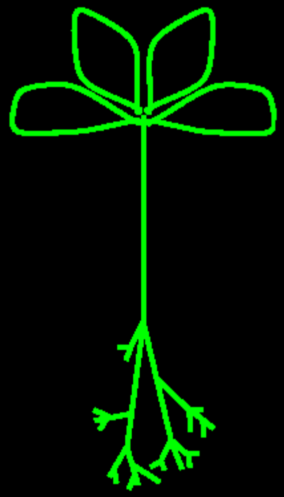
Biological Invasions in Heterogeneous Environments



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Outline

1. Background on biological invasions
2. Mathematical model for plant species
3. Results for homogeneous environments
4. Results for heterogeneous environments
   (a) Species persistence
   (b) Spread rate
5. Dispersal on multiple spatial scales
6. Summary

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]

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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 $\partial h/\partial n \leq 0$ 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

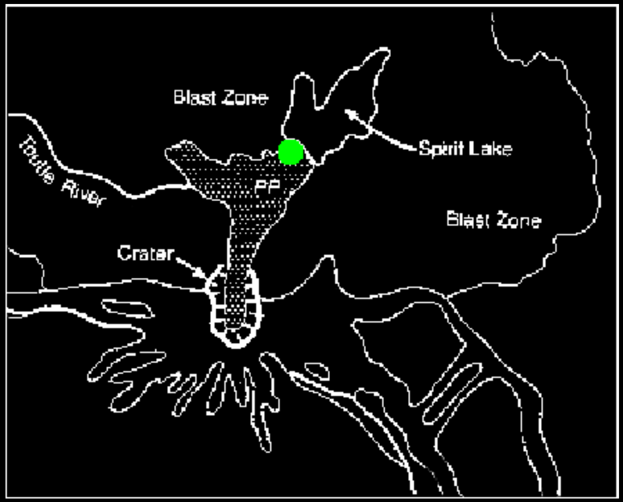
- $n = n(x,t)$ is the population density
- $D = D(x)$ is the spatially dependent, periodic diffusion coefficient
- $r_0 = r_0(x)$ is the spatially dependent, periodic intrinsic growth rate

- 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?

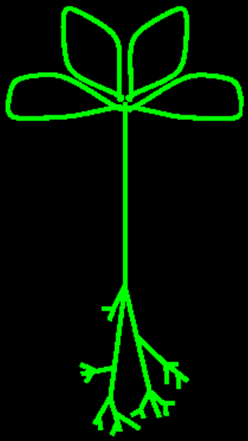
Mount St. Helens



- Mt. St. Helens erupted on May 18, 1980
- North of the crater, the *Pumice Plain* is a patchy environment, approximately 25 km^2, 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

[del Moral and Wood - 1987, 1993, 1995, Bishop]

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

- τ is the generation count
- $N_\tau(x)$ is the seed density at the start of generation τ
- f is the nonlinear growth function
- $k(x, y)$ is the dispersal kernel

IDE Models

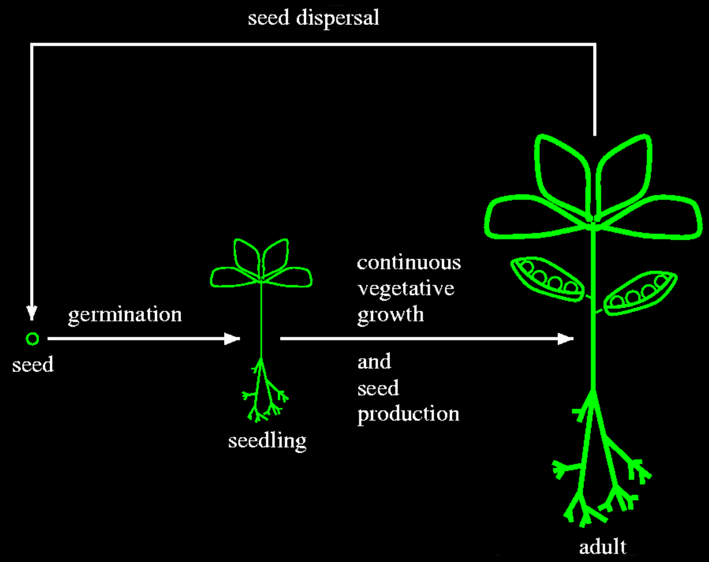
- Kot *et al.* - 1996:
  Spread of *D. pseudoobscura*, estimating the kernel from data

- 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



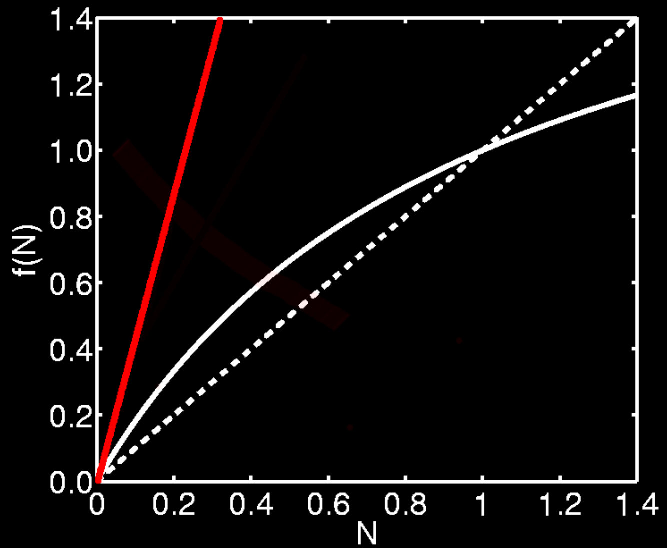
$$N_{\tau+\frac{1}{2}}(x) = f(N_\tau(x); x)$$

- $N_\tau(x)$ is the seed density at the start of generation τ,
  $N_{\tau+\frac{1}{2}}(x)$ is the seed density at the end of generation τ, 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

