*\}$.

One may now argue as in Alikakos (JDE '79) (Th3.1

that $\|u_2(x,t)\|_\infty \leq E^*(a_1+1, u_2(x,0))$

for $t \geq \tilde{t}$, where E^* is a constant depending on a_1 and $u_2(x,0)$. We now establish the following lemma, the proof of which is a refinement of the proof of Theorem 3.1 in Alikakos.

Lemma. Suppose that $u \geq 0$ satisfies

$$u_t = \mu \Delta u + a(x,t)u \quad \text{in } \Omega \times (0,\infty)$$

$$u \nabla u \cdot \eta \leq 0 \quad \text{on } \partial\Omega \times (0,\infty)$$

with $a(x,t)$ locally Lipschitz in (x,t) and satisfying $a(x,t) \leq A$ for some constant A. Suppose also that there exist constants B_0 independent of u and $E^*(B_0, u(x,0))$ so that $\|u(x,t)\|_1 \leq B_0$ and $\|u(x,t)\|_\infty \leq E^*(B_0, u(x,0))$ for t sufficiently large. Then there is a constant B^* independent of u so that $\|u(x,t)\|_\infty \leq B^*$ for t sufficiently large.

(Note: The Alikakos result gives global existence but is not sufficient to obtain dissipativity.)

Proof of Lemma:

Let $E_k = \int_\Omega u^{2^k} dx \quad , k = 0, 1, 2, \ldots$

For t large we get

$$\frac{dE_k}{dt} = \int_\Omega \frac{\partial}{\partial t} u^{2^k} dx$$

$$= \int_\Omega 2^k u^{2^k - 1} \frac{\partial u}{\partial t} dx$$

$$= \int_\Omega 2^k u^{2^k - 1} \left[\mu \Delta u + a(x,t) u \right] dx$$

$$= 2^k \mu \int_\Omega u^{2^k - 1} \Delta u \, dx + 2^k \int_\Omega a(x,t) u^{2^k}$$

$$= 2^k \mu \int_\Omega \left[\operatorname{div}(u^{2^k - 1} \nabla u) - (2^k - 1) u^{2^k - 2} |\nabla u|^2 \right]$$

$$+ 2^k \int_\Omega a(x,t) u^{2^k}$$

$$\leq -\mu 2^k (2^k - 1) \int_\Omega u^{2^k - 2} |\nabla u|^2 + 2^k A \int_\Omega u^{2^k}$$

Now $|\nabla(u^{2^{k-1}})|^2 = 2^{k-1} \cdot 2^{k-1} \cdot u^{2^{k-1} - 1} \cdot u^{2^{k-1} - 1} |\nabla u|^2$

$$= 2^{2(k-1)} u^{2^k - 2} |\nabla u|^2$$

$$\Rightarrow \quad u^{2^k - 2} |\nabla u|^2 = \frac{1}{2^{2k-2}} |\nabla(u^{2^{k-1}})|^2$$

$$\Rightarrow -\mu\, 2^k(2^k-1)\int_\Omega u^{2^k-2}|\nabla u|^2\,dx$$

$$= -\mu\,\frac{2^k(2^k-1)}{2^{2k-2}}\int_\Omega |\nabla(u^{2^{k-1}})|^2\,dx$$

$$= -\mu\,\frac{(2^k-1)}{2^{k-2}}\int_\Omega |\nabla(u^{2^{k-1}})|^2\,dx$$

Now $2^k-1 \geq 2^{k-1}$ for $k \geq 1 \Rightarrow$

$$-\mu\,\frac{(2^k-1)}{2^{k-2}}\int_\Omega |\nabla(u^{2^{k-1}})|^2\,dx$$

$$\leq -\mu\,\frac{2^{k-1}}{2^{k-2}}\int_\Omega |\nabla(u^{2^{k-1}})|^2\,dx$$

$$= -2\mu\int_\Omega |\nabla(u^{2^{k-1}})|^2\,dx$$

so that

$$(8) \qquad \frac{dE_k}{dt} \leq -\nu\int_\Omega |\nabla(u^{2^{k-1}})|^2\,dx + 2^k A\int_\Omega u^{2^k}\,dx,$$

where $\nu = 2\mu$.

For $\varepsilon \in (0, \tfrac{1}{2})$ and $v \in W^{1,2}(\Omega)$

we have the interpolation inequality

$$\|v\|_2^2 \leq \varepsilon \|\nabla v\|_2^2 + C_0 \varepsilon^{-(n/2)} \|v\|_1^2$$

where C_0 depends only on n and Ω, where n is the dimension of Ω.

$$\Rightarrow \; -\|\nabla v\|_2^2 \leq \frac{1}{\varepsilon}\|v\|_2^2 + C_0 \, \varepsilon^{-(\frac{n+2}{2})} \|v\|_1^2$$

Letting $v = u^{2^{k-1}}$, the preceding inequality applied to (8) yields

$$\frac{dE_k}{dt} \leq \left[-\left(\frac{\nu}{\varepsilon}\right) + 2^k A\right] \int_\Omega u^{2^k} dx + C_0 \varepsilon^{-(\frac{n+2}{2})} E_{k-1}^2$$

Choosing $\varepsilon_0 < \min\left\{\frac{1}{2}, \frac{2\nu}{2+A}\right\}$ and setting $\varepsilon = \varepsilon_k = 4^{-k}\varepsilon_0$

we have

$$-\frac{\nu}{\varepsilon_k} + 2^k A = \frac{-4^k \nu}{\varepsilon_0} + 2^k A \leq -4^k \nu \left(\frac{2+A}{2\nu}\right) + 2^k A$$

$$= -4^k\left(1 + \frac{A}{2}\right) + 2^k A \leq -4^k \quad \text{for } k \geq 1$$

$$\therefore \; \frac{dE_k}{dt} \leq -4^k E_k + C_0 \varepsilon_0^{-(\frac{n+2}{2})} 4^{[(\frac{n+2}{2})k]} E_{k-1}^2$$

$$= -4^k E_k + C_1 4^{[(\frac{n+2}{2})k]} E_{k-1}^2 \text{, where}$$

C_1 depends on Ω, n, ν and A but are independent of $u(x,0)$.

We hypothesize that for large t $E_0 \leq B_0$ and $\|u(x,t)\|_\infty \leq E^*(B_0, u(x,0))$. Hence $E_k \leq (E^*)^{2^k}$, where we replace the original bound on $\|u\|_\infty$ with $|\Omega| E^*$ if $|\Omega| > 1$.

We construct a sequence of bounds B_k and show $E_k \leq B_k$ for all k if t is large enough.

Let $\delta_k = \sum_{j=1}^{k} j 2^{k-j}$. Then $\delta_k = k + 2\delta_{k-1}$ and $\delta_k / 2^k \leq \sum_{j=1}^{\infty} j 2^{-j}$, which can be shown to equal 2 ($f(x) = \sum_{j=0}^{\infty} x^j$ for $x \in (0,1)$ $\Rightarrow$

$$f'(x) = \sum_{j=1}^{\infty} j x^{j-1}$$ and also that $$f(x) = \frac{1}{1-x}$$

$$\Rightarrow f'(x) = \frac{1}{(1-x)^2}.)$$

Let $B_k = C_1^{\,2^k-1}\, 2^{2^k-1}\, 4^{(n/2)\delta_k}\, B_0^{\,2^k}$.

