# Lecture 8

## Density Dependent Single Equation Models

Consider

(8.1)
$$\frac{\partial u}{\partial t} = \nabla \cdot d(x)\nabla u + \vec{b}(x)\cdot \nabla u + f(x, u) \quad \text{in } \Omega \times (0,\infty)$$

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

Proposition 8.1 (CC Proposition 3.1) Suppose that

$$f(x,u) \leq g_0(x) u \quad \text{for } x \in \Omega,$$

where $g_0(x) \in C^\alpha(\bar{\Omega})$. If the principal eigenvalue $\sigma_1$

of

(8.2)
$$\nabla \cdot d(x)\nabla \psi + \vec{b}(x)\cdot \nabla \psi + g_0(x)\psi = \sigma \psi \quad \text{in } \Omega$$

$$d(x)\frac{\partial \psi}{\partial \eta} + \beta(x)\psi = 0 \quad \text{on } \partial\Omega$$

is negative, then (8.1) has no positive equilibria and all nonnegative solutions to (8.1) decay exponentially to zero as $t \to \infty$.

Remark: We did not discuss principal eigenvalues in problems such as (8.2) in which there is an advective term. In general, variational formulations are not available. However, one can base the existence of such an eigenvalue on the elliptic maximum principle and the Krein-Rutman Theorem, the infinite dimensional analogue to Perron-Frobenius. See CC, Sections 2.3.2 and 2.5.2 for more detail.

Proof: Let $\bar{u} = c e^{\sigma_1 t} \psi_1$, where $\psi_1 > 0$ is an eigenfunction corresponding to $\sigma_1$ in (8.2) and $c > 0$ is a constant.

Then
$$\frac{\partial \bar{u}}{\partial t} - \nabla \cdot (d(x) \nabla \bar{u}) - \vec{b} \cdot \nabla \bar{u} - f(x, \bar{u})$$

$$= \sigma_1 \bar{u} - [\nabla \cdot d(x) \nabla \bar{u} + \vec{b}(x) \cdot \nabla \bar{u} + g_0(x) \bar{u}]$$

$$+ g_0(x) \bar{u} - f(x, \bar{u})$$

$$= g_0(x) \bar{u} - f(x, \bar{u}) \geq 0$$

So $\bar{u}$ is an uppersolution for (8.1). Let $u(x,t)$ be any nonnegative solution to (8.1). We may choose $c$ large enough so that $\bar{u}(x,0) > u(x,0)$.

Theorem 6.4 $\Rightarrow$ $\bar{u}(x,t) > u(x,t)$ for $t > 0$

$\sigma_1 < 0 \Rightarrow \bar{u}(x,t) \to 0$ exponentially as $t \to \infty$.

So $u(x,t)$ must decay toward 0 exponentially as well. So, in particular, there can be no positive equilibria.

Proposition 8.1 gives a criterion for extinction in models such as (8.1). In the linear (density independent) case, we have a prediction of extinction if $\sigma_1 < 0$ and growth at any density if $\sigma_1 > 0$. The density-dependent case is more complicated, since density dependent models may predict extinction for some initial densities and persistence for others. Such behavior is already present in non-spatial models such as the classic bi-stable model

$$\frac{du}{dt} = ru(u-a)\left(1-\frac{u}{K}\right)$$

$$u(0) = u_0$$

where $0 < a < K$. However, the sharp switch between predictions of extinction and predictions of persistence which occurs in linear models also occurs in reaction-diffusion models with growth terms of logistic type, since logistic models attain their highest population growth rates at low densities. Hence, if they allow population growth at any density at all then they predict invasibility at low densities. Such leads to predictions of persistence, as in our next result.