Growth Function: Example

- Example for a homogeneous environment: Beverton-Holt stock-recruitment curve

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



$r_0 = 2$

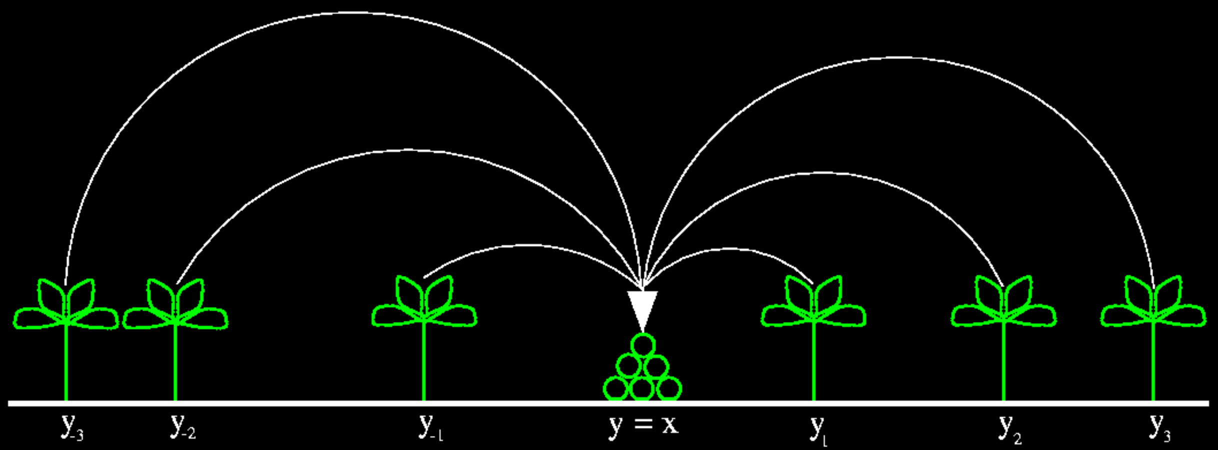
Dispersal Kernel

- $k(x, y)$ 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:

(1) $$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} - au$$

(2) $$\frac{\partial v}{\partial t} = au$$

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

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

  - 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 ∞:

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

- Integrate (1) from $t = 0$ to ∞:

$$\begin{aligned} \int_0^\infty \frac{\partial c}{\partial t} dt &= c(x,t;y)\Big|_{t=0}^{\infty} \\ &= -\delta(x-y) \\ &= D \int_0^\infty \left\{ \frac{\partial^2 c}{\partial x^2} \right\} dt - a \int_0^\infty c dt \\ &= D \frac{\partial^2}{\partial x^2} \left\{ \int_0^\infty c dt \right\} - a \int_0^\infty c dt \end{aligned}$$

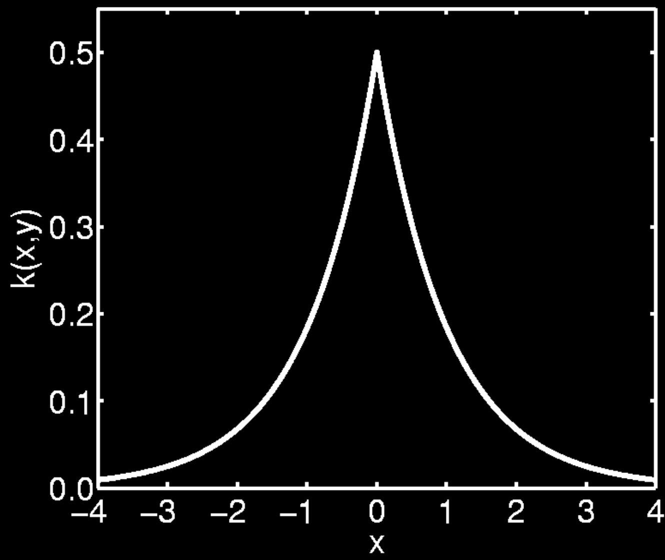
Laplace Dispersal Kernel

- 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

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



[Broadbent and Kendall - 1953, Neubert *et al.* - 1995]

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

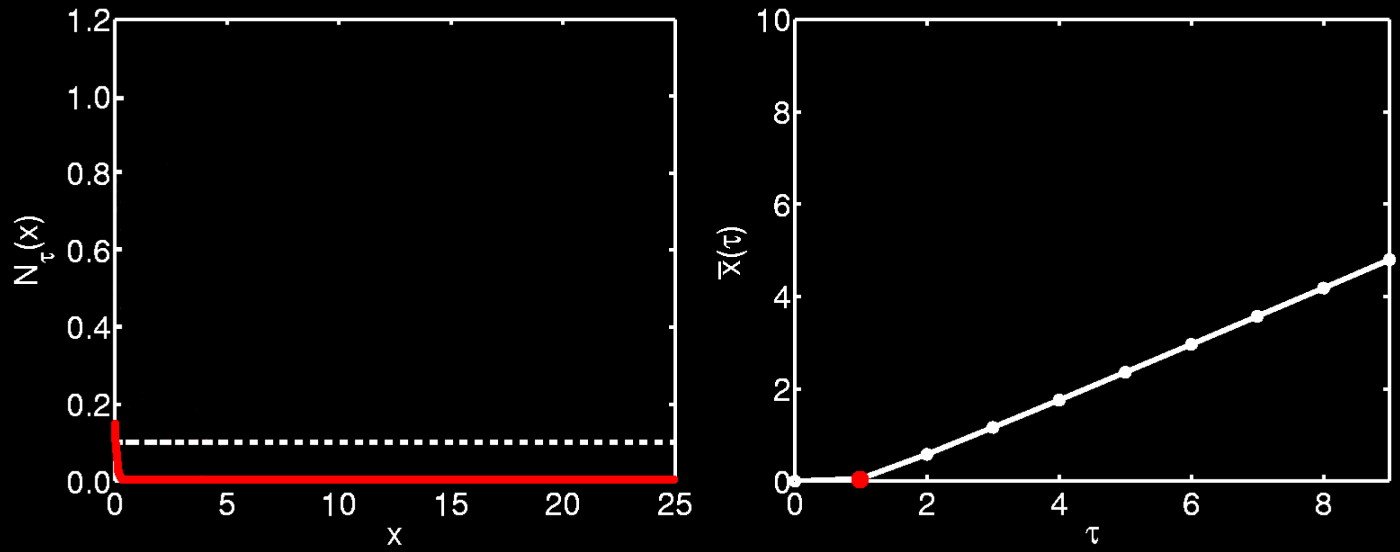
$$N_{\tau+1}(x) = \int_{-\infty}^{+\infty} f(N_\tau(y))k(x - y)dy$$

