Biological Invasions?

- What are biological invasions?
  - A biological invasion is the introduction and spread of an exotic species within an ecosystem
  - Estimated 450 million exotics imported into the US per year [Center et al. - 1995]

- Why are biological invasions important?
  - Economic impact:
    Cumulative $110 billion by 1991 to the US economy [Williamson - 1996]
  - Contribute to the loss of biodiversity
  - Threat to endangered species
Conceptual Framework

- Arrival and Establishment
  - Most invasions fail!
  - All communities are invasible
  - Invasion (or propagule) pressure is important

[Biological Invasions, Williamson - 1996]
Conceptual Framework

- Arrival and Establishment
  - Most invasions fail!
  - All communities are invasible
  - Invasion (or propagule) pressure is important

- Spread

[Biological Invasions, Williamson - 1996]
Conceptual Framework

- **Arrival and Establishment**
  - Most invasions fail!
  - All communities are invasible
  - Invasion (or propagule) pressure is important

- **Spread**

- **Equilibrium and effects**
  - Most invaders have only minor consequences
  - Few have disastrous consequences!

[Biological Invasions, Williamson - 1996]
Reaction–Diffusion Models

\[ \frac{\partial n}{\partial t} = D \frac{\partial^2 n}{\partial x^2} + (r_0 - \kappa n)n, \]

where

- \( n = n(x, t) \) is the frequency of the mutant allele
- \( D \) is the diffusion coefficient
- Logistic growth, \( r_0 \) is the intrinsic growth rate

- **Fisher, 1937**: Spread of an advantage gene within a homogeneous population
- **Skellam, 1951**
- **Aronson and Weinberger, 1975**
- **Shigesada et al., 1986**
Reaction–Diffusion Models

\[
\frac{\partial n}{\partial t} = D \left\{ \frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right\} + r_0 n,
\]

where

- \( n = n(x, y, t) \) is the population density
- \( D \) is the diffusion coefficient
- Malthusian growth, \( r_0 \) is the intrinsic growth rate

- Fisher, 1937
- **Skellam, 1951**: Modeled the range expansion of introduced muskrats in Europe
- Aronson and Weinberger, 1975
- Shigesada *et al.*, 1986
Reaction–Diffusion Models

\[ \frac{\partial n}{\partial t} = D \frac{\partial^2 n}{\partial x^2} + h(n)n, \]

where

- \( n = n(x, 0) \) has compact support
- \( D \) is the constant diffusion coefficient
- \( h \) is the intrinsic growth rate, \( h(0) > 0 \) and \( \frac{\partial h}{\partial n} \leq 0 \) for all \( n \geq 0 \)

- Fisher, 1937
- Skellam, 1951
- Aronson and Weinberger, 1975: ARS for population is \( c^* = 2\sqrt{h(0)D} \)
- Shigesada et al., 1986
Reaction–Diffusion Models

\[
\frac{\partial n}{\partial t} = \frac{\partial}{\partial x} \left\{ D(x) \frac{\partial n}{\partial x} \right\} + (r_0(x) - \kappa n)n,
\]

where

- \( n = n(x, t) \) is the population density
- \( D = D(x) \) is the spatially dependent, periodic diffusion coefficient
- \( r_0 = r_0(x) \) is the spatially dependent, periodic intrinsic growth rate

- Fisher, 1937
- Skellam, 1951
- Aronson and Weinberger, 1975
- Shigesada et al., 1986: Fisher equation with spatial heterogeneity
  Species persistence and dispersion relation for a Traveling Periodic Wave (TPW)
Biological Problem

- Consider the invasion of terrestrial plant species
- Assume spatial heterogeneity for local growth and dispersal ability
- How is invasibility and spread rates of the population affected by:
  - local growth rates?
  - seed deposition rates?
  - the ratio of local to long-distance seed dispersal?
- Can spread rates be increased or slowed down (possible stalled) by habitat heterogeneity?
Mount St. Helens

- Mt. St. Helens erupted on May 18, 1980
- North of the crater, the *Pumice Plain* is a patchy environment, approximately 25 km², with hills, valleys, craters and rivers
- *Lupinus lepidus* (Lupine) appeared in 1981, south of Spirit lake
- Lupine patches are located over much of the plain, with current estimates of over $10^8$ plants
- Lupine seeds are thought to be wind and water dispersed

Biological Model

- Terrestrial plant species
- Infinite, one-dimensional environment
- Assume that growth and dispersal occur in distinct, nonoverlapping stages
- Plant survival is limited to one cycle, with nonoverlapping generations
Mathematical Model