Proposition 8.2 (CC Proposition 3.2) Suppose that $f(x,u) = g(x,u)u$ with $g(x,u)$ of class $C^2$ in $u$ and $C^\alpha$ in $x$. Suppose there is $K > 0$ such that $g(x,u) < 0$ for $u > K$. If the principal eigenvalue $\sigma_1$ is positive in the problem

$$\nabla \cdot d(x) \nabla \psi + \vec{b} \cdot \nabla \psi + g(x,0)\psi = \sigma \psi \quad \text{in } \Omega \tag{8.3}$$

$$d(x) \frac{\partial \psi}{\partial \eta} + \beta(x) \psi = 0 \quad \text{on } \partial\Omega,$$

then (8.1) has a minimum positive equilibrium $u^*$, and all solutions to (8.1) which are initially nonnegative and positive on an open subset of $\Omega$ are eventually bounded below by orbits which increase toward $u^*$ as $t \to \infty$.

Notes: (i) The result holds for Dirichlet boundary conditions. (ii) The result gives a strong prediction of persistence in (8.1).

Proof: Write $f(x,u) = g(x,u)u$

$$= [g(x,0) + g(x,u) - g(x,0)]u$$

$$= [g(x,0) + g_1(x,u)u]u$$

where $g_1(x,u)$ is $C^1$ in $u$. Let $\psi_1 > 0$ be an eigenfunction for (8.3) corresponding to $\sigma_1$.

For $\varepsilon > 0$ sufficiently small,

$$\nabla \cdot d(x)\nabla(\varepsilon\psi_1) + \vec{b}(x)\nabla(\varepsilon\psi_1) + f(x,\varepsilon\psi_1)$$

$$= \varepsilon[\nabla \cdot d(x)\nabla\psi_1 + \vec{b}(x)\nabla\psi_1 + g(x,0)\psi_1]$$

$$+ g_1(x,\varepsilon\psi_1)\varepsilon^2\psi_1^2$$

$$= \sigma_1\varepsilon\psi_1 + g_1(x,\varepsilon\psi_1)\varepsilon^2\psi_1^2$$

$$= \varepsilon\psi_1[\sigma + \varepsilon g_1(x,\varepsilon\psi_1)\psi_1]$$

$$> 0$$

So for $\varepsilon > 0$ sufficiently small, $\varepsilon\psi_1$ is a sub-solution to the elliptic problem

$$\nabla \cdot d(x)\nabla u + \vec{b}(x)\cdot\nabla u + f(x,u) = 0 \qquad \text{in } \Omega$$

$$d(x)\frac{\partial u}{\partial \eta} + \beta(x)u = 0 \qquad \text{on } \partial\Omega$$

Then the appropriate analogue to Theorem 6.7 $\Rightarrow$ if $\underline{u}(x,t)$ is the solution to (8.1) with $\underline{u}(x,0) = \varepsilon\psi_1$, then $\underline{u}(x,t)$ is increasing in $t$. Since $K > \varepsilon\psi_1$ for $\varepsilon$ sufficiently small and $K$ is a supersolution, we may invoke Theorem 6.7 (actually its analogue) to assert that $\underline{u}(x,t) \nearrow u^*(x)$ as $t\to\infty$, where $u^*$ is the minimal positive equilibrium of (8.1).

So now if $u(x,t)$ is a solution to (8.1) which is initially nonnegative and is positive on an open subset of $\Omega$, the strong (or Hopf) maximum principle $\Rightarrow u(x,t) > 0$ on $\bar{\Omega}$ for $t > 0$. Choosing any $t_0 > 0$ we can take $\varepsilon > 0$ small enough so that $\varepsilon\psi_1 < u(x,t_0)$

So $\underline{u}(x,t-t_0) < u(x,t)$ for $t=t_0$, and by the maximum principle for $t > t_0$. So $u(x,t)$ is bounded below by $\underline{u}(x,t-t_0)$ and $\underline{u}(x,t-t_0) \uparrow u^*$ as $t\to\infty$, as desired.