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:



$r_0 = 6$, $D = 1$ and $a = 10$

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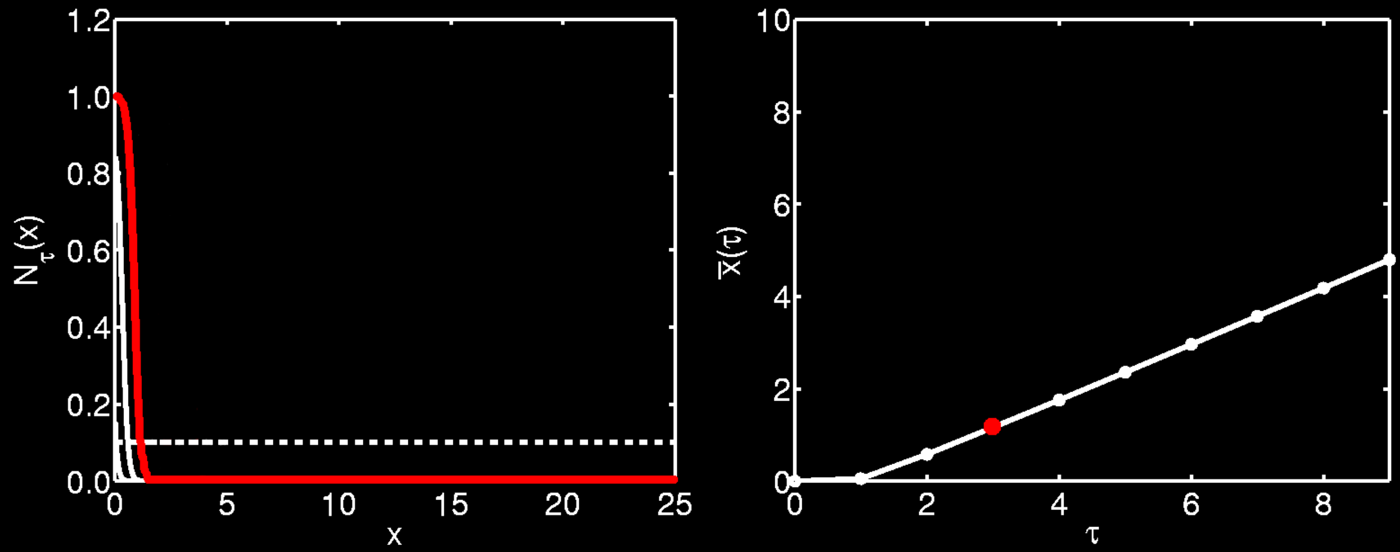

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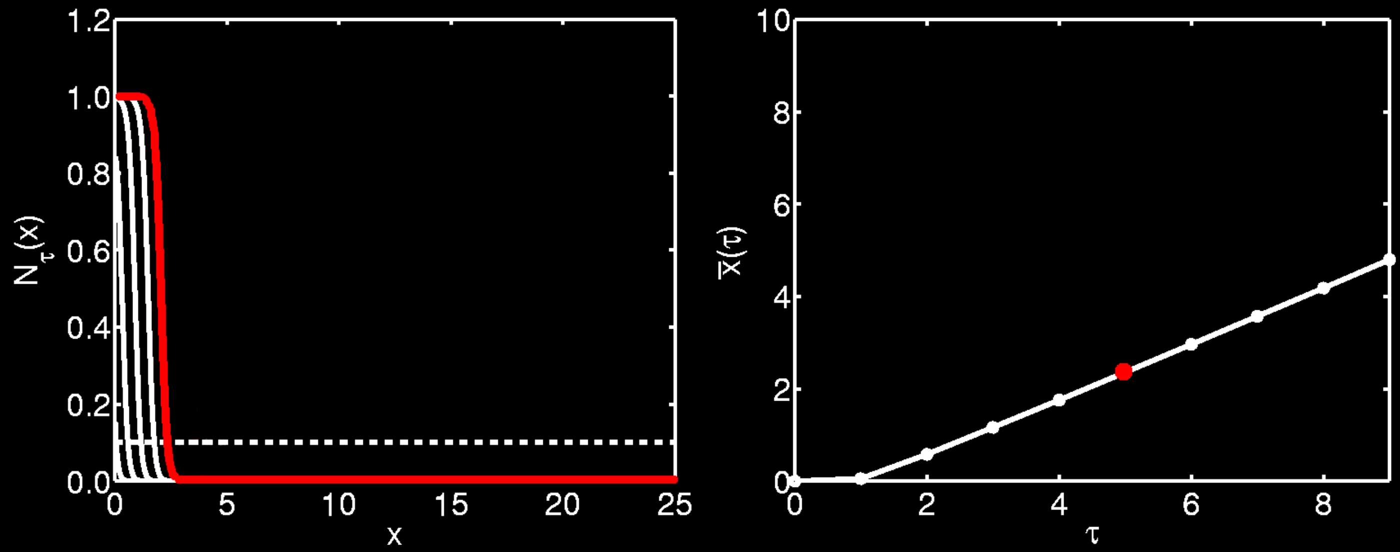