Integrodifference equation (IDE) model for the population density

\[ N_{\tau+1}(x) = \int_{-\infty}^{+\infty} f(N_\tau(y); y) k(x, y) dy \]

where

- \( \tau \) is the generation count
- \( N_\tau(x) \) is the seed density at the start of generation \( \tau \)
- \( f \) is the nonlinear growth function
- \( k(x, y) \) is the dispersal kernel
• Kot *et al.* - 1996: Spread of *D. pseudoobscura*, estimating the kernel from data

• Van Kirk and Lewis - 1997, Lutscher and Lewis - 2003: Species persistence in fragmented habitats

• Clark - 1998: Model tree migration in response to climate change

• Neubert and Caswell - 2000, Neubert and Parker - 2004: Model the spread of invasive plant species
Growth Function

\[ N_{\tau + \frac{1}{2}}(x) = f(N_\tau(x); x) \]

- \( N_\tau(x) \) is the seed density at the start of generation \( \tau \),
  \( N_{\tau + \frac{1}{2}}(x) \) is the seed density at the end of generation \( \tau \), before dispersal
- \( f \) is continuous, monotone increasing and bounded above
- The maximum per capita reproductive ratio, \( r_0 \), occurs at arbitrarily low population densities, is positive and bounded away from 0
Example for a homogeneous environment: Beverton-Holt stock-recruitment curve

\[ f(N) = \frac{r_0 N}{1 + [(r_0 - 1)N]} \]
Dispersal Kernel

• \( k(x, y) \) is a pdf for a seed released from a location \( y \) and being deposited at a location \( x \), i.e., for some \( y \),

\[
\int_{-\infty}^{+\infty} k(x, y) \, dx = 1
\]

• The IDE is the sum of all seeds dispersed to \( x \), i.e., for some \( x \),

\[
\int_{-\infty}^{+\infty} N_{\tau + \frac{1}{2}}(y) k(x, y) \, dy < \infty
\]
Model for Seed Dispersal

• The dispersal model:

\[
\begin{align*}
\frac{\partial u}{\partial t} &= D \frac{\partial^2 u}{\partial x^2} - au \\
\frac{\partial v}{\partial t} &= au \\
\end{align*}
\]

\( u(x, 0; y) = \delta(x - y) \)

\( v(x, 0; y) = 0 \)

• \( u \) is the airborne seed density

• \( v \) is the seed density on the ground

• \( a \) is the deposition rate

\( k(x, y) = \lim_{t \to \infty} v(x, t; y) \)

[Neubert et al. - 1995]
Laplace Dispersal Kernel

- Let $a(x) \equiv a$

- Integrate (2) from $t = 0$ to $\infty$:

  $$
  \int_0^\infty \frac{\partial d}{\partial t} dt = d(x, t; y) \Bigr|_{t=0}^\infty \\
  = k(x, y) \\
  = a \int_0^\infty c dt
  $$

- Integrate (1) from $t = 0$ to $\infty$:

  $$
  \int_0^\infty \frac{\partial c}{\partial t} dt = c(x, t; y) \Bigr|_{t=0}^\infty \\
  = -\delta(x - y) \\
  = D \int_0^\infty \left\{ \frac{\partial^2 c}{\partial x^2} \right\} dt - a \int_0^\infty c dt \\
  = D \frac{\partial^2}{\partial x^2} \left\{ \int_0^\infty c dt \right\} - a \int_0^\infty c dt
  $$
Laplace Dispersal Kernel

• \( k \) is the Greens function for

\[
D \frac{\partial^2}{\partial x^2} \left\{ \frac{1}{a} k(x, y) \right\} - k(x, y) = -\delta(x - y)
\]

• The dispersal kernel is given by the Laplace distribution

\[
k(x - y) = \sqrt{\frac{a}{4D}} \exp \left\{ -\sqrt{\frac{a}{D}} |x - y| \right\}
\]

Homogeneous Environment

- Infinite flow, one-dimensional homogeneous environment
- Growth function of the form
  \[ f(N; y) = f(N) \]
- The dispersal kernel is translation invariant, i.e.,
  \[ k(x, y) = k(x - y) \]
- The IDE model reduces to the convolution integral
  \[ N_{\tau+1}(x) = \int_{-\infty}^{+\infty} f(N_{\tau}(y)) k(x - y) dy \]
Traveling Wave Solution

