How Individual Dispersal in Patchy Landscapes Affects Population Spread

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Patchy Landscapes

- Anthropogenic disturbances lead to fragmented landscapes
- Recent work has suggested that population dynamics in heterogeneous habitats depends on the interplay between fragmentation and dispersal ability
- Major challenges: What are the possible mechanisms for individual movement behavior at an interface? How do these mechanisms affect population spread rates?

Invasive Forest Insects

- Invasive forest insects are a class of non-native species that have the ability to easily establish and spread rapidly
- Examples include the brown spruce longhorn beetle, asian longhorn beetle and emerald ash borer (EAB)
- EAB was first found near Detroit in 2002
- EAB has spread to sixteen other states, as well as, parts of Ontario and Quebec
- Invasions have severe economic impact - removal costs and treatment of infested trees are estimated to be between $20 and $60 billion
- EAB has two dispersal vectors: local dispersal (flying) and non-local anthropogenic dispersal

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We aim to study how local dispersal behaviour influences population spread

EAB Life Cycle

Integrodifference Equations

Integrodifference equations are discrete-time, continuous space equations

$N_t(x)$: Density of individuals in generation t

$$N_t \xrightarrow{\text{dynamics}} f(N_t) \xrightarrow{\text{dispersal}} N_{t+1}$$

$$N_{t+1}(x) = \int_{\Omega} k(x,y) f(N_t(y); y)\, dy$$

$f(N; x)$: Growth function, $k(x,y)$: Dispersal kernel

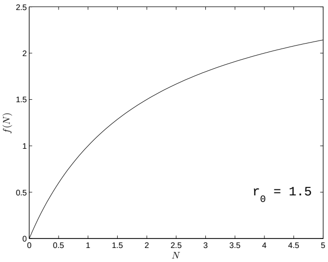
Ω : Landscape in which population resides

Discrete time, non-overlapping generations

$$N_{t+\tau} = f(N_t)$$

f is continuous, monotone increasing, and is bounded above

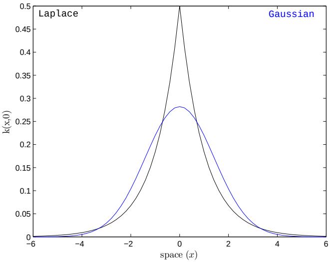
Beverton-Holt: $f(N) = \frac{r_0 N}{1+(r_0-1)N}$



Dispersal Kernel: Homogeneous Landscape

Probability of moving from y to x

$$k(x,y) = k(x-y) = k(z)$$



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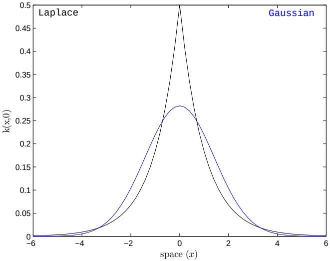


Dispersal kernels can be derived from mechanistic movement models in the form of diffusion equations (Neubert et al. 1995):

$$u_t = Du_{xx}, \qquad u(x,0;y) = \delta(x-y)$$

$$u_t = Du_{xx} - \alpha u, \qquad u(x,0;y) = \delta(x-y)$$

Spread in Homogeneous Landscapes

Minimal speed of spread (Weinberger, 1982)

$$c^* = \min_{s>0} \frac{1}{s} \ln(RM(s))$$

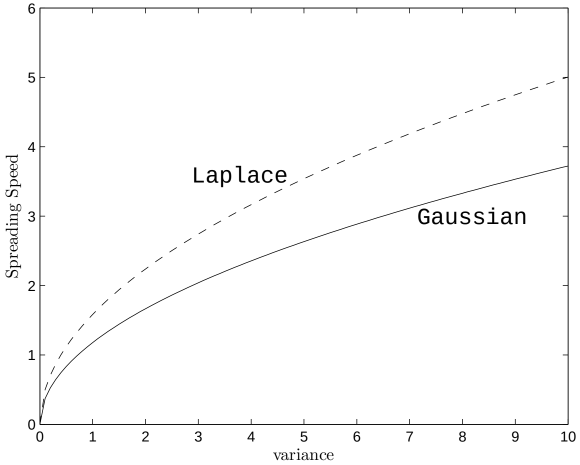
asymptotic speed of spread if initial population has compact support