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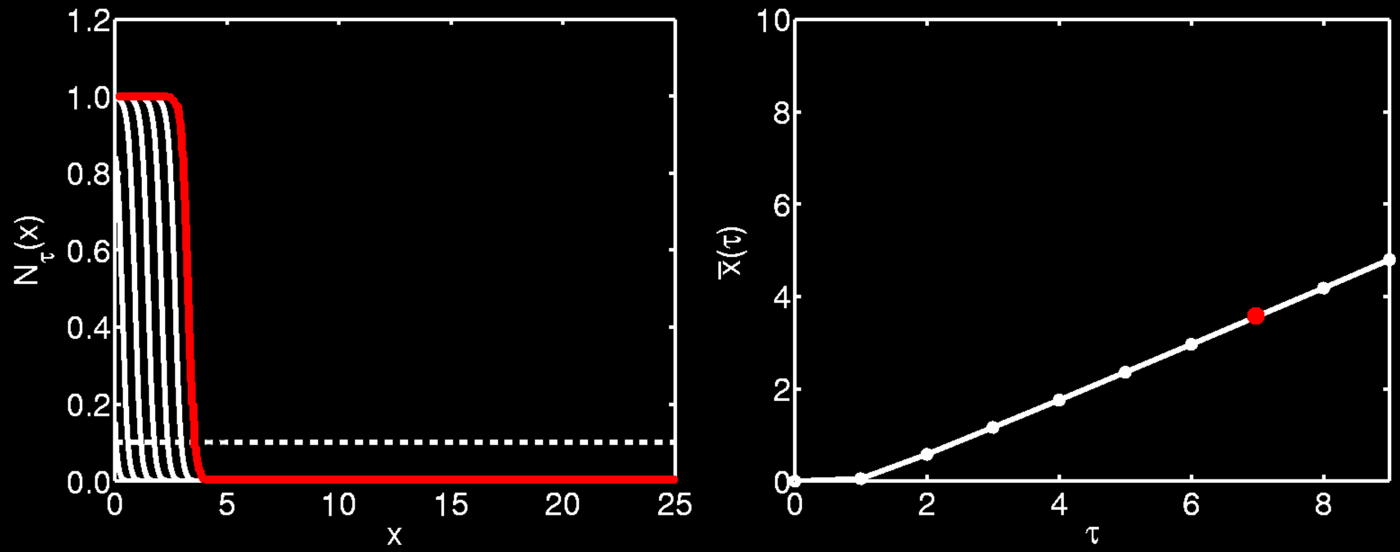

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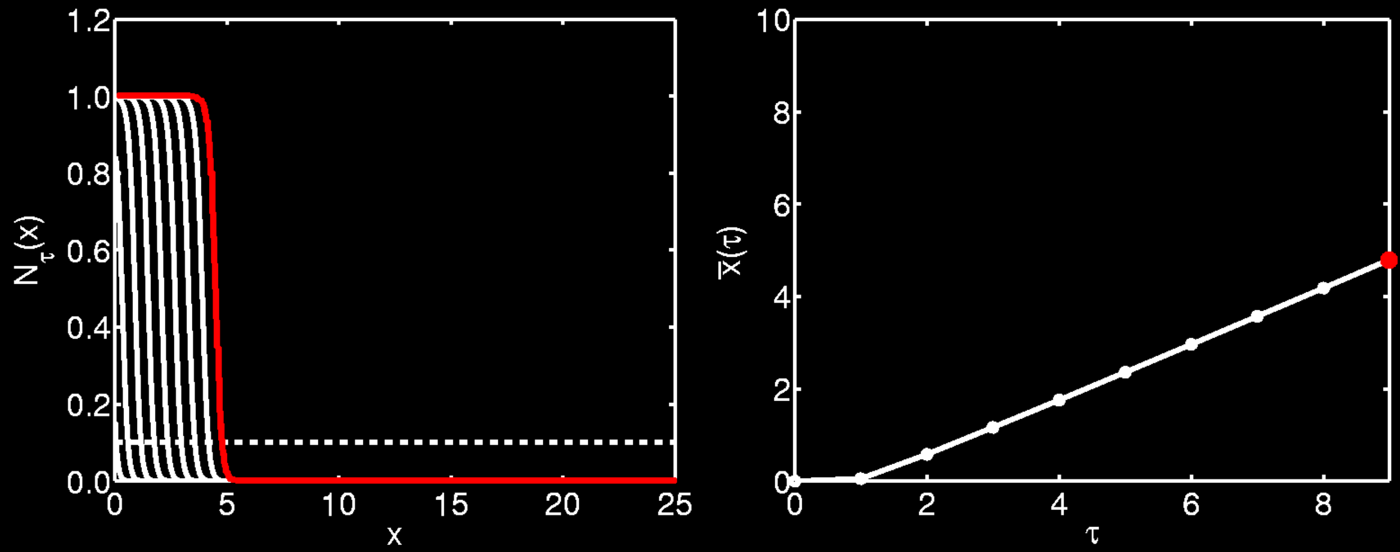


$r_0 = 6$, $D = 1$ and $a = 10$

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

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

[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]

