Lecture 1

Introduction and Mathematical Background

Our aim in this series of lectures is to consider

the asymptotic predictions, and biological consequences

thereof, of models of the form

$$\frac{\partial u_i}{\partial t} = L_i u_i + f_i(x, u_1, \ldots, u_m) \qquad \text{in} \quad \Omega \times (0, \infty)$$

(1.1)
$$B_i u_i = 0 \qquad \text{on} \quad \partial \Omega \times (0, \infty)$$

$$u_i(x, 0) = w_i(x) \qquad \text{on} \quad \Omega,$$

$$i = 1, \ldots, m$$

The context is as follows. Ω denotes a bounded

habitat patch in which m biological species

interact. Mathematically, Ω will be a

bounded domain in Euclidean space $\mathbb{R}^N$, where

N is usually 1, 2 or 3. The population density

of the ith species (or species i) at location $x \in \Omega$ at time $t \geq 0$ is given by $u_i(x,t)$. ¶ The terms $L_i u_i$ and $f_i(x, u_1, \cdots, u_m)$ represent the dispersal and growth components of the rate of change in density u_i with respect to time at location x and time t. Usually $f_i(x, u_1, \cdots, u_m)$ will have the so-called Kolmogorov form

$$(1.2) \qquad f_i(x, u_1, \cdots, u_m) = u_i \, \hat{f}_i(x, u_1, \cdots u_m).$$

The three most basic ecological interactions among species are competition, predation and mutualism (cooperation). The term (1.2) allows a range of combinations of such interactions with the potential that the particular combination might be different in different parts of the

focal habitat patch. Generally speaking, in ecology, we consider only pairwise interactions. An interaction between two species that serves to reduce the densities of both species is termed competitive. Predation refers to interactions, such as those of consumer and resource, in which the interaction serves to increase the density of one species and decrease that of the other. If the interaction serves to increase the densities of both species, we term it to be mutualistic (or cooperative). One could allow f_i or $\tilde{f}_i$ to depend on time t (e.g. with time periodicity) but we will not have time to discuss such non-autonomous models in these lectures. Clearly, allowing for temporal

as well as spatial variation in the rates of change of species'

densities is desirable, and very substantial

mathematical advances in this direction are due

to Shen and Yi (1998 a-c) and Zhao (2002), among

others. Much work remains, however, in order

to harness these results to address specific ecological

questions of interest.

The dispersal terms L_i in (1.1) can be derived as

the large scale limits of dispersal models based on

random walks, as in Okubo (1980) and Turchin (1998).

They can also be derived from Fick's law (which

describes the flux of a diffusing subtance in terms

of its gradient), as discussed in Okubo (1980) or

Murray (1993), from stochastic differential equations

as in Gardiner (1985), or via hydrodynamic limits of interacting particle systems, as in Durrett and Levin (1994). The mapping that assigns $L_i u_i$ to u_i is called an operator, specifically an elliptic differential operator. The general form here is

$$(1.3) \qquad L_i u_i(x,t) = \sum_{j,k=1}^{N} a_{jk}^i(x) \frac{\partial^2 u_i(x,t)}{\partial x_j \partial x_k}$$

$$+ \sum_{j=1}^{N} b_j^i(x) \frac{\partial u_i(x,t)}{\partial x_j}$$

$$+ c^i(x) u_i(x,t)$$

where, due to the equality of mixed partial derivatives, one may assume $a_{jk}^i(x) = a_{kj}^i(x)$ for all j, k. We assume L_i is strongly uniformly elliptic, by which we mean

there are constants $A_1^i \geq A_0^i > 0$ so that

$$A_0^i \left(\sum_{j=1}^{N} z_j^2 \right) \leq \sum_{j,k=1}^{N} a_{j,k}^i(x) z_j z_k \leq A_1^i \left(\sum_{j=1}^{N} z_j^2 \right)$$

for any $z \in \mathbb{R}^n$ and $x \in \overline{\Omega}$.

Importantly, (1.3) includes all models

of the form

(1.4)
$$\nabla \cdot \left[d_i(x) \nabla u_i - \vec{b}^i(x) u_i \right]$$

where $d_i(x)$ is a positive smooth function on

$\overline{\Omega}$. The form (1.4) is useful in delineating

random versus advective dispersal. It reduces

to

$$d_i \nabla^2 u_i = d_i \Delta u_i$$

when $d_i(x)$ is a positive constant and $\vec{b}^i = \vec{0}$.

Of course, some degree of continuity or

smoothness is needed in the analysis of our

models. We will be more specific about our assumptions

as appropriate as we move along.