For the initial population density

\[ N_0(x) = \delta(x) \]

with the Laplace dispersal kernel and Beverton-Holt growth dynamics \( r_0 > 1 \)
the solution of the IDE approaches a traveling wave:

\[ r_0 = 6, \quad D = 1 \quad \text{and} \quad a = 10 \]
Traveling Wave Solution

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with the Laplace dispersal kernel and Beverton-Holt growth dynamics \((r_0 > 1)\) the solution of the IDE approaches a traveling wave:

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Traveling Wave Solution

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the solution of the IDE approaches a traveling wave:

\[ r_0 = 6, \ D = 1 \text{ and } a = 10 \]
Traveling Wave Result

- Homogeneous, one-dimensional environment
- $N_0(x)$ has compact support
- $f$ is monotonic, bounded above and no Allee effect
- The dispersal kernel has a moment generating function

$$U(s) = \int_{-\infty}^{+\infty} k(x) \exp\{xs\} \, dx$$

- The asymptotic rate of spread is given by

$$c^* = \min_{0<s} \left[ \frac{1}{s} \ln (r_0 U(s)) \right]$$

[Weinberger - 1982]
Dispersion Relation

• A traveling wave, with positive wave speed $c$, is of the form

$$N_{\tau + 1}(x) = N_{\tau}(x - c)$$

• Near the front, population densities are low, so the IDE can be approximated by

$$N_{\tau}(x - c) = r_0 \int_{-\infty}^{+\infty} k(x - y) N_{\tau}(y) dy$$

where $r_0 = f'(0)$

• TW ansatz: near the leading edge of the wave

$$N_{\tau}(x) \propto e^{-sx}$$

for $s > 0$
Dispersion Relation

- From this assumption

\[ e^{-sx} e^{sc} = r_0 \int_{-\infty}^{+\infty} k(x - y) e^{-sy} dy \]

- Make the change of variables \( u \equiv x - y \)

- We have the characteristic equation

\[ e^{sc} = r_0 \int_{-\infty}^{+\infty} k(u) e^{su} du \]

- Solving for \( c \) as a function of \( s \)

\[ c(s) = \frac{1}{s} \ln \left( r_0 U(s) \right) \]

[Kot et al. - 1996]
Dispersion Relation: Laplace Kernel

- The moment generating function:

\[
U(s) = \frac{a}{D} \left[ \frac{1}{a/D - s^2} \right]
\]

- For the Laplace dispersal kernel, the dispersion relation is:

\[
c(s) = \frac{1}{s} \ln \left\{ r_0 \frac{a}{D} \left[ \frac{1}{a/D - s^2} \right] \right\}
\]
Homogeneous Environment: Application?

- UL: Exponentially bounded kernel
- UR: Fat-tailed kernel
- LL: Dispersal kernels
- LR: Location of wave front
Heterogeneous Environment

• Growth function of the form \( f = f(N; x) \), e.g.,

\[
f(N; y) = \frac{r_0(x)N}{1 + [(r_0(x) - 1)N]}
\]

• The dispersal model:

\[
\frac{\partial c}{\partial t} = D \frac{\partial^2 c}{\partial x^2} - a(x)c
\]

\[
\frac{\partial d}{\partial t} = a(x)c
\]

\[
c(x, 0; y) = \delta(x - y)
\]

\[
d(x, 0; y) = 0
\]

• The IDE model is of the form

\[
N_{\tau+1}(x) = AN_{\tau} = \int_{-\infty}^{+\infty} f(N_{\tau}(y); y)k(x, y)dy
\]
Periodic Heterogeneity

- Periodically divide the environment into *good* \( (r_0 > 1) \) and *bad* \( (r_0 < 1) \) patches:

  \[
  r_0(x) = \begin{cases} 
  r_1 & \text{if } 0 \leq x < x_a \\
  r_2 & \text{if } x_a \leq x < l 
  \end{cases}
  \]

  \[
  r_0(x + l) = r_0(x)
  \]

- Divide the environment into *high* \( (a = 1) \) and *low* \( (a < 1) \) deposition patches:

  \[
  a(x) = \begin{cases} 
  a_1 & \text{if } 0 \leq x < x_a \\
  a_2 & \text{if } x_a \leq x < l 
  \end{cases}
  \]

  \[
  a(x + l) = a(x)
  \]

[Shigesada *et al.* - 1986, Weinberger - 2002]
Dispersal Kernel

- $k(x, y)$ for the homogeneous environment and heterogeneous environment:

\[ D = 1, \ a_1 = 1, \ a_2 = 0.4, \ l = 1, \ x_h = 0.4 \]
Colony Persistence

- A colony is said to persist in an environment if when initially introduced at low densities, the population density eventually increases.
Colony Persistence

- A colony is said to persist in an environment if when initially introduced at low densities, the population density eventually increases.