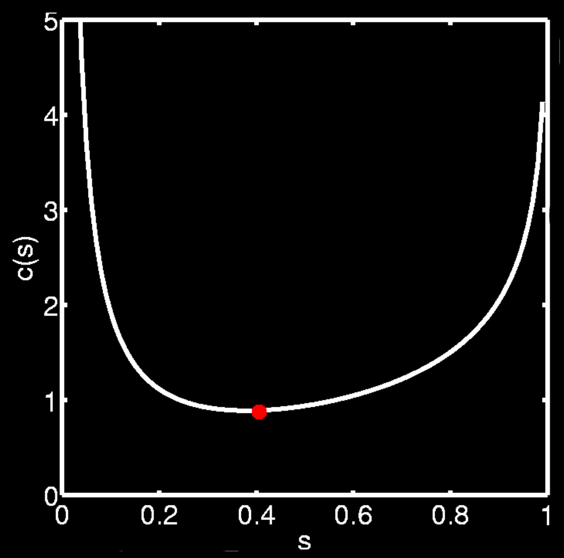
Dispersion Relation: Laplace Kernel

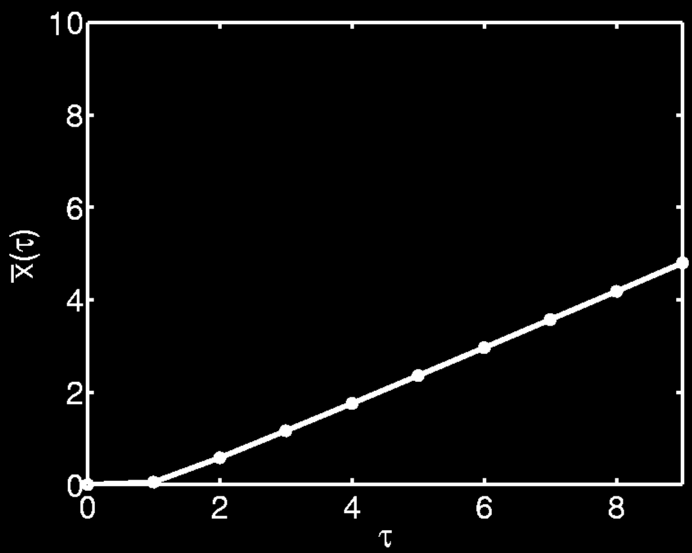
- The moment generating function:

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

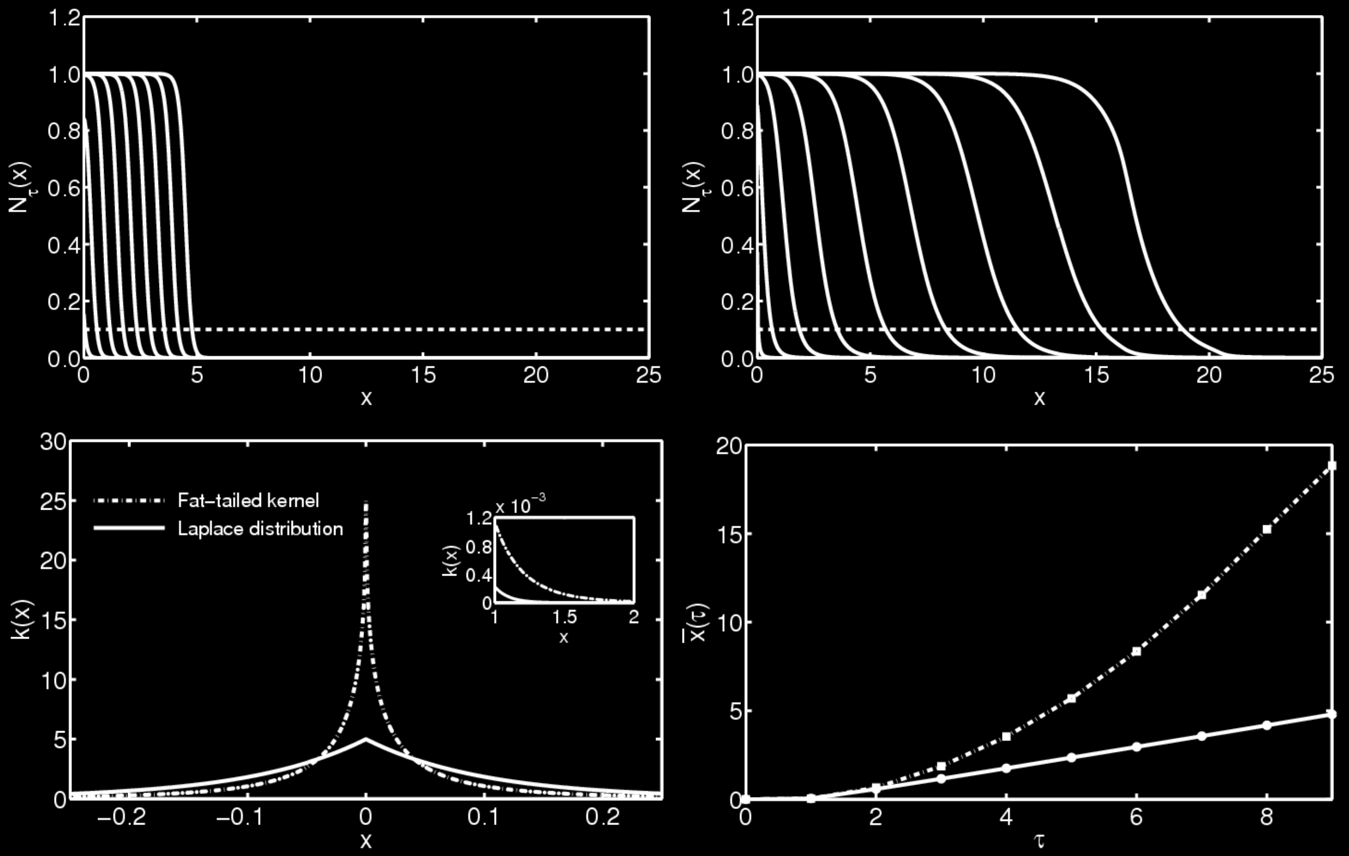
- For the Laplace dispersal kernel, the dispersion relation is:

$$c(s) = \frac{1}{s}\ln\left\{r_0\frac{a}{D}\left[\frac{1}{a/D - s^2}\right]\right\}$$