The equation $B_i u_i = 0$ on $\partial\Omega \times (0,\infty)$

in (1.1) governs the density of species i.

along the interface of the focal habitat patch with

the territory or environs surrounding it (frequently

referred to as "matrix" habitat). In the models

we consider here the boundary condition

is homogeneous (i.e. we have 0 on the r.h.s.

of the defining equation). Important examples

include

(1.5)
$$B_i u_i = u_i \qquad\qquad (\text{Dirichlet})$$

in which individuals that go to the boundary

are absorbed into the surrounding matrix.

Dirichlet boundary conditions are often referred to as "absorbing" boundary conditions in the ecology literature. This interpretation encompasses viewing them as designating a lethal boundary. Dirichlet boundary conditions are thus dissipative.

In contrast, the Neumann boundary condition

$$(1.6) \qquad B_i u_i = \nabla u_i \cdot \vec{\eta}$$

where $\vec{\eta}$ is a unit outer normal along $\partial\Omega$ is referred to as "reflecting" in the ecological literature. Neumann boundary conditions are sometimes designated "no-flux" boundary conditions, and such is the case for operators of the form (1.4) with $\vec{b^i} \equiv 0$. In general, however,

a no-flux boundary condition has

$$d_i(x)\nabla u_i \cdot \eta + u_i \vec{b} \cdot \eta = 0$$

on $\partial\Omega \times (0,\infty)$. Robin boundary

conditions, in which

(1.7)
$$B_i u_i = \beta \nabla u_i \cdot \eta + (1-\beta) u_i$$

where $\beta = \beta(x) \in [0,1]$, represent

a trade-off between absorption and

reflection (the larger β the more the

balance is toward reflection).

The last term in (1.1) represents the

initial density profile of species i across

the focal habitat patch. Assuming appropriate

smoothness of the coefficients in the dispersal

and growth terms, the model (1.1) is well-posed

meaning it has a unique solution over some

positive time interval with appropriate

continuity in the dependence of said solution

on the parameters (coefficients) and

initial conditions.

What Can Reaction-Diffusion Models Tell Us?

Can help to explain three types of spatial phenomena
relevant in ecology

(i) waves of invasion by exotic species
    Fisher (1937)   (genetics)
    Skellam (1951)   (ecology)
(ii) formation of patterns in homogeneous space
    Turing (1952)

(iii) the effects of the size, shape and heterogenity
    of the spatial environment on the persistence
    of species and the structure of communities
    Skellam (1951)
    Kierstead and Slobodkin (1953)
    KISS models; minimal patch size

(i) Traveling waves in reaction-diffusion models (math vpt)

      Fife (1979)

      Smoller (1982)

      Grindrod (1996)

        Murray (1993) (2002)   (bio vpt)

    Models for biological invasions

      Kawasaki and Shigesada (1997)

(ii) Pattern formation

      Grindrod (1996)

      Murray (2002)

(iii) Reaction - diffusion models in bounded

      spatial domains

      Leung (1989)

      Pao (1992)

      Hess (1991) (time periodic case)

* Focus of "Spatial ecology via reaction-diffusion
equations" (and hence these lectures):

    effects of habitat geometry and heterogeneity
    on the persistence, coexistence and extinction
    of species in finite habitats   (biogeography)

Other Approaches to Such Questions

    (i) Simulations, individual based models (IBM's),
      cellular automata, interacting particle systems

- good for predictions in specific situations; limited progress in terms of analyzing simulations mathematically so as to provide insight into mechanisms underlying predictions

    - general discussion: Tilman et al (1997)

    - spatial patterns via cellular automata:

            Comins et al (1992)

            Hassell et al (1994)

    - range expansion via interacting particle systems:

            Ellner et al (1998)

(ii) telegraph equations $\left(\varepsilon^2 \dfrac{\partial^2 u}{\partial t^2} + \dfrac{\partial u}{\partial t} = d \dfrac{\partial^2 u}{\partial x^2} + f(u) \right)$

    - addresses the perceived problem of infinite speed of propagation

    - predictions very close to corresponding r-d model:

            Holmes (1993)

(iii) integro-difference and integro-differential models:

    - allow for long-distance nonlocal dispersal

    - general discussion: Lewis (1997)

- more of an issue in invasive spread than
  in biogeography

- integral kernels have been used in biogeography:
  Van Kirk and Lewis (1997, 1999)

(iv) Metapopulation models

- primarily treat networks of patches, treating
  population dynamics implicitly, with
  state variable probability of occupancy
  of a patch or fraction of patch occupied,
  as opposed to population density