Since $\delta_k / 2^k$ is bounded and C_1 and B_0 are independent of $u(x,0)$,

$$B_k \le (B^*)^{2^k}$$

for some B^* independent of $u(x,0)$

Moreover, one may choose $t_0 > 0$ so that

$$(E^*)^{2^k} e^{-2^k t_0} \le B_k/2$$

(Here $(E^*)^{2^k} e^{-2^k t_0} \le B_k/2$

$$\Leftrightarrow \quad \frac{2(E^*)^{2^k}}{B_k} \le e^{2^k t_0}$$

$$\Leftrightarrow \quad \ln 2 + 2^k \ln E^* - \ln B_k \le 2^k t_0$$

$$\Leftrightarrow \quad \ln 2 + 2^k \ln E^* - \ln\left(C_1^{\,2^{k-1}} \cdot 2^{2^{k-1}}\, 4^{(n/2)\delta_k}\, B_0^{\,2^k}\right) \le 2^k t_0$$

$$\Leftrightarrow \quad \ln 2 + 2^k \ln E^* - (2^k-1)\ln C_1 - (2^k-1)\ln 2 - \left(\frac{n\delta_k}{2}\right)\ln 4$$

$$- 2^k \ln B_0 \le 2^k t_0$$

$$\Leftrightarrow \quad t_0 \ge 2^{-k}\ln 2 + \ln E^* - \ln C_1 + 2^{-k}\ln C_1 - \ln 2 + 2^{-k}\ln 2$$

$$- \frac{n}{2}\left(\frac{\delta_k}{2^k}\right)\ln 4 - \ln B_0 \;)$$

So now suppose for $t \geq t^*$ that we have

$$E_k \leq (E^*)^{2^k} \quad \text{and} \quad E_{k-1} \leq B_{k-1}.$$

Now

$$\frac{dE_k}{dt} \leq -4^k E_k + C_1 4^{[(\frac{n+2}{2})]k} E_{k-1}^2$$

$$\leq -4^k E_k + C_1 4^{[(\frac{n+2}{2})]k} B_{k-1}^2$$

$$\Rightarrow \frac{dE_k}{dt} + 4^k E_k \leq C_1 4^{[(\frac{n+2}{2})]k} B_{k-1}^2$$

$$\Rightarrow \frac{d}{dt}\left(e^{4^k(t-t^*)} E_k\right) \leq C_1 4^{[(\frac{n+2}{2})]k} B_{k-1}^2 e^{4^k(t-t^*)}$$

$$\Rightarrow e^{4^k(t-t^*)} E_k - E_k \leq C_1 4^{(\frac{n}{2})k} B_{k-1}^2 e^{4^k(t-t^*)}$$

$$- C_1 (4^{n/2})^k B_{k-1}^2$$

$$\Rightarrow e^{4^k(t-t^*)} E_k \leq E_k + C_1 (4^{n/2})^k B_{k-1}^2 e^{4^k(t-t^*)}$$

$$\leq (E^*)^{2^k} + C_1 (4^{n/2})^k B_{k-1}^2 e^{4^k(t-t^*)}$$

(9) $$\Rightarrow E_k \leq C_1 (4^{n/2})^k B_{k-1}^2 + (E^*)^{2^k} e^{-4^k(t-t^*)}$$

For $t \geq t^* + (t_0/2^k)$, (9) yields

$$E_k \le C_1 (4)^{(n/2)k} B_{k-1}^2 + (E^*)^{2^k} e^{-2^k t_0}$$

$$\le C_1 (4)^{(n/2)k} B_{k-1}^2 + B_k/2$$

Now $$B_{k-1}^2 = C_1^{2(2^{k-1}-1)} 2^{2(2^{k-1}-1)} \left(4^{(n/2)\delta_{k-1}}\right)^2 B_0^{2(2^{k-1})}$$

$$= C_1^{2^k-2} 2^{2^k-1} \left(4^{(n/2)}\right)^{2\delta_{k-1}} B_0^{2^k}$$

$\Rightarrow$ $$C_1 (4)^{(n/2)k} B_{k-1}^2 = C_1^{2^k-1} 2^{2^k-2} \left(4^{n/2}\right)^{(k+2\delta_{k-1})} B_0^{2^k}$$

$$= C_1^{2^k-1} 2^{2^k-2} \left(4^{n/2}\right)^{\delta_k} B_0^{2^k}$$

$$= \frac{1}{2} B_k$$

$\Rightarrow$ $$E_k \le B_k \quad \text{for} \quad t \ge t^* + t_0/2^k$$

Since $E_0 \le B_0$ when $t \ge t^*$, $E_k \le B_k$ when

$$t \ge t^* + t_0 \sum_{i=1}^{k} 2^{-i}$$

$\therefore$ for $t > t^* + t_0$,

$$\|u\|_{2^k} = E_k^{1/2^k} \le B_k^{1/2^k} \le B^*$$

for all k. $\therefore$ $\|u\|_\infty \le B^*$ for $t > t^* + t_0$

Lemma $\Rightarrow$ $\|u_2(x,t)\|_\infty \le B^*$ for $t >$ $\hat{t}^2((u_1(x,0), u_2(x,0)))$, where B^* is independent of $(u_1(x,0), u_2(x,0))$. So in (2), we may take $c_2 = B^*$.

So we now have that $\pi : Y \times [0,\infty) \to Y$ is dissipative and that $\pi(\cdot, t) : Y \to Y$ is compact for $t > 0$. As in the preceding lecture, π has a (compact) global attractor, a compact invariant subset U of Y so that

$$\lim_{t\to\infty} \sup_{u \in V} d(\pi((u_1, u_2), t), U) = 0$$

for any bounded subset V of Y. Consequently, given any $\varepsilon > 0$, the neighborhood $\mathcal{B}(U, \varepsilon)$ of U is such that there is a positive time $t_0 = t_0(\varepsilon)$ so that by time t_0, all orbits beginning in V reach $\mathcal{B}(U, \varepsilon)$ and remain there for all subsequent times.

We may restrict our attention to the restriction of π to $\mathcal{B}(U, \varepsilon)$, set $\tilde{X} = \overline{\pi(\mathcal{B}(U, \varepsilon), [t_0, \infty))}$ for some $t_0 > 0$ and $X = \pi(\tilde{X}, t')$ for some $t' > 0$. Then $\tilde{X}$ and X are compact and forward invariant under π, and if $S = X \cap \partial Y$, S and $X \setminus S$ are forward invariant under π. If $(u_1, u_2) \in S$, then either $u_1 = 0$ or $u_2 = 0$ in Y. Let $\omega(S) = \{\omega(u) \mid u \in S\}$ (nonstandard definition).

Let us consider (1). We set $d = 1$, as the value of $d > 0$ will not affect the remainder of the analysis. As noted earlier, (4) admits a unique globally attracting positive equilibrium solution $\bar{u}_1$ provided $a_1 > \lambda_0^1(\Omega)$.

(The same holds true for

(8) $$\frac{\partial u_2}{\partial t} = \Delta u_2 + u_2(a_2 - u_2) \qquad \text{in } \Omega \times (0,\infty)$$

$$u_2 = 0 \qquad \text{on } \partial\Omega \times (0,\infty)$$

so long as $a_2 > \lambda_0^1(\Omega)$.) Now

(9) $$a_i > \lambda_0^1(\Omega) \iff \sigma_i > 0,$$

$i = 1, 2$, where σ_i is the principal eigenvalue in

(10) $$\Delta w_i + a_i w_i = \sigma_i w \qquad \text{in } \Omega$$

$$w_i > 0 \qquad \text{in } \Omega$$

$$w_i = 0 \qquad \text{on } \partial\Omega$$

Let us now assume $\sigma_1 > 0$ and $\sigma_2 > 0$, and let $\bar{u}_1$ and $\bar{u}_2$ be the unique globally attracting positive equilibria for (4) and (8), respectively. We have

$$\omega(S) = \{(0,0), (\bar{u}_1, 0), (0, \bar{u}_2)\}.$$

The prey species can invade when the predator has density $\bar{u}_2$ provided that the principal eigenvalue σ_3 of

$$\Delta w_3 + (a_1 - b_1 \bar{u}_2) w_3 = \sigma_3 w_3 \quad \text{in } \Omega$$

$$w_3 = 0 \quad \text{on } \partial\Omega$$

is positive, and the predator species can invade when the prey has density $\bar{u}_1$ provided the principal eigenvalue σ_4 of

$$\Delta w_4 + (a_2 - b_2 \bar{u}_1) w_4 = \sigma_4 w_4 \quad \text{in } \Omega$$

$$w_4 = 0 \quad \text{on } \partial\Omega$$

is positive.

$$\boxed{\text{Assume now } \sigma_1 > 0,\ \sigma_2 > 0,\ \sigma_3 > 0 \text{ and } \sigma_4 > 0}$$

We restrict our attention to the compact set X.