f is linearly bounded, $R = f'(0)$

Moment generating function, $M(s) = \int k(x)e^{sx}\, dx$

For Gaussian kernel: $c_G = \sqrt{2\sigma^2 \ln(R)}$

Spread in Homogeneous Landscapes



IDEs in Patchy Landscapes

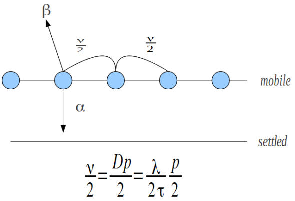
- Kawasaki and Shigesada used a Laplace kernel for a fragmented landscape; they assumed the growth function to be spatially dependent.
- Dewhirst and Lutscher included heterogeneity by allowing the variance of the kernel to depend on initial location.
- More mechanistically, VanKirk and Lewis derived kernels on a single patch with a semi-permeable boundary from a random walk model.
- Powell and Zimmerman considered a random walk model with patch dependent diffusion and settling, and used homogenization methods to derive approximate spread rates
- Robbins used almost the same model, but analyzed exact persistence conditions and spread rates

Outline

- Individual dispersal model
- Dispersal kernel
- Patchy landscapes
- Population spread

Dispersal Model

Individuals are dispersing in an infinite, one-dimensional landscape



- λ is the step size, p is the movement probability, τ is the time step
- β is the probability of dying
- α is the probability of settling
- ν is the motility coefficient

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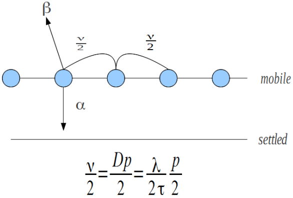

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$u(x, t; y)$: probability density of finding an individual located at any location x at any time t given an initial location y

$$\frac{\partial u}{\partial t} = \frac{\partial^2}{\partial x^2}(\nu(x)u) - (\alpha(x) + \beta(x))u$$
$$u(x, 0; y) = \delta(x - y)$$

Dispersal Kernel

- $k(x, y)$: probability density that a successful disperser settles at location x at the end of the dispersal period given an initial location y
- $\alpha(x)u(x, t; y)$ is the instantaneous rate an individual is settling at some time t

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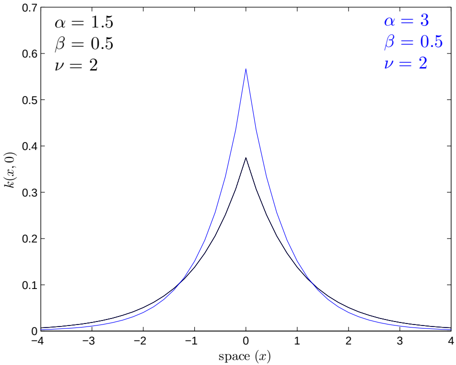
$k(x, y)$ is the Green's function of a second-order, linear differential operator

$$-\delta(x - y) = \frac{\partial^2}{\partial x^2}\left(\frac{\nu(x)}{\alpha(x)}k(x, y)\right) - \frac{\alpha(x) + \beta(x)}{\alpha(x)}k(x, y)$$

Homogeneous Landscape

The dispersal kernel is given by

$$k(x,0) := k(x) = \frac{\alpha}{2\sqrt{\nu(\alpha+\beta)}} \exp\left(-\sqrt{\frac{\alpha+\beta}{\nu}}|x| \right)$$



Patchy Habitats

- Landscape ecologists typically study populations on patchy or fragmented landscapes
- Patches are classified according to local population growth: good (source) and bad (sink)
- Parameter functions are piecewise constant
- At the boundary of a good and bad patch, we require interface conditions

Behaviour at an Interface

- Movement decisions at the interface may be different than movement rules within a particular patch

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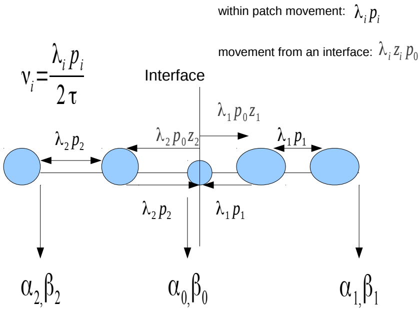

