

PATCHY INVASION OF
ALIEN SPECIES IN
THE PRESENCE OF
LONG-DISTANCE DISPERSAL

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- Introduction
- Modelling patchy invasion with long-distance dispersal: integro-difference equations
- Computational issues related to modelling invasion with long-distance dispersal
- Conclusions

Introduction

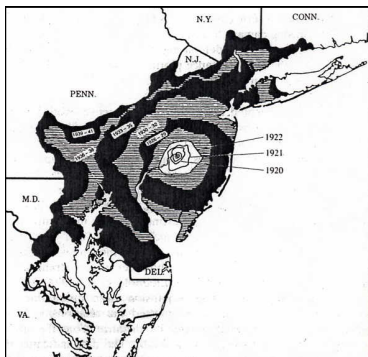
Why do we study biological invasion?

The term **biological invasion** refers to a variety of phenomena arising as a result of introduction and proliferation of alien (or 'exotic') species.

Consequences of alien species invasion:

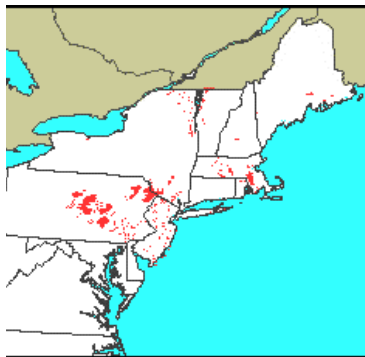
- The new species often appears to be a strong competitor or a very efficient predator to the native species, which may lead to extinction and severe **damage to biodiversity**
- The new species often becomes a dangerous pest and that can result in huge direct and indirect **economic losses**
Also
- The new species can be a vector for a certain disease.

Traveling front vs. patchy invasion



Invasion of Japanese beetle
(*Popillia japonica*)
in the United States

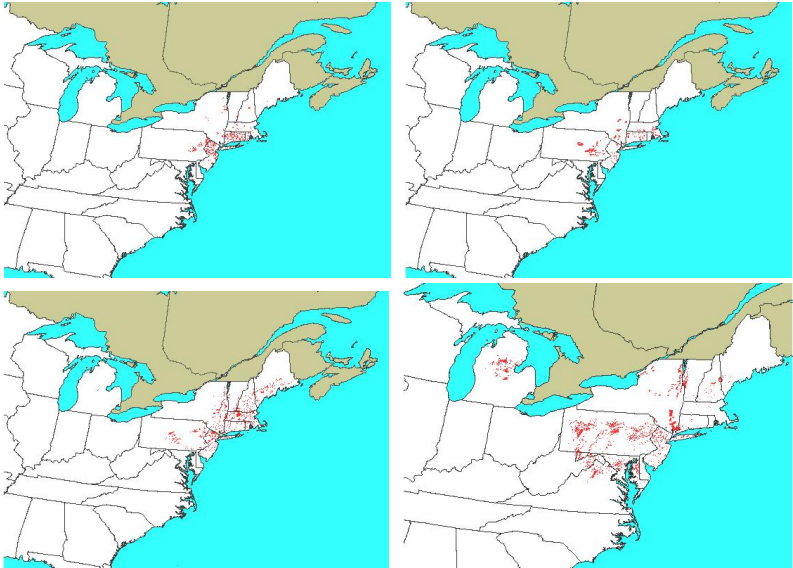
2-D traveling front



Invasion of Gypsy moth
(*Lymantria dispar*)
in the United States

Patchy invasion

Geographic spread of Gypsy moth



(by courtesy of Andrew Liebhold)

Modelling patchy invasion: diffusion-reaction system

A predator-prey system:

$$\frac{\partial U(\mathbf{R}, T)}{\partial T} = D_1 \nabla^2 U(\mathbf{R}, T) + f(U)U - r(U)V,$$

$$\frac{\partial V(\mathbf{R}, T)}{\partial T} = D_2 \nabla^2 V(\mathbf{R}, T) + \kappa r(U)V - MV,$$

where U and V are the densities of prey and predator, respectively, at position $\mathbf{R} = (X, Y)$ and time T ,

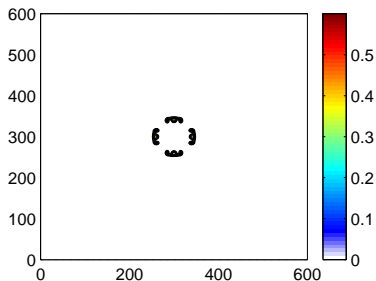
$f(U) = \alpha(U - U_0)(K - U)$, α is the maximum growth rate, K is the carrying capacity, U_0 is the Allee threshold,