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.,

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

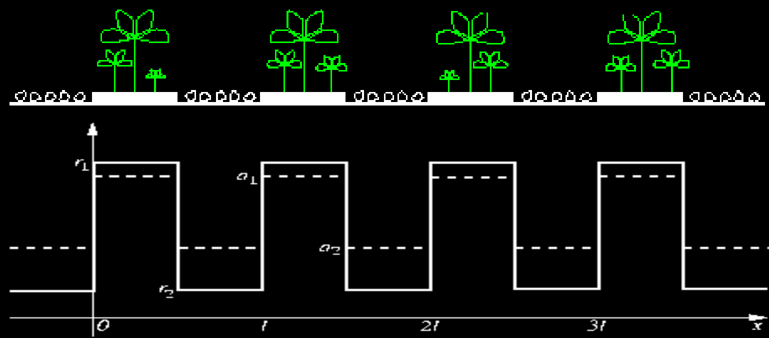
- The dispersal model:

$$\begin{aligned} \frac{\partial c}{\partial t} &= D\frac{\partial^2 c}{\partial x^2} - a(x)c \\ \frac{\partial d}{\partial t} &= a(x)c \\ c(x,0;y) &= \delta(x-y) \\ d(x,0;y) &= 0 \end{aligned}$$

- The IDE model is of the form

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

Periodic Heterogeneity



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

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

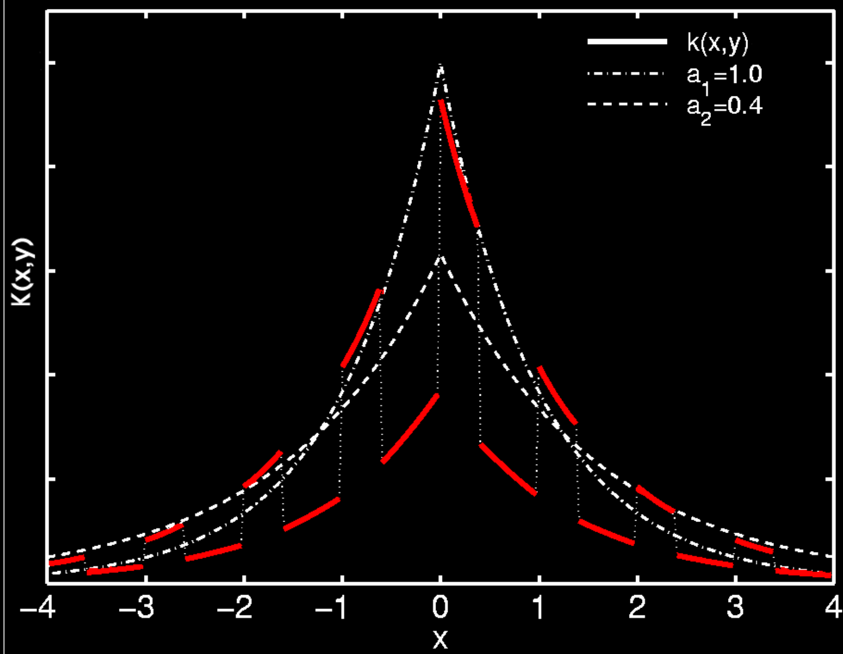
- Divide the environment into *high* ($a = 1$) and *low* ($a < 1$) deposition patches:

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

[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

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

$$N^* = \mathcal{A} N^*,$$

i.e., for all $\xi_0(x)$ such that $\|\xi_0\| < \epsilon$, does $\|\mathcal{A}^\tau \xi_0\| \to 0$?

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- This is equivalent to studying the spectrum of the linearization of $\mathcal{A}$ 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 λ_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:

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

where $\mu_1 = 1/\lambda_1$

[Van Kirk and Lewis - 1997]

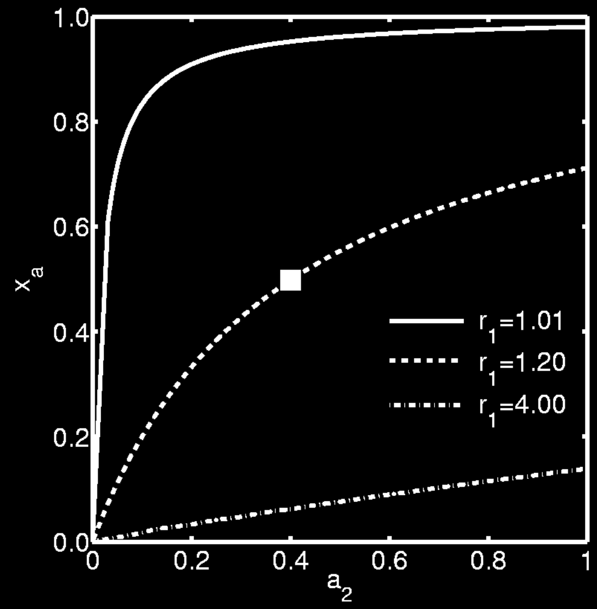
Colony Persistence

The resulting condition for $\lambda_1 = 1$ is:

$$
\begin{aligned}
0 &= F(a_2, r_1, r_2, x_a, l) \\
&:= 1 - \cos\left(x_a \sqrt{[r_1 - 1]}\right) \times \\
&\qquad \cos\left((l - x_a)\sqrt{a_2\,[r_2 - 1]}\right) \\
&\quad + \frac{[r_1 - 1] + a_2\,[r_2 - 1]}{2\sqrt{[r_1 - 1]}\sqrt{a_2\,[r_2 - 1]}} \times \\
&\qquad \sin\left(x_a \sqrt{[r_1 - 1]}\right) \times \\
&\qquad \sin\left((l - x_a)\sqrt{a_2\,[r_2 - 1]}\right)
\end{aligned}
$$

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)