Notes: (i) If our model has Dirichlet boundary conditions on all or part of $\partial\Omega$, nonnegative nonzero solutions to (8.1) cannot satisfy $u(x,t) > 0$ on $\bar{\Omega}$ for $t>0$. In that case $u(x,t) > 0$ on $\Omega$ and those parts of $\partial\Omega$ where the boundary conditions are not Dirichlet. On the parts of the boundary where $u=0$, the strong or Hopf maximum principle $\Rightarrow$ $\frac{\partial u}{\partial \eta} < 0$, so for $\varepsilon > 0$ sufficiently small, we have

$$\frac{\partial u}{\partial \eta}\Big|_{t=t_0} < \varepsilon \frac{\partial \varphi_1}{\partial \eta} = \frac{\partial \underline{u}}{\partial \eta}\Big|_{t=t_0}.$$

Hence we may still conclude that if $\varepsilon$ is sufficiently small $u(x,t_0) > \underline{u}(x,0)$, so that $u(x,t) > \underline{u}(x, t-t_0)$ as before

(ii) The regularity assumptions with respect to $x$ can be weakened if we work in Sobolev spaces such as $W^{1,p}(\Omega)$ instead of seeking classical solutions. For example, suppose that

$$f(x,u) = m(x)u + h(x,u)u^2$$

where $m(x)$ is a bounded measurable function, $h(x,u)$ is bounded and measurable on bounded subsets of $\Omega \times \mathbb{R}$, $h(x,u)$ is continuous in $u$ for almost all $x$, and that

$$m(x) + h(x,u)u < 0$$

for $u > K_0$. The existence of a positive equilibrium when $\sigma_1 > 0$ follows from results (extensions of maximum principles to weak solutions) such as Thm 1.24 in CC (originally due to Berestycki and Lions. Sub- and supersolution arguments then proceed as in the proof of Proposition 3.2.

## Minimal Patch Sizes

Notice that in Propositions 8.1 and 8.2 the eigenvalue problem used to predict extinction may be different from the one used to predict persistence. The two problems coincide when

(8.4) $$g_0(x) = \max_{u \geq 0}\left[\frac{f(x,u)}{u}\right] = \lim_{u \to 0^+}\left[\frac{f(x,u)}{u}\right] = \left.\frac{\partial f}{\partial u}\right|_{u=0} = g(x,0)$$

Certainly (8.4) holds in the logistic case

$$\frac{f(x,u)}{u} = a(x) - c(x)u$$

with $c > 0$, but may fail if $f(x,u)/u$ is increasing for some values of $u$, as in the case of an Allee effect.

Suppose now the coefficients in (8.1) are constant in $x$, and let $\Omega = \ell\,\Omega_0$ where $|\Omega_0| = 1$. Consider the model

$$u_t = d\Delta u + f(u) \quad \text{in } \Omega \times (0,\infty) = \ell\Omega_0 \times (0,\infty)$$

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

Let $\lambda_0$ be the principal eigenvalue for

$$\Delta\phi + \lambda\phi = 0 \quad \text{in } \Omega_0$$

$$\phi = 0 \quad \text{on } \partial\Omega_0$$

Let $g_0 = \max\limits_{u \geq 0} f(u)/u$ and $g = \lim\limits_{u\to 0} \dfrac{f(u)}{u} = f'(0)$

The principal eigenvalue in (8.2) in this case is

$$g_0 - d\lambda_0/\ell^2$$

while the principal eigenvalue in (8.3) in this case is

$$g - d\lambda_0/\ell^2$$

If we let $f(u) = u(1-u)$, they coincide with $g_0 = g = 1$

We then have extinction in (8.1) from any initial density if $\ell < \sqrt{d\lambda_0}$ and persistence starting at any initial density that is positive somewhere if $\ell > \sqrt{d\lambda_0}$.

However, if $f(u) = u(1+u-u^2)$, then

$$g_0 = \max_{u \geq 0} (1+u-u^2) = 5/4$$

while

$$g = 1.$$

So in this case we get a prediction of extinction when

$$\ell < \frac{2\sqrt{5}}{5} (\sqrt{d\lambda_0})$$

but we need

$$\ell > \sqrt{d\lambda_0}$$

to get a prediction of persistence.

$\sigma_1 < 0$ will mean that $u \equiv 0$ is locally stable, so population whose initial densities are too small will go extinct, but that does not rule out the possibility that larger populations may persist.