$r(U) = \eta \frac{U}{H + U}$, η is the predation rate, H is the half-saturation prey density, κ is the efficiency,

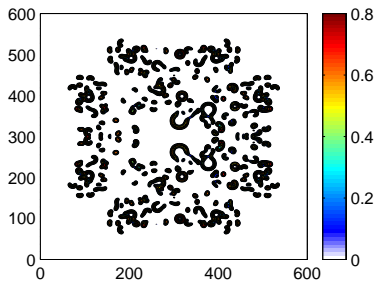
M is the mortality rate

S. Petrovskii, A. Morozov and E. Venturino. Allee effect makes possible patchy invasion in a predator-prey system. *Ecology Letters*, (2002) 5:345–352.

Simulation of patchy invasion: example

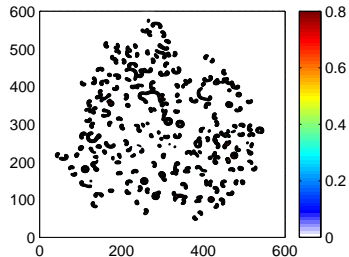
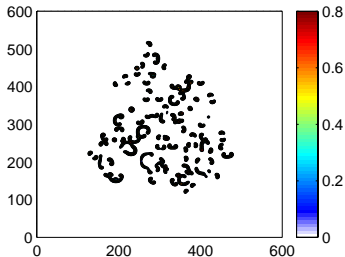
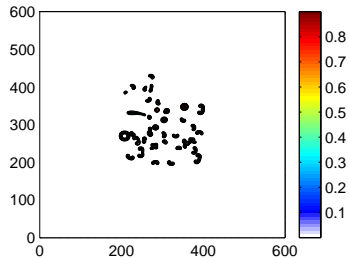
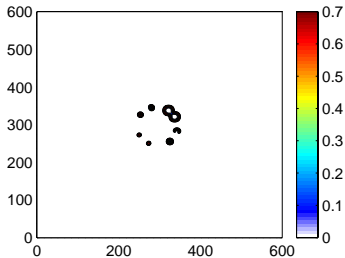


$t = 100$



$t = 1000$

Simulation of patchy invasion: example



Long-distance dispersal (LDD)

- Long-distance dispersal is not a well-studied phenomenon.
- There is the conceptual complexity in defining LDD.
- If sufficient biological information is available, the frequency distribution of dispersal distances may be obtainable from either direct measurements or indirect estimates.
- The LDD may be defined on the base of a certain threshold of absolute dispersal distance that is much longer than the median dispersal distance.

Long-distance dispersal (LDD) is important!

- "Invading organisms may spread through **local movements** (giving rise to a diffusion-like process) and by **long-distance jumps...**"

A. V. Suarez, D.A. Holway, T.J. Case. Patterns of spread in biological invasions dominated by long-distance jump dispersal: Insights from Argentine ants. *Proc Natl Acad Sci USA*. (2001) 98(3): 1095–1100.

- "The main threats to global biodiversity involve **excessive LDD of elements alien to ecosystems** and insufficient dispersal of native species..."

A. Trakhtenbrot, R. Nathan, G. Perry, D.M. Richardson. The importance of long-distance dispersal in biodiversity conservation. *Divers. Distrib.* (2005) 11: 173–181.

- "The relative importance of **diffusion** (expanding front) vs. **long-distance dispersal** can inform management of invasive species..."

M.E. Moody, R.N. Mack. Controlling the spread of plant invasions: the importance of nascent foci. (1988) *J Appl Ecol* 25:1009–1021

How does LDD contribute to patchy invasion?

- Patchy invasion is observed in the diffusion-reaction model(s).
- Effect of long-distance dispersal?
- Long-distance dispersal is important yet diffusion approximation neglects it.
- The need for an alternative framework where long-distance dispersal can be modelled.