Define $P : X \to [0, \infty)$ by

$$P((v_1, v_2)) = \left(\int_\Omega w_3 v_1 \, dx \right)^{\beta_1} \left(\int_\Omega w_4 v_2 \, dx \right)^{\beta_2}$$

Notes: (i) $w_3 > 0$ and $w_4 > 0$ in Ω.

(ii) We require $\sigma_1 > 0$ and $\sigma_2 > 0$, respectively, for the equations which define w_3 and w_4, respectively, to be meaningful.

(iii) Having $\sigma_3 > 0$ and $\sigma_4 > 0$ is an additional hypothesis that will be needed.

(iv) β_1 and β_2 are positive constants yet to be determined.

(v) $P((v_1, v_2)) = 0$ if and only if $v_1 \equiv 0$ or $v_2 \equiv 0$; i.e., if and only if $(v_1, v_2) \in S$.

Now let $\alpha(t, u)$ for $t \geq 0$ and $u \in S$ be given by

$$Q(t,u) = \liminf_{\substack{v \to u \\ v \in X \setminus S}} \left(\frac{P(\Pi(v,t))}{P(v)} \right).$$

Π is permanent if $\sup_{t>0} Q(t,u) > \begin{cases} 1 & u \in \omega(S \\ 0 & u \in S \end{cases}$

Let $(u_1, u_2) \in S$. Now

$$P((v_1, v_2)) = \exp\left[\beta_1 \log \int_\Omega w_3 v_1 \, dx + \beta_2 \log \int_\Omega w_4 v_2 \, dx\right.$$

Let $(z_1(x,t), z_2(x,t)) = \Pi((v_1(x), v_2(x), t)$

$$\frac{P(\Pi((v_1, v_2), t))}{P((v_1, v_2))}$$

$$= \exp\left[\beta_1 \left(\log \int_\Omega w_3(x) z_1(x,t)\, dx - \log \int_\Omega w_3(x) z_1(x,0)\, dx\right)\right.$$

$$\left. + \beta_2 \left(\log \int_\Omega w_4(x) z_2(x,t)\, dx - \log \int_\Omega w_4(x) z_2(x,0)\, dx\right)\right]$$

Now $\log f(t) - \log f(0) = \int_0^t \frac{f'(s)}{f(s)}$

for a smooth positive function.

So the preceding equals

$$\exp\left[\beta_1 \int_0^t \left[\int_\Omega w_3(x) \frac{\partial z_1}{\partial s}(x,s)\,dx \Big/ \int_\Omega w_3(x) z_1(x,s)\,dx \right] ds\right.$$

$$\left. + \beta_2 \int_0^t \left[\int_\Omega w_4(x) \frac{\partial z_2}{\partial s}(x,s)\,dx \Big/ \int_\Omega w_4(x) z_2(x,s)\,dx \right] ds \right]$$

$$= \exp\left[\beta_1 \int_0^t \left[\frac{\int_\Omega w_3(x) \{ \Delta z_1(x,s) + z_1(x,s)[a_1 - z_1(x,s) - b_1 z_2(x,s)]\}\,dx}{\int_\Omega w_3(x) z_1(x,s)\,dx} \right] \right.$$

$$\left. + \beta_2 \int_0^t \left[\frac{\int_\Omega w_4(x) \{ \Delta z_2(x,s) + z_2(x,s)[a_2 + b_2 z_1(x,s) - z_2(x,s)]\}\,dx}{\int_\Omega w_4(x) z_2(x,s)\,dx} \right] \right.$$

Now $\int_\Omega w_3(x)\Delta z_1(x,s)\,dx \underset{(GSI)}{=} \int_\Omega \Delta w_3(x) z_1(x,s)$

$$= \int_\Omega (\sigma_3 - a_1 + b_1 \bar{u}_2(x))\, w_3(x)\, z_1(x,s)\,dx$$

and $\int_\Omega w_4(x)\Delta z_2(x,s)\,dx = \int_\Omega \Delta w_4(x) z_2(x,s)\,dx$

$$= \int_\Omega (\sigma_4 - a_2 - b_2 \bar{u}_1(x))\, w_4(x) z_2(x,s)\,dx$$

So the preceding yields

$$= \exp\left[\beta_1 \int_0^t \left[\frac{\int_\Omega w_3(x) z_1(x,s)\{\sigma_3 + b_1\bar{u}_2(x) - b_1 z_2(x,s) - z_1(x,s)\}dx}{\int_\Omega w_3(x) z_1(x,s)\,dx}\right] ds\right.$$

(11)

$$\left. + \beta_2 \int_0^t \left[\frac{\int_\Omega w_4(x) z_2(x,s)\{\sigma_4 - b_2\bar{u}_1(x) + b_2 z_1(x,s) - z_2(x,s)\}dx}{\int_\Omega w_4(x) z_2(x,s)\,dx}\right] ds\right]$$

We have restricted ourselves to the compact set X which contains the global attractor to the system. The functional expressions $\sigma_3 + b_1\bar{u}_2(x) - b_1\hat{v}_2(x) - \hat{v}_1(x)$ and $\sigma_4 - b_2\bar{u}_1(x) + b_2\hat{v}_1(x) - \hat{v}_2(x)$ appearing above must be bounded below as $(\hat{v}_1, \hat{v}_2)$ range over X, since X is compact.

In particular,

$$\sigma_3 + b_1\bar{u}_2(x) - b_1\hat{v}_2(x) - \hat{v}_1(x) \geq d_1$$

$$\sigma_4 - b_2\bar{u}_1(x) + b_2\hat{v}_1(x) - \hat{v}_2(x) \geq d_2$$

independent of $(\hat{v}_1, \hat{v}_2) \in X$.

So $$\frac{P(\pi((v_1, v_2), t)}{P((v_1, v_2))} \geq \exp((\beta_1 d_1 + \beta_2 d_2)t)$$

Notice that d_1 and d_2 need not be positive.

So the ratio $P(\pi((v_1,v_2),t))/P(v_1,v_2)$ need only exceed a decaying exponential.

So we have if $(u_1,u_2) \in S$

$$a(t,(u_1,u_2)) \geq \exp((\beta_1 d_1 + \beta_2 d_2)t)$$

$$\Rightarrow \sup_{t>0} a(t,(u_1,u_2)) > 0 \quad \text{if } (u_1,u_2) \in S$$

Note: We may argue that $\sup_{t>0} a(t,(u_1,u_2)) > c$ for any number $c \in (0,1)$, even when d_1 and d_2 are negative, by choosing t close enough to 0.

If d_1 and d_2 were positive, we would be through at this point, for then $a(t,(u_1,u_2)) > 1$ for any t. Unfortunately, we have no means of discerning d_1 and d_2 are positive.

So now we must turn to $\omega(S)$

$= \{ (0,0), (\bar{u}_1(x), 0), (0, \bar{u}_2(x)) \}$ and establish

that $\sup_{t>0} a(t, (u_1, u_2)) > 1$ if $(u_1, u_2) \in \omega(S)$

Basic Problem: we encounter an indeterminate form.

How so? Since X is compact, $\Pi : X \times [0,1] \to X$

is uniformly continuous. So if $(v_1, v_2) = (z_1(x,0), z_2(x,0))$

is near enough to $(\bar{u}_1, 0) = (\tilde{z}_1(x,0), \tilde{z}_2(x,0))$, for

example, their images under the semiflow,

$(z_1(x,t), z_2(x,t))$ and $(\tilde{z}_1(x,t), \tilde{z}_2(x,t))$

will remain close on $\bar{\Omega}$ for all $t \in [0,1]$.

But since $(\bar{u}_1, 0)$ is an equilibrium,

$(\tilde{z}_1(x,t), \tilde{z}_2(x,t)) = (\bar{u}_1(x), 0)$ for all $t \in [0,1]$.