- describe spatial effects on a different set
  of spatial scales than r-d models

- Hanski (1999)
- Hanski and Ovaskainen (2000)
  Metapopulation capacity

(v) Discrete-diffusion models (aka island
  chain models)

Edges, Boundary Conditions and Environmental
  Heterogeneity

Phenomena of traveling waves and pattern formation

differ from that of a minimal patch in a fundamental way, as they may occur in homogeneous space, whereas the very notion of "patch" requires at least enough spatial heterogeneity to distinguish the patch from its surroundings

A defining feature of any finite habitat is that it has a boundary or edge

Edges: (i) mediate numerous features in population dynamics (Fagan et al 1999)

(a) affect movement patterns
(b) act as a source of mortality or resource
(c) function as a unique environment
(d) have different effects on different species

Reaction-diffusion models are a natural framework for the study of edge mediated effects

(a) boundary conditions are needed to have a well-posed reaction-diffusion-advection model (one must specify not only how the population disperses through the focal patch but what it does when it gets to the edge or boundary)
(b) r-d models can readily incorporate effects of edges

(c) also incorporate effects of internal heterogeneity within a patch

Formulating boundary conditions:

Fick's Law: rate of diffusion across an interface is given by by

$$\vec{J} \cdot \vec{\eta}$$

where $\vec{\eta}$ is the unit normal to the interface

If we are describing the density u of a population that diffuses at a rate $d(x)$ and are advected or engage in directed movement with velocity $\vec{v}(x)$,

$$\vec{J} = -d(x)\nabla u + \vec{v}(x) u$$

and the diffusion equation is then

$$\frac{\partial u}{\partial t} = -\nabla \cdot \vec{J} = \nabla \cdot [d(x)\nabla u - u\vec{v}(x)]$$

Standard boundary condition for the equation relate the flux of individuals across the boundary to the density at the boundary

To wit: Let Ω be a bounded region with smooth boundary $\partial \Omega$ and let $\vec{\eta}$

denote the outward pointing unit normal. Then the flux across the boundary $\partial\Omega$ at any given point is proportional to the density with constant of proportionality $\beta(x)$ if

$$\vec{J} \cdot \vec{\eta} = \beta u$$

so that

(1.8)
$$\left[-d(x)\nabla u + u\vec{V}(x) \right] \cdot \vec{\eta} = \beta(x) u$$

$\Rightarrow$

$$d(x)\frac{\partial u}{\partial \eta} + \left[\beta(x) - \vec{V}(x) \cdot \vec{\eta} \right] u = 0$$

If $\beta = 0$, there is no flux across the boundary.

As β increases a larger proportion of individuals who encounter the boundary cross it in the outward direction:

$$u = \frac{1}{\beta} \left[\vec{J} \cdot \vec{\eta} \right] \quad \rightarrow \quad u = 0 \quad \text{as } \beta \rightarrow \infty$$

Note also that we can re-write (1.8) as:

$$\frac{1}{\beta(x)+1}\left[d(x)\frac{\partial u}{\partial \eta}-\vec{v}\cdot\vec{\eta}\,u\right]+\frac{\beta(x)}{\beta(x)+1}\,u=0$$

Setting $\alpha=\dfrac{1}{\beta(x)+1}$, we have (1.8) as equivalent to

$$\alpha\left[d(x)\frac{\partial u}{\partial \eta}-\vec{v}\cdot\vec{\eta}\,u\right]+(1-\alpha)u=0$$

with $0\le \alpha \le 1$.

Brief Summary and Example

Once we have specified a patch Ω, the dispersal properties and local population dynamics of a species inhabiting the patch Ω, and the behavior or fate of individuals encountering the boundary of Ω, we can assemble a complete reaction-diffusion model

Example: Model for the density of a population

Dispersal: diffusion at a rate $d(x)$ which may vary in space

Population dynamics: reproduce or die logistically with a net per capita birth-death rate of $a(x)-b(x)u$

Boundary behavior: leave Ω when they encounter $\partial\Omega$

$$\frac{\partial u}{\partial t} = \nabla \cdot \left[d(x) \nabla u \right] + \left[a(x) - b(x)u \right] u$$

$$\text{in } \Omega \times (0, \infty)$$

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

To obtain a specific solution we add $u(x, 0)$.

Fifty-two years ago, Skellam (1951) said of models such as the preceding that "orthodox analytical models appear inadequate"

To a large extent the purpose of these lectures is to say "J.D., we've come a very long way!..."