L.A.D. Rodrigues, D.C.Mistro, E.R.Cara, N.B.Petrovskaya, S.V.Petrovskii. Patchy Invasion of Stage-Structured Alien Species with Short-Distance and Long-Distance Dispersal. Bull Math Biol (2015) 77:1583–1619

Modelling patchy invasion
with long-distance dispersal:
integro-difference equations

The IDE-based framework

We consider a system of integro-difference equations:

$$u_{t+1}(\mathbf{r}) = \int_{\Omega} k^{(u)}(|\mathbf{r} - \mathbf{r}'|) f(u_t(\mathbf{r}'), v_t(\mathbf{r}')) d\mathbf{r}',$$

$$v_{t+1}(\mathbf{r}) = \int_{\Omega} k^{(v)}(|\mathbf{r} - \mathbf{r}'|) g(u_t(\mathbf{r}'), v_t(\mathbf{r}')) d\mathbf{r}',$$

- The dispersal kernel $k(|\mathbf{r} - \mathbf{r}'|)$ gives the probability density of the event that an individual located at the position \mathbf{r}' before the dispersal will be found at the position \mathbf{r} after the dispersal.
- Hence long-distance dispersal can be modelled.

The IDE-based framework

We assume that both species have a similar life cycle so that they interact during their maturation stage:

$$\tilde{u}_t(\mathbf{r}) = f(u_t(\mathbf{r}), v_t(\mathbf{r})), \quad \tilde{v}_t(\mathbf{r}) = g(u_t(\mathbf{r}), v_t(\mathbf{r})),$$

where $\tilde{u}_t(\mathbf{r})$ and $\tilde{v}_t(\mathbf{r})$ are the population densities prior the dispersal stage,

$$f(u, v) = \frac{a(u(\mathbf{r}))^2}{1 + b(u(\mathbf{r}))^2} \cdot \exp(-v(\mathbf{r})),$$

$$g(u, v) = u(\mathbf{r})v(\mathbf{r}),$$

$a = A/\delta$, $b = (B/\delta)^2$, A is the prey intrinsic growth rate, $1/B$ is the prey density for which its per capita growth rate reaches its maximum, and δ is the predator growth rate.

Dispersal kernel: the 'reference case'

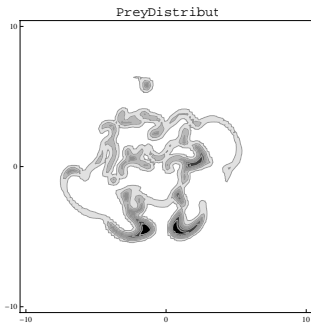
- The Gaussian kernel

$$k_G(|\mathbf{r} - \mathbf{r}'|) = \frac{1}{2\pi\alpha_j^2} \exp\left(-\frac{|\mathbf{r} - \mathbf{r}'|^2}{2\alpha_j^2}\right).$$

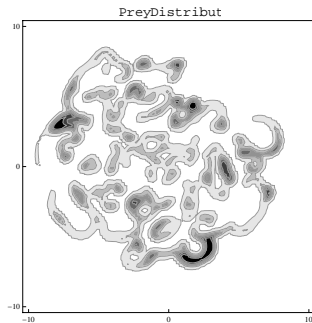
- The diffusion-reaction model:
the distances individuals move over a given length of time are drawn from a normal distribution.
- Hence dispersal with the Gaussian kernel is equivalent (in some sense) to diffusion.

Dispersal kernel: the 'reference case'

$$k_G(|\mathbf{r} - \mathbf{r}'|) = \frac{1}{2\pi\alpha_i^2} \exp\left(-\frac{|\mathbf{r} - \mathbf{r}'|^2}{2\alpha_i^2}\right).$$



t=140



t=200

Long-distance asymptotics for the Gaussian kernel:

$$k(x) \sim e^{-ax^2}.$$

Fat-tailed kernels – **power-law** decay:

$$k(x) \sim x^{-\mu} \quad (1 < \mu < 3)$$

The Cauchy distribution ($\mu = 2$):

$$k_C(x) = \frac{\beta}{\pi(\beta^2 + x^2)} \sim x^{-2}.$$

Fat-tailed kernels in 2 – D

Long-distance asymptotics: $k(\mathbf{r}) \sim r^{-(\mu+1)}$ ($1 < \mu < 3$)

Extension onto the 2 – D case is ambiguous.