Consequently, in all three cases,

at least one of the ratios

$$\frac{\int_\Omega w_3(x)\, z_1(x,s)\left\{\sigma_3 + b_1\bar{u}_2(x) - b_1 z_2(x,s) - z_1(x,s)\right\}dx}{\int_\Omega w_3(x)\, z_1(x,s)\, dx}$$

and $\dfrac{\int_\Omega w_4\, z_2(x,s)\left\{\sigma_4 - b_2\bar{u}_1(x) + b_2 z_1(x,s) - z_2(x,s)\right\}}{\int_\Omega w_4\, z_2(x,s)\, dx}$

is a $\frac{0}{0}$ indeterminate form as

(v_1, v_2) approaches $(0,0)$ or $(\bar{u}_1, 0)$ or $(0, \bar{u}_2)$.

Indeed, such was the case for any $(u_1, u_2) \in S$.

However, we only need fairly crude lower bounds arising from the compactness and invariance of X to get the estimate on S.

Consider $(\bar{u}_1, 0)$. Let $t=1$ in (11).

For all $s \in [0,1]$, the ratio

$$\frac{\int_\Omega w_3(x)\, z_1(x,s)\left\{\sigma_3 + b_1\bar{u}_2(x) - b_1 z_2(x,s) - z_1(x,s)\right.}{\int_\Omega w_3(x)\, z_1(x,s)\, dx}$$

converges (as $(v_1, v_2) \to (\bar{u}_1, 0)$) to

$$\frac{\int_\Omega w_3(x)\bar{u}_1(x)\{\sigma_3 + b_1\bar{u}_2(x) - \bar{u}_1(x)\}dx}{\int_\Omega w_3(x)\bar{u}_1(x)}$$

$$= \frac{\int_\Omega [w_3(x)\bar{u}_1(x)\{\sigma_3 - a_1 + b_1\bar{u}_2(x)\} + w_3(x)\bar{u}_1(x)(a_1 - \bar{u}_1(x))]dx}{\int_\Omega w_3(x)\bar{u}_1(x)dx}$$

$$= \frac{\int_\Omega [\bar{u}_1(x)\Delta w_3(x) - \Delta\bar{u}_1(x) w_3(x)]dx}{\int_\Omega w_3(x)\bar{u}_1(x)dx} = 0$$

So the $\exp(\beta_1 \int_0^1 \cdot\, ds)$ tends to 1 as $(v_1, v_2) \to (\bar{u}_1, 0)$.

So now consider the remaining factor.

$$\sigma_4 - b_2\bar{u}_1(x) + b_2 z_1(x,s) - z_2(x,s)$$

converges to $\sigma_4 - b_2\bar{u}_1(x) + b_2\bar{u}_1(x) = \sigma_4$

uniformly on $\bar{\Omega}$ for all $s \in [0,1]$ as $(v_1, v_2) \to (\bar{u}_1, 0)$. So if (v_1, v_2) is close enough to $(\bar{u}_1, 0)$, $\sigma_4 - b_2 \bar{u}_1(x) + b_2 z_1(x,s) - z_2(x,s)$ will exceed $\frac{\sigma_4}{2} > 0$ for all $s \in [0,1]$ and

$$a(1, (\bar{u}_1, 0)) > \exp\left(\beta_2 \frac{\sigma_4}{2}\right) > 1$$

for any choice of $\beta_2 > 0$.

If $(u_1, u_2) = (0, \bar{u}_2)$, a completely analogous argument allows us to conclude

$$a(1, (0, \bar{u}_2)) > \exp\left(\beta_1 \frac{\sigma_3}{2}\right) > 1$$

for any choice of $\beta_1 > 0$.

Let $(u_1, u_2) = (0,0)$. Again $(z_1(x,t), z_2(x,t))$ converges uniformly to $(0,0)$ for $x \in \bar{\Omega}$ and $t \in [0,1]$ as (v_1, v_2) converges in X to $(0,0) \in \omega(S)$. As a result, we have that

$$\sigma_3 + b_1 \bar{u}_2(x) - b_1 z_2(x,s) - z_1(x,s) \geq \frac{\sigma_3}{2}$$

and

$$\sigma_4 - b_2\bar{u}_1(x) + b_2 z_1(x,s) - z_2(x,s) \geq \sigma_4 - b_2\bar{u}_1(x) - 1$$

if (v_1, v_2) is sufficiently close to $(0,0)$ in X.

From (11) with $t=1$,

$$\exp\Big\{\beta_1 \int_0^1 \Big[\frac{\int_\Omega w_3(x) z_1(x,s)\{\sigma_3 + b_1\bar{u}_2(x) - b_1 z_2(x,s) - z_1(x,s)\}dx}{\int_\Omega w_3(x) z_1(x,s)\,dx}\Big] ds$$

$$+ \beta_2 \int_0^1 \Big[\frac{\int_\Omega w_4(x) z_2(x,s)\{\sigma_4 - b_2\bar{u}_1(x) + b_2 z_1(x,s) - z_2(x,s)\}dx}{\int_\Omega w_4(x) z_2(x,s)\,dx}\Big] ds$$

$$\geq \exp\Big\{\beta_1 \int_0^1 \left[\frac{\int_\Omega w_3(x) z_1(x,s)\,(\sigma_3/2)\,dx}{\int_\Omega w_3(x) z_1(x,s)\,dx}\right] ds$$

$$+ \beta_2 \int_0^1 \left[\frac{\int_\Omega w_4(x)\, z_2(x,s)\,(\sigma_4 - b_2 \sup_\Omega \bar{u}_1 - 1)\,dx}{\int_\Omega w_4\, z_2(x,s)}\right] ds$$

$$\geq \exp\Big\{\beta_1 \frac{\sigma_3}{2} + \beta_2\big(\sigma_4 - b_2 \sup_\Omega \bar{u}_1 - 1\big)\Big\}$$

Recall that β_1 and β_2 are only required to be positive. So we are free to choose them to our advantage. Fix β_2 at some positive value.

Since $\sigma_3 > 0$, we may choose $\beta_1 > 0$ so that

$$\beta_1 \frac{\sigma_3}{2} + \beta_2 \left(\sigma_4 - b_2 \sup_{\bar{\Omega}} \bar{u}_1 - 1 \right) > 0$$

Hence $a(1,(0,0)) \geq \exp\left\{ \beta_1 \frac{\sigma_3}{2} + \beta_2 \left(\sigma_4 - b_2 \sup_{\bar{\Omega}} \bar{u}_1 - 1 \right) \right.$

> 1

What about (2)? Assume $\sigma_1 > 0$,

we have $\omega(S) = \{(0,0), (\bar{u}_1, 0)\}$. The

predator here is a specialist and tends to extinction

in the absence of the prey.

Now σ_4 is defined. So if $\sigma_4 > 0$,

we may define a candidate for average Lyapunov

function $P : X \to [0, \infty)$ by

$$P((v_1, v_2)) = \left(\int_\Omega w_1 v_1 dx \right)^{\beta_1} \left(\int_\Omega w_4 v_2 dx \right)^{\beta_2}$$

where $w_1 > 0$ and $w_4 > 0$ in Ω, and

β_1 and β_2 are positive constants to be

determined.

In this case we need

$$\beta_1 \frac{\sigma_1}{2} + \beta_2 \left(\sigma_4 - b_2 \sup_{\bar{\Omega}} \bar{u}_1 - 1 \right) > 0$$

and

$$\beta_2 \frac{\sigma_4}{2} > 0 ,$$

which is again immediate.

II. How Two Dominant Competitors May Mediate Persistence of an Inferior Competitor

Idea: There are three competing species A, B, C. A or B exclude C, while A and B coexist (permanent subsystem). Is it possible for the competition between A and B to reduces their abundances enough to allow coexistence of all 3 species?

Cantrell and Ward, SIAM J. Appl. Math 1997

Ayala (1969): famous bottle on Drosophila that showed two species could coexist on a single resource, contradicting the dominant ecological theory at the time, due in large part to Robert MacArthur and based primarily on Lotka-Volterra models.

Ayala et al (1973): employed a number of 2 species competition models in a data fitting exercise with Drosophila results. The isoclines of models that fit the data have intersections below line joining carrying capacities. Coexistent L-V models don't have this property.