Uniqueness of Equilibria

Under the hypotheses of Proposition 8.2, there are orbits of (8.1) starting arbitrarily close to zero (at $\varepsilon \psi_1$) which increase toward a minimal equilibrium $u^*$. If $f(x,u) < 0$ for $u > K$, any constant $C$ is a super-solution to the equilibrium problem and solutions with initial data $u(x,0) = C$ will decrease toward a maximal equilibrium $u^{**} \geq u^*$. If (8.1) has a unique equilibrium, all orbits of (8.1) are "squeezed" toward $u^*$ and $u^*$ is globally asymptotically stable.

Proposition 8.3. (CC Proposition 3.3) (Hess 1977). Suppose that the hypotheses of Proposition 8.2 are satisfied and that $f(x,u) = g(x,u)u$ where $g(x,u)$ is strictly decreasing in $u$ for $u \geq 0$. Then the minimal positive equilibrium $u^*$ is the only positive equilibrium for (8.1). If $g_1(x,u)$ and $g_2(x,u)$ are both strictly decreasing in $u$ and if $u_1^*$ and $u_2^*$ are the unique positive equilibria corresponding to (8.1) with $g_1$ and $g_2$, respectively, then having $g_1(x,u) \le g_2(x,u)$ for $u > 0$ implies $u_1^* \le u_2^*$. If $g_1(x,u) < g_2(x,u)$ for $u>0$, then $u_1^* < u_2^*$.

Proof: If $u^{**}$ is a positive equilibrium of (8.1) with $u^{**} \neq u^*$, then since $u^*$ is minimal we must have $u^{**} > u^*$ somewhere in $\Omega$. Since $u^* > 0$ is an equilibrium of (8.1), it is a positive solution to

$$\nabla \cdot d(x)\nabla\psi + \vec{b}(x)\cdot\nabla\psi + g(x,u^*)\psi = \sigma\psi \quad \text{in } \Omega$$

$$(8.5) \qquad d(x)\frac{\partial\psi}{\partial\eta} + \beta(x)\psi = 0 \quad \text{on } \partial\Omega$$

with $\sigma = 0$. So $\sigma_1 = 0$ is the principal eigenvalue for (8.5)

Similarly, $u^{**} > 0$ satisfies

$$\nabla \cdot d(x)\nabla\psi + \vec{b}(x)\cdot\nabla\psi + g(x,u^{**})\psi = \sigma\psi \quad \text{in } \Omega$$

$$(8.6) \qquad d(x)\frac{\partial\psi}{\partial\eta} + \beta(x)\psi = 0 \quad \text{on } \partial\Omega$$

with $\sigma = 0$.

However, since $g(x,u)$ is strictly decreasing in $u$ and

$u^{**} > u^{*}$ on at least part of $\Omega$, the principal eigenvalue in (8.6) must exceed 0. (If $\vec{b} \not\equiv 0$, we would employ Corollary 2.19 in CC.) So $u^*$ is the only positive equilibrium.

If $g_1(x,u) \le g_2(x,u)$, then $u_1^*$ is a subsolution of the equilibrium problem for (8.1) with $f(x,u) = g_2(x,u)u$. Any constant larger than $K$ is a supersolution. So (8.1) with $f(x,u) = g_2(x,u)u$ must have an equilibrium $\ge u_1^*$. So the uniqueness of equilibria ($g_2(x,u)$ is strictly decreasing) $\Rightarrow u_1^* \le u_2^*$. If $g_1 < g_2$, $u_1^*$ is a strict subsolution, so that $u_2^* > u_1^*$.

Notes: (i) The same argument applies in the case of Dirichlet boundary conditions.

(ii) <u>Example</u>.