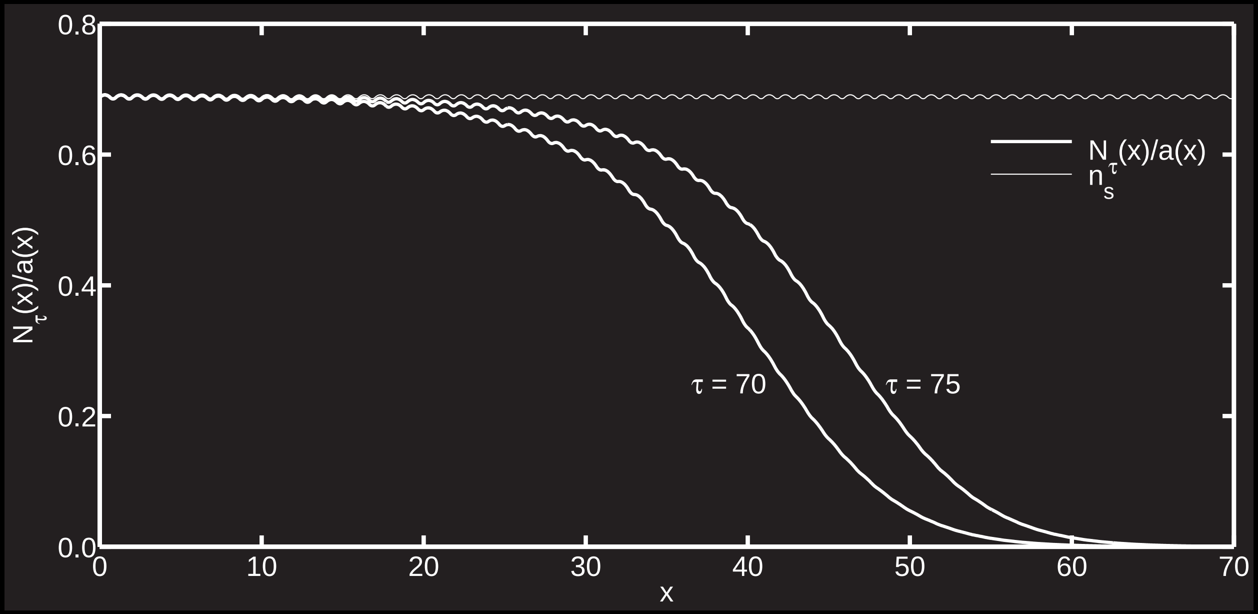


$$a_1 = 1,\, l = 1,\, r_2 = 0.5$$

- Stable region is below the curve

Traveling Periodic Wave

- $N_0(x)$ has compact support
- $N^* \equiv 0$ is unstable
- $N_\tau(x)/a(x)$ for τ 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

$$\hat{N}(x) \ll 1$$

Traveling Periodic Wave

- 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

$$e^{sc}\left(e^{-sx} g(x)\right) = \int_{-\infty}^{+\infty} r_0(y) e^{-sy} g(y) k(x,y) dy$$

- Apply the linear operator $\mathcal{L}$
- Hill's equation:

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

where $\varphi(x) = e^{-sx} g(x)/a(x)$

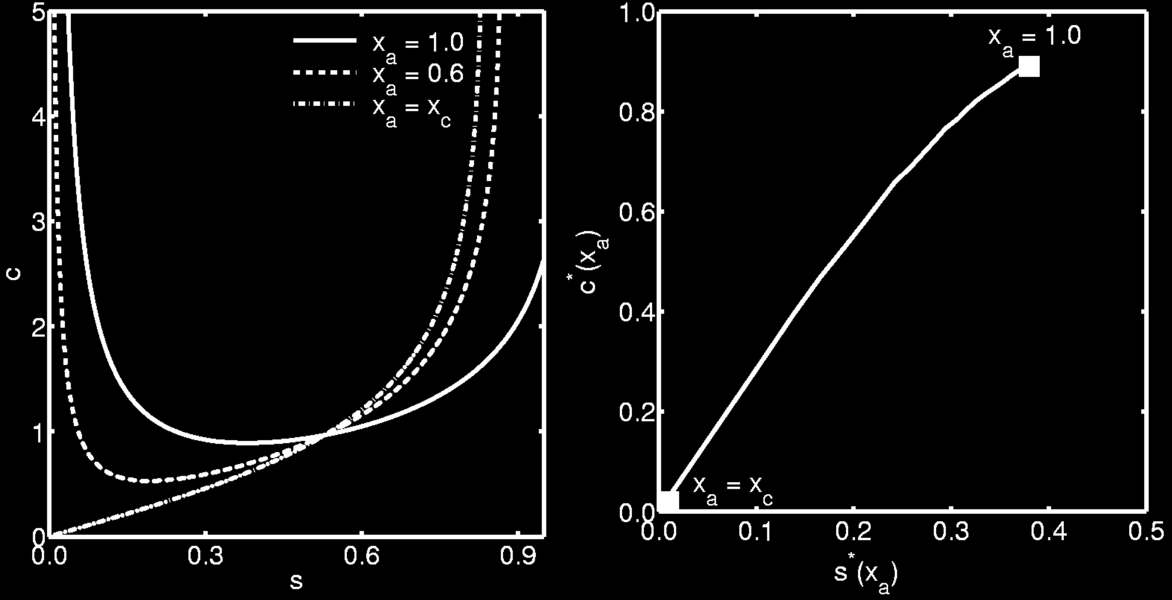
Dispersion Relation for the TPW

Assume a traveling periodic wave and derive the dispersion relation:

$$
\begin{aligned}
0 &= G(s, c\,; a_2, r_1, r_2, x_a, l) \\
&:= \cosh(sl) - \cos\left(x_a\sqrt{[r_1 e^{-sc} - 1]}\right) \times \\
&\qquad \cos\left((l - x_a)\sqrt{a_2\left[r_2 e^{-sc} - 1\right]}\right) \\
&\quad + \frac{[r_1 e^{-sc} - 1] + a_2\left[r_2 e^{-sc} - 1\right]}{2\sqrt{[r_1 e^{-sc} - 1]}\sqrt{a_2\left[r_2 e^{-sc} - 1\right]}} \times \\
&\qquad \sin\left(x_a\sqrt{[r_1 e^{-sc} - 1]}\right) \times \\
&\qquad \sin\left((l - x_a)\sqrt{a_2\left[r_2 e^{-sc} - 1\right]}\right)
\end{aligned}
$$