Objective: Find such a reaction-diffusion model.

Preliminary Observation:

Consider

$$\frac{du_1}{dt} = u_1(a - u_1 - \alpha_{12}u_2 - \beta_{12}u_2^2)$$

$$\frac{du_2}{dt} = u_2(a - \alpha_{21}u_1 - \beta_{21}u_1^2 - u_2)$$

In the absence of species j, species i is subject to a logistic growth law and converges to a.

Permanence here requires that species j can invade when species i is at density a. So we require

$$a - \alpha_{12} a - \beta_{12} a^2 > 0$$

and

$$a - \alpha_{21} a - \beta_{21} a^2 > 0$$

which requires first that $\alpha_{12} < 1$ and $\alpha_{21} < 1$

and then that

$$\beta_{12} < \frac{1 - \alpha_{12}}{a} \quad \text{and} \quad \beta_{21} < \frac{1 - \alpha_{21}}{a}$$

Observe that a positive (componentwise) equilibrium (u_1, u_2) satisfies

$$u_1 + \alpha_{21} u_2 = a - \beta_{12} u_2^2$$

$$\alpha_{21} u_1 + u_2 = a - \beta_{21} u_1^2$$

But if (u_1, u_2) is to approach $(0, 0)$

it must be the case that

$$\beta_{12} \sim \frac{a}{u_2^2} \gg 1 \quad \text{and} \quad \beta_{21} \sim \frac{a}{u_1^2} \gg 1$$

as $(u_1, u_2) \to (0,0)$. So if we think of modifying a L-V model with higher order terms, we need the coefficients β_{12} and β_{21} to impact the location of (but not existence of) the global attractor. In this instance $-\beta_{12} u_2^2 u_1$ and $-\beta_{21} u_1^2 u_2$ are linear in u_1 and u_2, respectively, so that β_{12} and β_{21} play a role in whether the system is permanent or not.

With this observation in mind, we consider

$$\begin{aligned}
\frac{\partial u_1}{\partial t} &= \Delta u_1 + u_1 (a - u_1 - \alpha_{12} u_2 - \beta_{12} u_1 u_2 - \alpha_{13} u_3) \\
\frac{\partial u_2}{\partial t} &= \Delta u_2 + u_2 (a - \alpha_{12} u_1 - \beta_{21} u_1 u_2 - u_2 - \alpha_{23} u_3) \\
\frac{\partial u_3}{\partial t} &= \Delta u_3 + u_3 (a' - \alpha_{31} u_1 - \alpha_{32} u_2 - u_3)
\end{aligned} \tag{12}$$

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

subject to

$$u_1 = u_2 = u_3 = 0 \qquad \text{on } \partial\Omega \times (0,\infty).$$

Here the parameters satisfy

$$a \geq a' > \lambda_0^1(\Omega)$$

$$\alpha_{12}, \alpha_{13}, \alpha_{21}, \alpha_{23} \in (0,1)$$

$$\alpha_{31} > 1, \quad \alpha_{32} > 1$$

$$\beta_{12} \geq 0, \quad \beta_{21} \geq 0$$

As before, $(\theta_a, 0, 0)$, $(0, \theta_a, 0)$ and $(0, 0, \theta_{a'})$ are the global attractors for (12), where θ_a denotes the unique solution of

$$\Delta\theta_a + \theta_a(a - \theta_a) = 0 \qquad \text{in } \Omega \tag{13}$$

$$\theta_a > 0 \qquad \text{in } \Omega$$

$$\theta_a = 0 \qquad \text{on } \partial\Omega$$

which exists when $a > \lambda_0^1(\Omega)$ by (9) and (10).

Observe now that (13) $\Rightarrow$ the principal eigenvalue $\sigma = \sigma_a$ in

(14) $$\Delta\phi + \phi(a - \theta_a) = \sigma\phi \qquad \text{in } \Omega$$
$$\phi = 0 \qquad \text{on } \partial\Omega$$

is 0.

So now consider the subsystem of (12) with $u_1 \equiv 0$:

(15) $$\frac{\partial u_2}{\partial t} = \Delta u_2 + u_2(a - u_2 - d_{23}u_3)$$
$$\frac{\partial u_3}{\partial t} = \Delta u_3 + u_3(a' - d_{32}u_2 - u_3) \qquad \text{in } \Omega \times (0,\infty)$$
$$u_2 = u_3 = 0 \qquad \text{on } \partial\Omega \times (0,\infty)$$

Observe that whether species 2 can invade when species 3 is its equilibrium $\theta_{a'}$ is determined by the value of $\tilde{\sigma}$ in

$$\Delta\phi + \phi(a - d_{23}\theta_{a'}) = \tilde{\sigma}\phi \qquad \text{in } \Omega$$

$$\phi = 0 \qquad \text{on } \partial\Omega$$

$$\phi > 0 \qquad \text{in } \Omega$$

Method of upper and lower solutions $\Rightarrow \theta_{a'} \leq \theta_a$

whenever $\lambda_0^1(\Omega) < a' \leq a$.

So $\alpha_{23} < 1 \Rightarrow a - \alpha_{23}\theta_{a'} > a - \theta_a$

Green's Second Identity $\Rightarrow \tilde{\sigma} > \sigma_a = 0$.

So species 2 can invade when species 3

is at its equilibrium $\theta_{a'}$.

On the other hand, whether species 3 can invade

when species 2 is at its equilibrium is determined

by the value of $\tilde{\tilde{\sigma}}$ in

$$\Delta\phi + \phi(a' - \alpha_{32}\phi_a) = \tilde{\tilde{\sigma}}\phi \qquad \text{in } \Omega$$

$$\phi = 0 \qquad \text{on } \partial\Omega$$

$$\phi > 0 \qquad \text{in } \Omega.$$

But now $\alpha_{32} > 1 \Rightarrow -\alpha_{32}\phi_a < -\phi_a$

$\Rightarrow \quad a' - \alpha_{32}\phi_a < a - \phi_a \quad \Rightarrow \quad \tilde{\sigma} < \sigma_a = 0$

So species 3 can not invade when species 2 is at its equilibrium density θ_a.

It follows that species 2 excludes species 3 provided there is no componentwise positive equilibrium to (15). Suppose there is such an equilibrium (u_2, u_3)

Then
$$u_3 \Delta u_2 + u_2 u_3 (a - u_2 - \alpha_{23} u_3) = 0$$
$$u_2 \Delta u_3 + u_2 u_3 (a' - \alpha_{32} u_2 - u_3) = 0$$

$$\Rightarrow \quad 0 = \int_\Omega (u_3 \Delta u_2 - u_2 \Delta u_3)$$
$$+ \int_\Omega u_2 u_3 (a - u_2 - \alpha_{23} u_3 - a' + \alpha_{32} u_2 + u_3)$$
$$= \int_\Omega u_2 u_3 [a - a' + (\alpha_{32} - 1) u_2 + (1 - \alpha_{23}) u_3]$$
$$> 0 \quad (*) \qquad (\text{since } \alpha_{31} > 1,\ \alpha_{23} < 1 \text{ and } a > a')$$

So there is no such equilibrium and species 2 excludes species 3.

Similarly, species 1 excludes species 3

Now consider the subsystem that arises

when $u_3 \equiv 0$.

(16) $$\frac{\partial u_1}{\partial t} = \Delta u_1 + u_1 [a - u_1 - \alpha_{12} u_2 - \beta_{12} u_1 u_2]$$

$$\frac{\partial u_2}{\partial t} = \Delta u_2 + u_2 [a - \alpha_{21} u_1 - \beta_{21} u_1 u_2 - u_2]$$

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

$u_1 = u_2 = 0$ on $\partial\Omega \times (0, \infty)$

whether species 1 can invade when species 2 is at its equilibrium density is determined by the value of σ_1 in

$$\Delta \phi + \phi [a - \alpha_{12} \theta_a] = \sigma_1 \phi \quad \text{in } \Omega$$

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

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

(Note that the term $-\beta_{12} u_1^2 u_2$ is higher order in u_1

and so does not affect the value of σ_1.)