Consider the diffusive logistic equation

(8.7) $$\frac{\partial u}{\partial t} = \nabla \cdot d(x) \nabla u + \vec{b}(x) \cdot \nabla u + a(x) u - c(x) u^2$$

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

$$d(x)\frac{\partial u}{\partial \eta} + \beta(x)u = 0 \qquad \text{on } \partial\Omega\times(0,\infty)$$

Here we have $g(x,u) = a(x) - c(x)u$, which is strictly decreasing in $u$ if $c(x) > 0$. Let $\sigma_1$ be the principal eigenvalue for

(8.8) $$\nabla\cdot d(x)\nabla\psi + \vec{b}(x)\cdot\nabla\psi + a(x)\psi = \sigma\psi \qquad \text{in } \Omega$$

$$d(x)\frac{\partial\psi}{\partial\eta} + \beta(x)\psi = 0 \qquad \text{on } \partial\Omega$$

If $\sigma_1 < 0$, Proposition 8.1 $\Rightarrow$ all positive solutions to (8.7) decline toward zero as $t\to\infty$. If $\sigma_1 > 0$, (8.7) has a unique positive equilibrium $u^*$ and all positive solutions approach $u^*$ as $t\to\infty$.

Suppose now that $\sigma_1 = 0$. The adjoint to (8.8) is

$$\nabla\cdot d(x)\nabla\rho - \nabla\cdot(\rho\vec{b}) + a(x)\rho = \sigma\rho \qquad \text{in } \Omega$$

$$d(x)\frac{\partial\rho}{\partial\eta} + \beta(x)\rho - \vec{b}\cdot\vec{\eta}\,\rho = 0 \quad \text{on } \partial\Omega$$

Arguments used to establish Corollary 2.13 in CC will tell us that the principal eigenvalue here will be 0. Let $\rho^*$ be the eigenfunction. Multiply (8.7) by $\rho^*$ and integrate. We have

$$\frac{d}{dt}\int_\Omega \rho^* u\,dx = \int_\Omega \rho^* \frac{d}{dt} u\,dx$$

$$= \int_\Omega \rho^* \left[\nabla\cdot d(x)\nabla u + \vec{b}(x)\cdot\nabla u + a(x)u - c(x)u^2\right]dx$$

Now $\int_\Omega \rho^*[\nabla\cdot d(x)\nabla u] - u[\nabla\cdot d(x)\nabla\rho^*]$

$$= \int_\Omega \left[\operatorname{div}(\rho^* d(x)\nabla u) - \operatorname{div}(u\,d(x)\nabla\rho^*)\right]$$

$$= \int_{\partial\Omega} \rho^* d(x)\nabla u\cdot\eta - \int_{\partial\Omega} u\,d(x)\nabla\rho^*\cdot\eta$$

$$= -\int_{\partial\Omega}\beta\rho^* u - \int_{\partial\Omega} u\,d(x)\nabla\rho^*\cdot\eta$$

So $\int_\Omega \rho^*[\nabla\cdot d(x)\nabla u]$

$$= \int_\Omega u[\nabla\cdot d(x)\nabla\rho^*] - \int_{\partial\Omega}\left[d(x)\nabla\rho^*\cdot\eta + \beta\rho^*\right]u$$

Next $\int_\Omega \rho^* \vec{b}(x) \cdot \nabla u = \int_\Omega \operatorname{div}(u\rho^* \vec{b}) - \int_\Omega \nabla \cdot (\rho^* \vec{b}(x))\, u$

$$= -\int_\Omega \nabla \cdot (\rho^* \vec{b}(x)) u + \int_{\partial\Omega} u \rho^* \vec{b} \cdot \eta$$

So $\int_\Omega \rho^* \left[ \nabla \cdot d(x) \nabla u + \vec{b}(x) \cdot \nabla u + a(x) u - c(x) u^2 \right] dx$

$$= \int_\Omega u \left[ \nabla \cdot d(x) \nabla \rho^* - \nabla \cdot (\rho^* \vec{b}(x)) + a(x) \rho^* \right]$$

$$- \int_{\partial\Omega} u \left[ d(x) \nabla \rho^* \cdot \eta + (\beta - \vec{b} \cdot \eta) \rho^* \right]$$