Interface Conditions

- If movement decisions at an interface are the same as movement decisions within a patch (Nagylaki, 1976):

$$u(x,0^-) = u(x,0^+), \qquad u_x(x,0^-) = \frac{\nu_1}{\nu_2} u_x(x,0^+)$$

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Different Movement Probabilities (p_i):

$$u(x,0^-) = \frac{(1-z)\nu_1}{(1+z)\nu_2} u(x,0^+), \quad u_x(x,0^-) = \frac{\nu_1}{\nu_2} u_x(x,0^+)$$

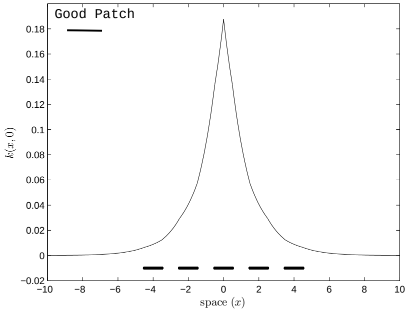
$z_1 = \frac{1-z}{2}$, $z_2 = \frac{1+z}{2}$

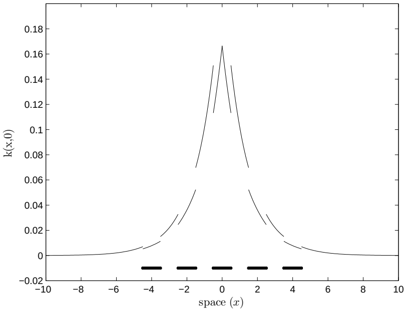
Different Step Sizes (λ_i):

$$u(x,0^-) = \frac{(1-z)\sqrt{\nu_1}}{(1+z)\sqrt{\nu_2}} u(x,0^+), \quad u_x(x,0^-) = \frac{\nu_1}{\nu_2} u_x(x,0^+)$$

Dispersal Kernel in a Patchy Landscape

- For illustrative purposes, we consider a patchy landscape with five good patches
- $\nu_1 = 2$, $\nu_2 = 1.5$

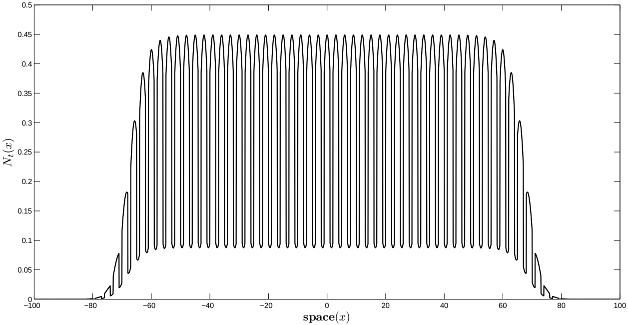




Traveling Periodic Waves and the Spreading Speed

- Assuming that a population persists, perhaps the most important quantity to consider is the spread rate of the population and its dependence on parameters
- We analyze an IDE on an l-periodic landscape consisting of good patches (source) of length l_1 and bad patches (sink) of length l_2
- Model parameters are assumed to be l-periodic, piecewise constant and $f(\cdot; x) = f(\cdot; x + l)$
- Source: Beverton-Holt growth, i.e. $f(N) = \frac{r_0 N}{1+(r_0-1)N}$
- Sink: $f(N) = r_0 N$, $0 \leq r_0 < 1$

Traveling Periodic Waves: Numerical Example



- $\nu_1 = 1$, $\nu_2 = 2$, $\alpha_1 = 1$, $\alpha_2 = 0.5$, $\beta_1 = 0.3$, $\beta_2 = 1$

Traveling Waves and Spreading Speeds

- Recall, the IDE is given by

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

- Existence of a traveling periodic wave and corresponding spreading speed follows from Weinberger, 2002; look for solutions of the form $N_t(x) = N_t(x - c)$

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- Near the wave front, we make the traveling wave ansatz

$$N_t(x) = \exp(-s(x - ct))g(x)$$

where $g(x) = g(x + l)$, s is the shape parameter and c is the wave speed

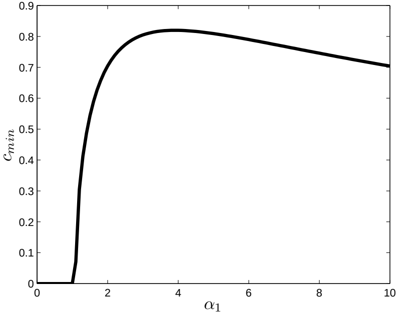
- Linearizing the IDE, substituting in the ansatz, and recalling properties of $k(x, y)$, one can derive the following ODE relating c and s