Moreover, since $\alpha_{12} < 1$, $\sigma_1 > \sigma_a = 0$.

So species 1 can invade when species 2 is at its equilibrium density θ_a. Similarly, $\sigma_2 > 0$ in

$$\Delta\phi + \phi[a - \alpha_{21}\theta_a] = \sigma_2\phi \quad \text{in } \Omega$$

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

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

So species 2 can invade when species 1 is at its equilibrium density. So we have mutual invasibility and (16) is permanent for all values $\beta_{12} \geq 0$, $\beta_{21} \geq 0$. Indeed, it is compressive.

We let $\pi((u_1(x,0), u_2(x,0), u_3(x,0)), t)$ denote the unique solution to (12) which is such $\pi((u_1(x,0), u_2(x,0), u_3(x,0)), 0) = (u_1(x,0), u_2(x,0), u_3(x,0))$

Then we may regard π as a semi-dynamical system on the positive cone K in $[C_0^1(\bar{\Omega})]^3$. Since the density of each species is governed by a diffusive logistic law in the absence of the other two species, it follows readily that π is dissipative and that $\pi(\cdot, t)$ is compact for $t > 0$. As in Part I, we have a global attractor U in K. We may define X and S in a manner analogous to Part I of this lecture, and restrict our attention to $X \subseteq K$ and $S \subseteq \partial K$. We now have

$$\omega(S) = \{(0,0,0), (\theta_a, 0, 0), (0, \theta_a, 0), (0, 0, \theta_a), M_5$$

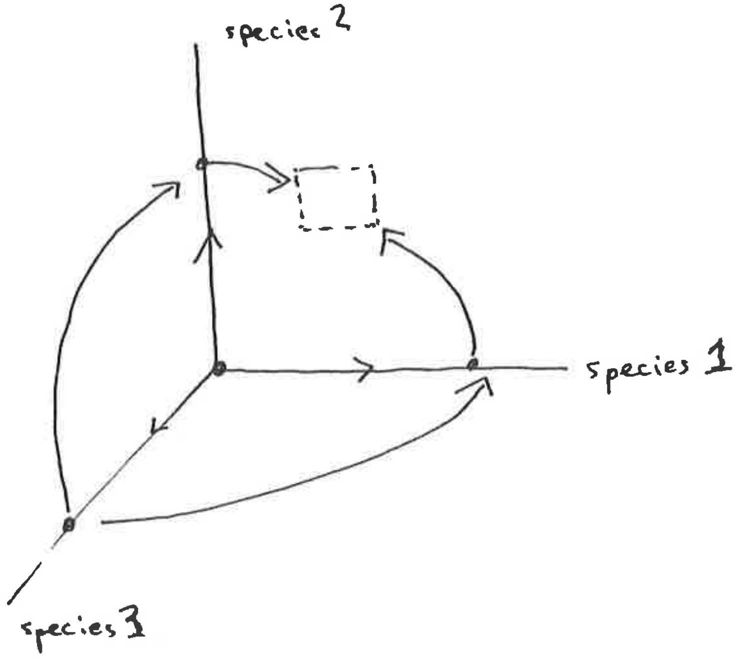
where M_5 denotes the global attractor for solutions to (16) corresponding to componentwise positive initial data.

Since (16) is compressive, M_5 is contained in an order interval in the skew ordering

(17) $$(u_1, u_2) \preceq (\bar{u}_1, \bar{u}_2) \iff \underline{u}_1 \le \bar{u}_1 \text{ and } \bar{u}_2 \le \underline{u}_2$$

whose endpoints are componentwise positive equilibria.

So $\pi \,|\, \partial K$ is as in the following diagram:



It is evident that the covering

$$\{(0,0,0),\ (\theta_a,0,0),\ (0,\theta_a,0),\ (0,0,\theta_{a'}),\ M_5\}$$

of $\omega(S)$ is acyclic. Moreover

$$a \ge a' > \lambda_0^1(\Omega) \Rightarrow \text{the stable manifold}$$

$$W^s(\{(0,0,0\}) \cap X \setminus S = \phi$$

$\tilde{\sigma} > 0$ for (15) (and its analogue for the $u_1 u_3$ subsystem) $\Rightarrow W^s(\{(0,0,\theta_{a'})\}) \cap X \setminus S = \phi$.

$\sigma_1 > 0 \Rightarrow W^s(\{(0,\theta_a,0)\}) \cap X \setminus S = \phi$

and

$\sigma_2 > 0 \Rightarrow W^s(\{(\theta_a,0,0)\}) \cap X \setminus S = \phi$

So the Acyclicity Theorem $\Rightarrow \Pi$ is permanent provided

(18) $$W^s(M_5) \cap X \setminus S = \phi.$$

Now (18) holds so long as there is a $c > 0$ so that the principal value $\sigma_3 \geq c$ in

(19) $$\Delta\phi_3 + (a' - d_{31}\hat{u}_1 - d_{32}\tilde{u}_2)\phi_3 = \sigma_3\phi_3 \quad \text{in } \Omega$$
$$\phi_3 = 0 \quad \text{on } \partial\Omega$$

for any $(\hat{u}_1, \tilde{u}_2) \in M_5$. As noted, M_5 is contained in an order interval $[(u_{1*}, u_{2*}), (u_1^*, u_2^*)]$ with $u_{1*} \leq u_1^*$ and $u_2^* \leq u_2^*$. There is such a c provided $\sigma_3 > 0$ in (19) when $\hat{u}_1 = u_1^*$ and $\hat{u}_2 = u_{2*}$.

Note that (u_1^*, u_{2*}) is an equilibrium only in the case when $M_5 = \{(u_{1*}, u_{2*})\} = \{(u_1^*, u_2^*)\}$.

However, if $(\hat{u}_1, \hat{u}_2) \in M_5$, $\hat{u}_1 \le u_1^*$ and $\hat{u}_2 \le u_{2*}$ and u_1^* and u_{2*} are the smallest functions for which these inequalities hold seperately.

Setting $\hat{u}_1 = u_1^*$ and $\hat{u}_2 = u_{2*}$ over-estimates the competitive pressure on species 3 when the densities of species 1 and 2 lie in M_5, in essence giving "competitive overkill" or a "worst-case scenario" vis-a-vis the possibility of species 3 invading the habitat Ω when species 1 and 2 are established.

The value of σ_3 we get with $\hat{u}_1 = u_1^*$ and $\hat{u}_2 = u_{2*}$ is less than the actual σ, since

$$\alpha_{31}\hat{u}_1 + \alpha_{32}\hat{u}_2 < \alpha_{31}u_1^* + \alpha_{32}u_{2*}$$

However, our goal here is to show two things:

(i) Π in (12) is not permanent when

$$\beta_{12} = 0 = \beta_{21}$$

(ii) Π is permanent for appropriate large enough values of β_{12} and β_{21}.

Let's deal with the case $\beta_{12} = 0 = \beta_{21}$.

We need the following result from

Cosner and Lazer, SIAM J. Appl. Math 1984

Lemma. When $\beta_{12} = 0$ and $\beta_{21} = 0$, (16) has a unique componentwise positive equilibrium

$$u_1 = \frac{1 - d_{12}}{1 - d_{12} d_{21}} \theta_a, \quad u_2 = \frac{1 - d_{21}}{1 - d_{12} d_{21}} \theta_a$$

Proof: Suppose (u_1, u_2) is a componentwise positive equilibrium for (16). Suppose z is a smooth function satisfying

$$\Delta z + z[a - u_1 - u_2] = 0 \qquad \text{in } \Omega$$

$$z = 0 \qquad \text{on } \partial\Omega$$

Claim: $z \equiv 0$.