- Consider when $N^* \equiv 0$ is unstable, where

$$N^* = AN^*, $$

i.e., for all $\xi_0(x)$ such that $\|\xi_0\| < \epsilon$, does $\|A^T \xi_0\| \to 0$?
• A colony is said to persist in an environment if when initially introduced at low densities, the population density eventually increases.

• Consider when $N^* \equiv 0$ is unstable, where

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• This is equivalent to studying the spectrum of the linearization of $A$ near $N^*$.
Colony Persistence

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- For the linear IDE, we analyze the eigenvalue problem.
A colony is said to persist in an environment if when initially introduced at low densities, the population density eventually increases.

Consider when \( N^* \equiv 0 \) is unstable, where

\[
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\]

i.e., for all \( \xi_0(x) \) such that \( \|\xi_0\| < \epsilon \), does \( \|A^T \xi_0\| \to 0 \)?

This is equivalent to studying the spectrum of the linearization of \( A \) near \( N^* \).

For the linear IDE, we analyze the eigenvalue problem.

\( N^* \) is stable if \( \lambda_1 < 1 \) and unstable if \( \lambda_1 > 1 \), where \( \lambda_1 \) is the dominant eigenvalue.
Colony Persistence

- The eigenvalue problem is

\[ \lambda_1 \phi_1(x) = \int_{-\infty}^{+\infty} r_0(y) \phi_1(y) k(x, y) dy \]

- Recall the linear operator \( \mathcal{L} \), where

\[ \mathcal{L}k = \frac{\partial^2}{\partial x^2} \left\{ \frac{k(x, y)}{a(x)} \right\} - k(x, y) = -\delta(x - y) \]

- Apply \( \mathcal{L} \) to the eigenvalue problem

- Hill’s equation:

\[ \frac{d^2}{dx^2} \left\{ \frac{\phi_1(x)}{a(x)} \right\} + a(x) [\mu_1 r_0(x) - 1] \left\{ \frac{\phi_1(x)}{a(x)} \right\} = 0 \]

where \( \mu_1 = 1/\lambda_1 \)

[Van Kirk and Lewis - 1997]
The resulting condition for $\lambda_1 = 1$ is:

\[ 0 = F(a_2, r_1, r_2, x_a, l) := 1 - \cos \left( x_a \sqrt{r_1 - 1} \right) \times \]
\[ \cos \left( (l - x_a) \sqrt{a_2 [r_2 - 1]} \right) \]
\[ + \frac{[r_1 - 1] + a_2 [r_2 - 1]}{2 \sqrt{r_1 - 1} \sqrt{a_2 [r_2 - 1]}} \times \]
\[ \sin \left( x_a \sqrt{r_1 - 1} \right) \times \]
\[ \sin \left( (l - x_a) \sqrt{a_2 [r_2 - 1]} \right) \]
Colony Persistence: Example

- *high* deposition in *good* patches

- Deposition rate in *bad* patch \((a_2)\) vs. relative fraction of *good* patches \((x_a)\):
  
  fixed growth rate in the *good* patch \((r_1)\)

\[
 a_1 = 1, \quad l = 1, \quad r_2 = 0.5
\]

- Stable region is below the curve
• $N_0(x)$ has compact support

• $N^* \equiv 0$ is unstable

• $N_\tau(x)/a(x)$ for $\tau$ large

\[ a_2 = 0.4, \ R_1 = 1.2, \ R_2 = 0.5, \ l = 1 \]

[Shigesada et al. - 1986, Weinberger - 2002]
Traveling Periodic Wave

• Consider the IDE model

\[ N_{\tau+1}(x) = \int_{-\infty}^{+\infty} k(x, y) f(N_t(y); y) \, dy \]

• Assume the existence of a traveling periodic wave (TPW)

\[ \hat{N}(x - c) = \int_{-\infty}^{+\infty} k(x, y) f(\hat{N}(y); y) \, dy \]

• Traveling wave ansatz:

Near the leading edge of the TPW

\[ \hat{N}(x) \propto e^{-s(x-c\tau)} g(x), \]

where \( g(x + l) = g(x) \)

• Near the leading edge of the TPW

\[ \hat{N}(x) \ll 1 \]
Consider the linearized IDE

\[
N_\tau(x) = \int_{-\infty}^{+\infty} r_0(y) N_\tau(y) k(x, y) dy
\]