Dispersion Relation: Example

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



$$a_2 = 0.4,\ r_1 = 1.2,\ r_2 = 0.5,\ l = 1$$

Multiple Dispersal Scale Model

- The dispersal model:

$$\begin{aligned} \frac{\partial u_1}{\partial t} &= D_\eta \frac{\partial^2 u_1}{\partial x^2} - a(x)u_1 & \frac{\partial u_2}{\partial t} &= D \frac{\partial^2 u_2}{\partial x^2} - a(x)u_2 \\ \frac{\partial v_1}{\partial t} &= a(x)u_1 & \frac{\partial v_2}{\partial t} &= a(x)u_2 \\ u_1(x,0;y) &= \delta(x-y) & u_2(x,0;y) &= \delta(x-y) \\ v_1(x,0;y) &= 0 & v_2(x,0;y) &= 0 \end{aligned}$$

- $D_\eta \ll D$

- Define the dispersal ratio

$$w(x) = \begin{cases} w_1 & \text{if } 0 \le x < x_a \\ w_2 & \text{if } x_a \le x < l\,; \qquad w(x+l) = w(x) \end{cases}$$

- 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

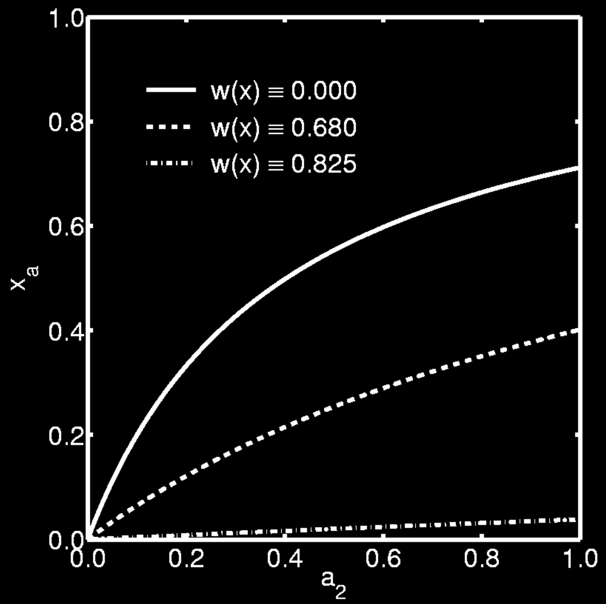
- The IDE model is

$$
\begin{aligned}
N_{\tau+1}(x) &= \int_{-\infty}^{+\infty} f(N_\tau(y);y)k_1(x,y;D_\epsilon)dy \\
&+ \int_{-\infty}^{+\infty} f(N_\tau(y);y)k_2(x,y;D)dy
\end{aligned}
$$

- 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)

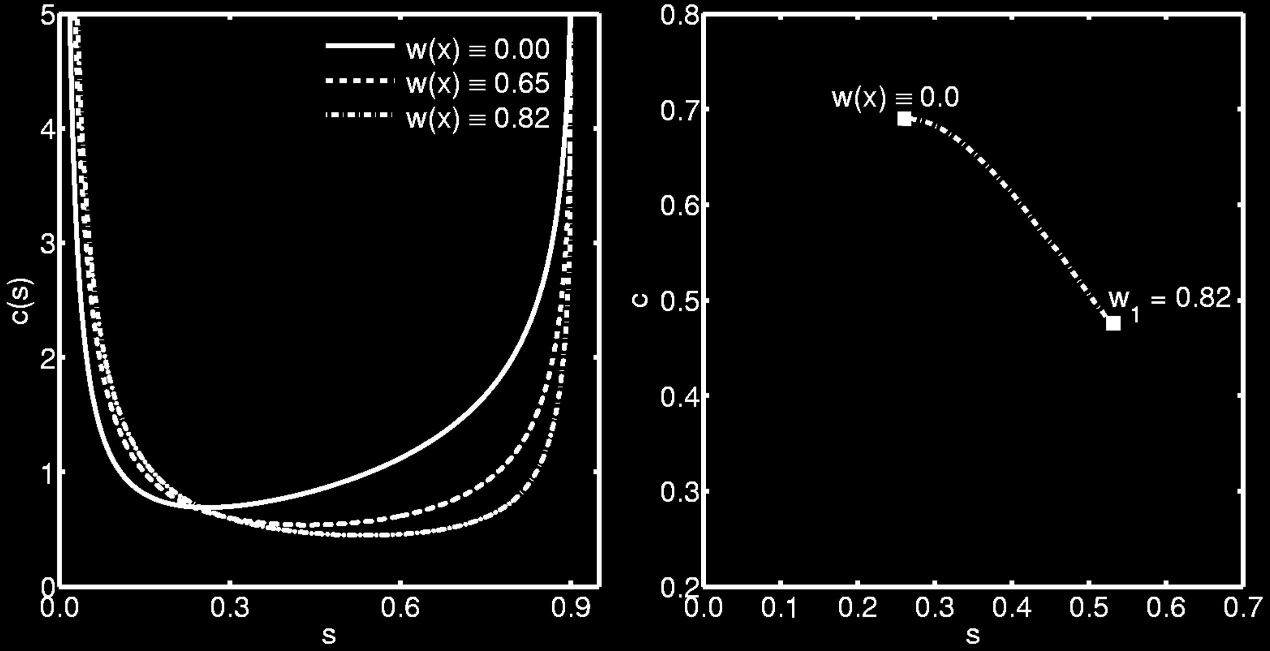


$$a_1 = 1.0,\ r_1 = 1.2,\ r_2 = 0.5,\ l = 1$$

- 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:



$$a_2 = 0.4,\ r_1 = 1.2,\ r_2 = 0.5,\ w_2 = 0,\ l = 1$$

- 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