Notice that $w = u_1$ satisfies

$$-\Delta w - w[a - u_1 - d_{12} u_2] = \alpha w \qquad \text{in } \Omega$$

$$w = 0 \qquad \text{on } \partial\Omega$$

$\therefore$ $\alpha = 0$ is the principal eigenvalue of the problem and hence for any smooth function ψ we have the variational inequality

$$0 \leq \frac{\int_\Omega (|\nabla\psi|^2 - [a - u_1 - d_{12} u_2]\psi^2)\,dx}{\int_\Omega \psi^2\,dx}$$

Now

$$-z\Delta z - z^2[a - u_1 - u_2] = 0$$

$$\Rightarrow 0 = \int_\Omega (-z\Delta z - z^2[a - u_1 - u_2])$$

$$= \int_\Omega (|\nabla z|^2 - z^2[a - u_1 - d_{12}u_2])\,dx + \int_\Omega u_2(1 - d_{12}) z^2\,dx$$

$$\geq \int_\Omega u_2 (1 - d_{12}) z^2\,dx \qquad \text{Since } u_2 > 0 \text{ and } d_{12} < 1,$$

$z \equiv 0$ as claim.

Now $\quad \Delta u_1 + u_1[a - u_1 - d_{12}u_2] = 0$

$\Delta u_2 + u_2[a - d_{21}u - u_2] = 0$

can be re-written as

$$\Delta u_1 + u_1[a - u_1 - u_2] + (1-d_{12})u_1u_2 = 0$$

$$\Delta u_2 + u_2[a - u_1 - u_2] + (1-d_{21})u_1u_2 = 0$$

$$\Rightarrow \Delta\left[(1-d_{21})u_1 - (1-d_{12})u_2\right]$$
$$+ [(1-d_{21})u_1 - (1-d_{12})u_2][a - u_1 - u_2] = 0$$

$$\Rightarrow \quad (1-d_{21})u_1 - (1-d_{12})u_2 = 0 \quad \text{in } \bar{\Omega}$$

$$\Rightarrow \quad u_1 = \frac{(1-d_{12})u_2}{1-d_{21}}$$

$$\Rightarrow \quad \Delta u_2 + u_2\left[a - \frac{d_{21}(1-d_{12})u_2}{1-d_{21}} - u_2\right] = 0 \quad \text{in } \Omega$$

$$\Rightarrow \quad \Delta u_2 + u_2\left[a - \left(\frac{1-d_{21}d_{12}}{1-d_{21}}\right)u_2\right] = 0 \quad \text{in } \Omega$$

$$u_2 = 0 \quad \text{on } \partial\Omega$$

$$u_2 > 0 \quad \text{in } \Omega$$

$$\Rightarrow \quad u_2 = \frac{1-d_{21}}{1-d_{12}d_{21}}\,\theta_a$$

$$\Rightarrow \quad u_1 = \frac{1-d_{12}}{1-d_{21}} \cdot \frac{1-d_{21}}{1-d_{12}d_{21}}\,\theta_a = \frac{1-d_{12}}{1-d_{12}d_{21}}\,\theta_a$$

So we have that when $\beta_1 = 0$, $\beta_2 = 0$, solutions to (16) converge over time to $\left(\frac{1-d_{12}}{1-d_{12}d_{21}}\theta_a, \frac{1-d_{21}}{1-d_{12}d_{21}}\theta_a\right)$

So now there is only one choice of $(\hat{u}_1, \hat{u}_2) \in M_s$, namely $\left(\frac{1-d_{12}}{1-d_{12}d_{21}}\theta_a ; \frac{(1-d_{21})\theta_a}{1-d_{12}d_{21}}\right)$

σ_3 in (19) is negative (and hence $W^s(M_s) \cap (X \setminus S$ $\neq \phi$, if

$$d_{31}\left(\frac{1-d_{12}}{1-d_{12}d_{21}}\right) + d_{32}\left(\frac{1-d_{21}}{1-d_{12}d_{21}}\right) > 1$$

Note that

$$d_{31}\left(\frac{1-d_{12}}{1-d_{12}d_{21}}\right) + d_{32}\left(\frac{1-d_{21}}{1-d_{12}d_{21}}\right)$$

$$> \frac{1-d_{12}}{1-d_{12}d_{21}} + \frac{1-d_{21}}{1-d_{12}d_{21}} = \frac{2-d_{12}-d_{21}}{1-d_{12}d_{21}}$$

Now $(1-\alpha_{12})(1-\alpha_{21}) > 0$

$$\Rightarrow 1-\alpha_{12}-\alpha_{21} > -\alpha_{12}\alpha_{21}$$

$$\Rightarrow 2-\alpha_{12}-\alpha_{21} > 1-\alpha_{12}\alpha_{21}$$

$$\Rightarrow \frac{2-\alpha_{12}-\alpha_{21}}{1-\alpha_{12}\alpha_{21}} > 1$$

So π is not permanent when $\beta_1 = 0$, $\beta_2 = 0$ for any $a \geq a' > \lambda_0^1(\Omega)$ and any choice of $\alpha_{12}, \alpha_{21}, \alpha_{13}, \alpha_{23} \in (0,1)$ and $\alpha_{31}, \alpha_{32} \in (1,\infty)$.

Now consider the case when $\beta_{12} > 0$, $\beta_{21} > 0$.

Assume first that $\beta_{12} = \beta_{21} = \beta$.

Let $w = u_2 - \left(\frac{1-\alpha_{21}}{1-\alpha_{12}}\right)u_1$.

Then

(20) $$-\Delta w + (\beta u_1 u_2 + u_1 + u_2)w = \gamma w \quad \text{in } \Omega$$
$$w = 0 \quad \text{on } \partial\Omega$$

with $\gamma = a$.

Let γ_1 be the smallest eigenvalue of (20) and $z > 0$

a corresponding eigenfunction.

$$-\Delta z + (\beta u_1 u_2 + u_1 + u_2) z = \gamma_1 z$$

Multiply by u_1, integrate and employ Green's

Second Identity to obtain

$$\int (a + (1-d_{12}) u_2) u_1 z \, dx = \gamma_1 \int_\Omega u_1 z$$

Since u_1 and $(1-d_{12}) u_2 > 0$, we get $\gamma_1 > a$.

$$\therefore \quad u_2 - \left(\frac{1-d_{12}}{1-d_{21}}\right) u_1 \equiv 0$$

$$\Rightarrow \quad u_2 \equiv \left(\frac{1-d_{21}}{1-d_{12}}\right) u_1$$

So u_1 satisfies

(21) $$-\Delta u_1 = u_1 \left(a - u_1 - d_{12} \left(\frac{1-d_{21}}{1-d_{12}}\right) u_1 - \beta \left(\frac{1-d_{21}}{1-d_{12}}\right) u_1^2 \right)$$

$$= u_1 \left(a - \left(\frac{1-d_{12} d_{21}}{1-d_{12}}\right) u_1 - \beta \left(\frac{1-d_{21}}{1-d_{12}}\right) u_1^2 \right)$$

If we set $f(u) = a - \left(\frac{1-d_{12} d_{21}}{1-d_{12}}\right) u - \beta \left(\frac{1-d_{21}}{1-d_{12}}\right) u^2$,

then $f'(u) < 0$ for $u \geq 0$ and

$f(u) \leq 0$ when $u \geq K^*(\beta)$, where

(22) $$K^*(\beta) = \frac{-(1-d_{12}d_{21}) + \sqrt{(1-d_{12}d_{21})^2 + 4\alpha\beta(1-d_{12})(1-d_{21})}}{2\beta(1-d_{21})}$$

Now (21) has a unique positive solution u_1^*

and thus (16) has a unique componentwise positive

equilibrium $\left(u_1^*, \left(\frac{1-d_{21}}{1-d_{12}}\right)u_1^*\right)$.

Moreover, the maximum principle $\Rightarrow$

$$u_1^* \leq K^*(\beta)$$

So now $M_5 = \left\{\left(u_1^*, \left(\frac{1-d_{21}}{1-d_{12}}\right)u_1^*\right)\right\}$.

So Π is permanarenent provided the principal

eigenvalue σ_3 in (19) with $\tilde{u}_1 = u_1^*$

and $\tilde{u}_2 = \left(\frac{1-d_{21}}{1-d_{12}}\right)u_1^*$ is positive.