From the traveling wave ansatz

\[
e^{sc} (e^{-sx} g(x)) = \int_{-\infty}^{+\infty} r_0(y) e^{-s y} g(y) k(x, y) dy
\]

Apply the linear operator \( L \)

Hill’s equation:

\[
\frac{d^2 \varphi}{dx^2} + a(x) \left[ e^{-sc} r_0(x) - 1 \right] \varphi = 0
\]

where \( \varphi(x) = e^{-sx} g(x) / a(x) \)
Dispersion Relation for the TPW

Assume a traveling periodic wave and derive the dispersion relation:

\[ 0 = G(s, c; a_2, r_1, r_2, x_a, l) := \cosh(sl) - \cos \left( x_a \sqrt{r_1 e^{-sc} - 1} \right) \times \cos \left( (l - x_a) \sqrt{a_2 [r_2 e^{-sc} - 1]} \right) \]

\[ + \frac{[r_1 e^{-sc} - 1] + a_2 [r_2 e^{-sc} - 1]}{2 \sqrt{[r_1 e^{-sc} - 1]} \sqrt{a_2 [r_2 e^{-sc} - 1]}} \times \sin \left( x_a \sqrt{r_1 e^{-sc} - 1} \right) \times \sin \left( (l - x_a) \sqrt{a_2 [r_2 e^{-sc} - 1]} \right) \]
Dispersion Relation: Example

- high deposition in *good* patches, low deposition in *bad* patches
- Dispersion relation for TPW: fixed fraction of *good* patches \( (x_a) \)

\[
\begin{align*}
a_2 &= 0.4, \quad r_1 = 1.2, \quad r_2 = 0.5, \quad l = 1
\end{align*}
\]
Multiple Dispersal Scale Model

- The dispersal model:

\[
\begin{align*}
\frac{\partial u_1}{\partial t} &= D\eta \frac{\partial^2 u_1}{\partial x^2} - a(x)u_1 \\
\frac{\partial v_1}{\partial t} &= a(x)u_1 \\
u_1(x, 0; y) &= \delta(x - y) \\
v_1(x, 0; y) &= 0
\end{align*}
\]

\[
\begin{align*}
\frac{\partial u_2}{\partial t} &= D \frac{\partial^2 u_2}{\partial x^2} - a(x)u_2 \\
\frac{\partial v_2}{\partial t} &= a(x)u_2 \\
u_2(x, 0; y) &= \delta(x - y) \\
v_2(x, 0; y) &= 0
\end{align*}
\]

- \( D\eta \ll D \)

- Define the dispersal ratio

\[
w(x) = \begin{cases} 
  w_1 & \text{if } 0 \leq x < x_a \\
  w_2 & \text{if } x_a \leq x < l \\
\end{cases}
\]

\[
w(x + l) = w(x)
\]

- Let \( k(x - y) = \lim_{t \to \infty} \left\{ w(y)v_1(x, t; y) + (1 - w(y))v_2(x, t; y) \right\} \)
Multiple Dispersal Scale Model

- The IDE model is

\[ N_{\tau+1}(x) = \int_{-\infty}^{+\infty} f(N_\tau(y); y) k_1(x, y; D_\epsilon) \, dy \]

\[ + \int_{-\infty}^{+\infty} f(N_\tau(y); y) k_2(x, y; D) \, dy \]

- How does local dispersal affect invasibility?
- How does local dispersal affect the spread rate?
Invasion Model: Colony Persistence

- $0 \leq w(x) \leq 1$ and *high* deposition in *good* patches
- Deposition rate in *bad* patch ($a_2$) vs. relative fraction of *good* patches ($x_A$)

![Graph showing the relationship between $x_A$ and $a_2$ for different $w(x)$ values.]

$a_1 = 1.0$, $r_1 = 1.2$, $r_2 = 0.5$, $l = 1$

- Local dispersal increases species persistence
Invasion Model: Traveling Periodic Wave

- $0 \leq w(x) \leq 1$ and *high* deposition in *good* patches

- Dispersion relation for the speed of the wave:

\[
a_2 = 0.4, \quad r_1 = 1.2, \quad r_2 = 0.5, \quad w_2 = 0, \quad l = 1
\]

- Local dispersal can slow the invasion
Summary

- Use of the periodicity assumption to derive conditions for species persistence

- Dispersion relation for the traveling periodic wave without explicit knowledge of the dispersal kernel

- Invasibility:
  - *Bad* patches decrease invasibility
  - Local dispersal increases invasibility

- Spread rate:
  - *Bad* patches decrease spread rates
  - Local dispersal decreases spread rates