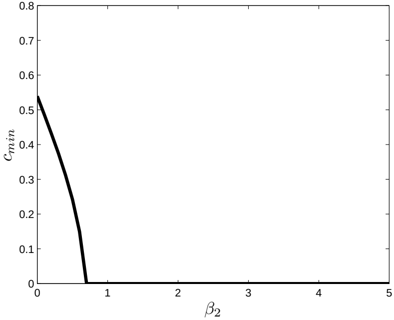
$$\Psi''(x) + m(x)\Psi(x)\left(\exp(-sc)\hat{r}(x) - 1 \right) = 0$$

where $\Psi(x) = \frac{\nu(x)}{\alpha(x)} g(x)\exp(-sx)$ and $m(x) = \frac{\alpha(x)+\beta(x)}{\nu(x)}$

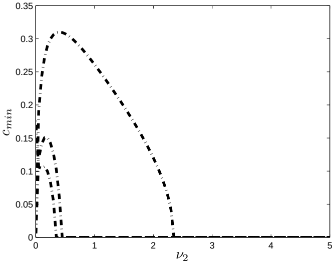
- From the ODE, we obtain a relation between the wave speed and the shape parameter of the wave. Minimizing this expression, we obtain the minimal wave speed.

Minimal Spreading Speed

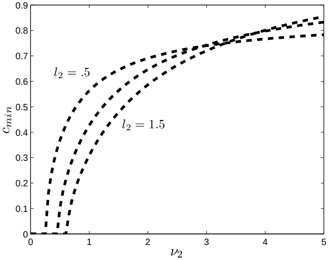


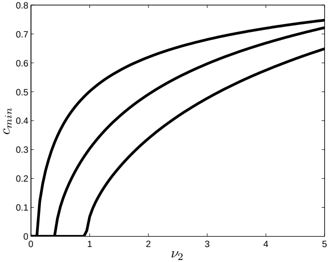


- If $\nu_1 = \nu_2$, qualitative behavior of obtained spreading speeds is the same



- **dashed-dot curve** - continuous density
  dashed curve - different movement probabilities
  solid curve - different step size





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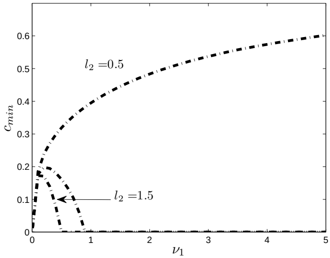

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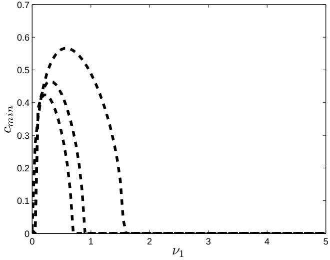

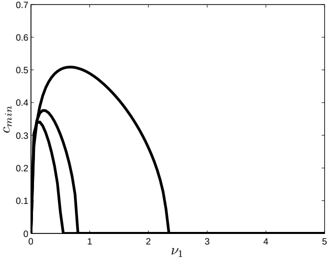

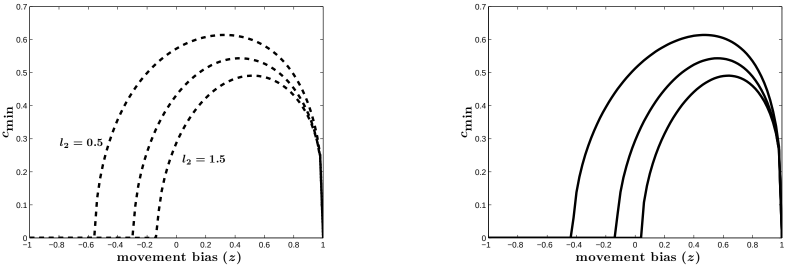

- $l_2 = 0.5, 1, 1.5$
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Discussion

- A useful characterization of the dispersal kernel is as the Green's function of a differential operator
- Explicit modelling of individual movement rules in patchy landscapes, in particular individual responses at an interface, may lead to discontinuous dispersal kernels
- Understanding individual movement behaviour at an interface is crucial when studying population spread (and persistence!)
- Recent studies on the Emerald Ash Borer have focused on studying understanding local dispersal behaviour of EAB in newly established populations - we hope to provide some insight here.

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Questions?