Since $u_1^* \le K^*(\beta)$, such will be the case provided $\sigma_5 > 0$ where σ_5 is the principal eigenvalue in

$$\Delta\phi_5 + \left(a' - \alpha_{31} K^*(\beta) - \alpha_{31}\left(\frac{1-\alpha_{21}}{1-\alpha_{12}}\right) K^*(\beta)\right)\phi_5 = \sigma_5 \phi \quad \text{in } \Omega$$

$$\phi_5 = 0 \quad \text{on } \partial\Omega$$

$$\sigma_5 = a' - \left(\alpha_{31} + \alpha_{32}\left(\frac{1-\alpha_{21}}{1-\alpha_{2}}\right)\right)K^*(\beta) - \lambda_0^1(\Omega)$$

It is clear from (22) that

$$\lim_{\beta\to\infty} K^*(\beta) = 0$$

It follows that Π is permanent if $\beta = \beta_{12} = \beta_{21}$ and β is sufficiently large.

Let us now assume that β_{12} and β_{21} are unequal. For the sake of specificity we assume $\beta_{12} < \beta_{21}$. As best we know, M_5 does not reduce to a single componentwise positive equilibrium. So what we are going to do in this case is show σ_3 is positive in (19) when $\tilde{u}_1 = u_1^*$ and $\hat{u}_2 = u_{2*}$. To do so, we will obtain upper bounds on both components of an arbitrary componentwise positive equilibrium (u_1, u_2) to (16) via the method of upper and lower solutions. Because of the nature of the skew ordering, two applications of the method will be needed.

Suppose

$$
\begin{aligned}
-\Delta u_1 &= u_1(a - u_1 - \alpha_{12}u_2 - \beta_{12}u_1u_2) && \text{in } \Omega \\
-\Delta u_2 &= u_2(a - \alpha_{21}u_1 - \beta_{21}u_1u_2 - u_2) && \\
u_1 &= 0 = u_2 && \text{on } \partial\Omega \\
u_1 &> 0, \; u_2 > 0 && \text{in } \Omega.
\end{aligned}
$$

Let ϕ be a positive eigenfunction for

$$
\begin{aligned}
-\Delta\phi &= \lambda_0^1(\Omega)\,\phi && \text{in } \Omega \\
\phi &= 0 && \text{on } \partial\Omega
\end{aligned}
$$

We have

$$-\Delta u_1 \geq u_1 (a - u_1 - d_{12} u_2 - \beta_{21} u_1 u_2)$$

in Ω

$$-\Delta u_2 \leq u_2 (a - d_{21} u_1 - \beta_{21} u_1 u_2 - u_2)$$

since $\beta_{12} < \beta_{21}$.

If $(\bar{u}_1, \bar{u}_2) = (\varepsilon\phi, a)$

$$-\Delta \bar{u}_1 \leq \bar{u}_1 (a - \bar{u}_1 - d_{12} \bar{u}_2 - \beta_{21} \bar{u}_1 \bar{u}_2)$$

$$-\Delta \bar{u}_2 \geq \bar{u}_2 (a - d_{21} \bar{u}_1 - \beta_{21} \bar{u}_1 \bar{u}_2 - \bar{u}_2)$$

for small enough values of $\varepsilon > 0$ provided

(23) $$(1 - d_{12}) a > \lambda_0^1(\Omega)$$

Provided (23) holds, the unique componentwise positive equilibrium to (16) when $\beta_{12} = \beta_{21}$, namely $\left(u_1^*(\beta_{21}), \left(\frac{1 - d_{21}}{1 - d_{12}}\right) u_1^*(\beta_{21})\right)$ satisfies

$$\bar{u}_1 \leq u_1^*(\beta_{21}) \leq u_1$$

$$u_2 \leq \left(\frac{1 - d_{21}}{1 - d_{12}}\right) u_1^*(\beta_{21}) \leq \bar{u}_2 .$$

(24) So $$u_2 \le \left(\frac{1-d_{21}}{1-d_{12}}\right) u_1^*(\beta_{21})$$

To obtain an upper bound on u_1, we make an additional assumption regarding β_{12} and β_{21}.

(25) $$\beta_{21} - \beta_{12} < \frac{1-d_{21}}{a}$$

If (25) holds,

$$a(\beta_{21} - \beta_{12}) < 1 - d_{21}$$

So there is a value $\tilde{d}_{21} \in (d_{21}, 1)$ so that

(25′) $$a(\beta_{21} - \beta_{12}) < \tilde{d}_{21} - d_{21}$$

Since $u_2 < a$,

(26) $$(\beta_{21} - \beta_{12})\, u_2 < \tilde{d}_{21} - d_{21}$$

$$\Rightarrow \quad d_{21} u_1 + \beta_{21} u_1 u_2 < \tilde{d}_{21} u_1 + \beta_{12} u_1 u_2$$

So (u_1, u_2) satisfie

$$-\Delta u_1 \leq u_1(a - u_1 - \alpha_{12}u_2 - \beta_{12}u_1u_2)$$
$$\text{in } \Omega$$
$$-\Delta u_2 \geq u_2(a - \hat{\alpha}_{21}u_1 - \beta_{12}u_1u_2 - u_2)$$

Set $(\hat{u}_1, \hat{u}_2) = (a, \varepsilon\phi)$ to get

$$-\Delta\hat{u}_1 \geq \hat{u}_1(a - \hat{u}_1 - \alpha_{12}\hat{u}_2 - \beta_{12}\hat{u}_1\hat{u}_2)$$
$$\text{in } \Omega$$
$$-\Delta\hat{u}_2 \leq \hat{u}_2(a - \tilde{\alpha}_{21}\hat{u}_1 - \beta_{12}\hat{u}_1\hat{u}_2 - \hat{u}_2)$$

provided

(27) $$(1 - \tilde{\alpha}_{21})a > \lambda_0^1(\Omega)$$

So now the unique componentwise positive equilibrium to (16) when $\beta_{21} = \beta_{12}$ and $\alpha_{21} = \tilde{\alpha}_{21}$, namely

$$\left(u_1^*(\beta_{12}), \left(\frac{1 - \tilde{\alpha}_{21}}{1 - \alpha_{12}}\right) u_1^*(\beta_{12})\right)$$

satisfies

$$u_1 \leq u_1^*(\beta_{12}) \leq \hat{u}_1$$

$$\hat{u}_2 \leq \left(\frac{1-\hat{d}_{21}}{1-d_{21}}\right) u_1^*(\beta_{12}) \leq u_2$$

so that

(28) $$u_1 \leq u_1^*(\beta_{12})$$

So Π is permanent when σ_3 in (19) is positive

when $\hat{u}_1 = u_{1\,\hat{d}_{21}}^*(\beta_{12})$ and $\hat{u}_2 = \left(\frac{1-d_{21}}{1-d_{12}}\right) u_1^*(\beta_{21})$

<u>Note</u>: Let d_{12}, d_{21} $\in (0,1)$ be arbitrary and let $\tilde{d}_{21}$ be any fixed value in $(d_{21}, 1)$.

(23) and (27) require

$$a > \lambda_0^1(\Omega) \cdot \max\left\{\frac{1}{1-d_{12}}, \frac{1}{1-\tilde{d}_{21}}\right\}$$

The larger d_{12} and d_{21} are the larger a must be.

Once such an a is identified, (25') holds if

$$\beta_{21} - \beta_{12} < \frac{\hat{\alpha}_{21} - \alpha_{21}}{a}$$

Note that if the pair of parameters (β_{12}, β_{21}) satisfies the preceding inequality, so does $(\beta_{12}+s, \beta_{21}+s)$ for any $s>0$. So (25') holds for (β_{12}, β_{21}) lying in a thin strip along the main diagonal $\beta_{12} = \beta_{21}$ in the (β_{12}, β_{21}) parameter space, and we can find β_{12} and β_{21} which are arbitrarily large and satisfy (25').

To what extent these restrictions are an artifact of our approach is not clear. However, size requirement on β_{12} and β_{21} are evidently needed as the phenomenone does not hold when $\beta_{12} = 0 = \beta_{21}$ (the Lotka-Volterra case).