$$- \int_\Omega c(x) u^2 \rho^*$$

$$= -\int_\Omega c(x) \rho^* u^2 \, dx$$

So $\frac{d}{dt}\int_\Omega \rho^* u\,dx = \int_\Omega u\left[\nabla\cdot d(x)\nabla\rho^* - \nabla\cdot(\rho^*\vec{b}(x)) + a(x)\rho^*\right]dx$

$$- \int_\Omega c(x)\rho^* u^2\,dx$$

$\Rightarrow$

$$\frac{d}{dt}\int_\Omega \rho^* u\,dx = -\int c(x)\rho^* u^2\,dx$$

Thus $\int_\Omega \rho^* u\,dx$ is strictly decreasing if $u > 0$.

So all positive solutions must decline toward 0.

So if $\sigma_1 \le 0$ in (8.8), all positive solutions decline toward zero as $t\to\infty$, while if $\sigma_1 > 0$, (8.7) has a unique positive equilibrium which is globally attracting among positive solutions.

If the problem

$$(8.9)\quad \nabla\cdot d(x)\nabla\phi + \vec{b}(x)\cdot\nabla\phi + \lambda\, a(x)\phi = 0 \quad \text{in } \Omega$$

$$d(x)\frac{\partial\phi}{\partial\eta} + \beta(x)\phi = 0 \quad \text{on } \partial\Omega$$

admits a positive principal eigenvalue $\lambda_1^+(a(x))$

(which it will except in the case of Neumann boundary conditions with $\int_\Omega a(x)dx \geq 0$), then we have by Theorem 7.6 (or Corollary 2.18 of CC when $\vec{b} \neq 0$) that

$$\sigma_1 > 0 \iff \lambda_1^+(a(x)) < 1$$

Suppose now that the coefficients of the differential operator in (8.1) are constant and that $f(u) = u\,g(u)$, where $g(0) > 0$, $g$ is decreasing and $g(u) < 0$ for $u > K > 0$. Suppose $\Omega = \ell\,\Omega_0$ where $\ell > 0$ and $\Omega_0$ is a fixed domain. Then

$$\lambda_1^+(g(0); \ell\Omega_0) = \frac{\lambda_1^+(g(0); \Omega_0)}{\ell^2}$$

So there is a critical size $\ell^*$ so that

$$\sigma_1 > 0 \iff \ell > \ell^*$$

The analysis for the diffusive logistic case above may be adapted to conclude that all positive solutions decline toward 0 when $\ell \leq \ell^*$ and converge to a unique positive equilibrium $u^*(\ell)$ when $\ell > \ell^*$. In particular, we have:

<u>Corollary 8.4</u> If the underlying domain for

$$(8.10) \qquad u_t = d\Delta u + g(u)u \qquad \text{in } \Omega \times (0,\infty)$$

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

is $\Omega = \ell\Omega_0 = \{\ell x \mid x \in \Omega_0\}$ and if $g(u)$ is Lipschitz and decreasing in $u$, with $g(0) > 0$ and $g(u) < 0$ for $u > K > 0$, then there is a number $\ell^* > 0$ such that for $\ell \leq \ell^*$ all positive solutions to (8.10) approach 0 as $t \to \infty$, while if $\ell > \ell^*$ there is a unique positive equilibrium $u^* = u^*(\ell)$ such that all positive solutions approach $u^*$ as $t \to \infty$.

Suppose we can linearize (8.10) about $u = 0$ and get the eigenvalue problem

$$d\Delta\psi + g(0)\psi = \sigma\psi \quad \text{in } \Omega$$

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

If $\lambda_0$ is the principal eigenvalue for

$$\Delta\phi + \lambda\phi = 0 \quad \text{on } \Omega_0$$

$$\phi = 0 \quad \text{on } \partial\Omega_0$$

then $\sigma_1 = g(0) - \frac{d\lambda_0}{\ell^2}$. So

$\sigma_1 \leq 0 \iff \ell \leq \sqrt{d\lambda_0 / g(0)}$. So $\ell^* = \sqrt{d\lambda_0 / g(0)}$.