Cauchy kernels Type I:

$$k_{C_I}(\mathbf{r}, \mathbf{r}') = \frac{\beta_i^2}{\pi(\beta_i + |\mathbf{r} - \mathbf{r}'|)^3} \sim |\mathbf{r} - \mathbf{r}'|^{-3},$$

Cauchy kernels Type II:

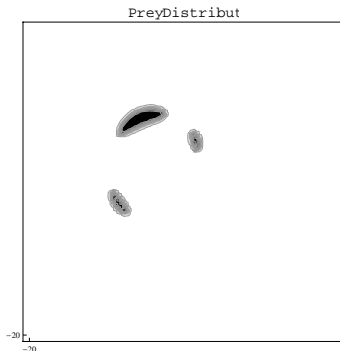
$$k_{C_{II}}(\mathbf{r}, \mathbf{r}') = \frac{\gamma_i}{2\pi(\gamma_i^2 + |\mathbf{r} - \mathbf{r}'|^2)^{3/2}} \sim |\mathbf{r} - \mathbf{r}'|^{-3}.$$

Questions arising:

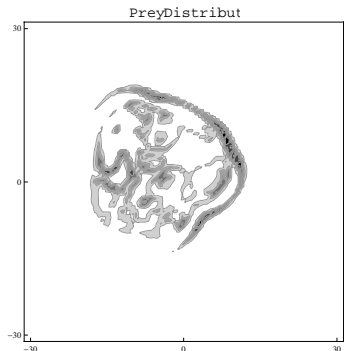
- Can patchy spread **occur** for the fat-tailed dispersal?
- How the **rate of spread** may differ between different kernels?

L.A.D. Rodrigues, D.C.Mistro, E.R.Cara, N.B.Petrovskaya, S.V.Petrovskii. Patchy Invasion of Stage-Structured Alien Species with Short-Distance and Long-Distance Dispersal. Bull Math Biol (2015) 77:1583–1619

Simulations, kernel Type I

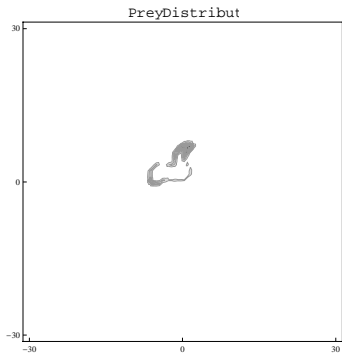


$t=100$

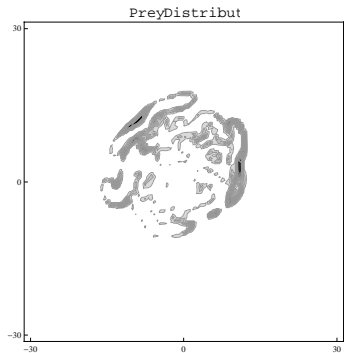


$t=190$

Simulations, kernel Type II



$t=80$



$t=200$

Computational issues related to modelling
invasion with long-distance dispersal

Computational issues arising in the problem are related to the fact that the kernel-based model is non-local.

Two issues to discuss:

- The choice of a numerical method: fast Fourier transform vs. numerical integration
- Numerical implementation of boundary conditions

Fast Fourier transform vs. numerical integration

$$u_{t+1}(\mathbf{r}) = \int_{\Omega} k^{(u)}(|\mathbf{r} - \mathbf{r}'|) f(u_t(\mathbf{r}'), v_t(\mathbf{r}')) d\mathbf{r}',$$

$$v_{t+1}(\mathbf{r}) = \int_{\Omega} k^{(v)}(|\mathbf{r} - \mathbf{r}'|) g(u_t(\mathbf{r}'), v_t(\mathbf{r}')) d\mathbf{r}',$$

Numerical integration:

- One time step on a grid of $K = 2^7$ nodes in each direction takes approximately 40 seconds.
(Intel(R)Core(TM)2Duo CPU T5870 @ 2.00GHz, 3.00GB of RAM)
- The number of operations is $O(K^4)$. Alternative numerical technique is required to compute the solution on finer grids ($K = 2^{12}$) at bigger times ($t \sim 200$).

Fourier transform

-

$$f * g = \int_{-\infty}^{+\infty} f(y)g(x-y)dy$$

- The convolution theorem

$$\widehat{f * g}(s) = \frac{1}{2\pi} \widehat{f}(s) \widehat{g}(s)$$

- The discrete Fourier transform (DFT) of the function $[f_k]$

$$F_s = \frac{1}{K} \sum_{k=0}^{K-1} f_k e^{2\pi iks/K}$$

- The inverse transform is

$$f_k = \sum_{s=0}^{K-1} F_s e^{-2\pi iks/K}$$

Fast Fourier transform vs. numerical integration

- Computing and inverting the DFT can be done efficiently with help of the fast Fourier transform (FFT) numerical algorithms.
- While the number of operations in a straightforward DFT computation is $O(K^2)$, an FFT algorithm reduces that number to $O(K \log_2 K)$.
- The FFT is superior to methods of numerical integration. (Numerical integration by a composite trapezoidal rule can be done in $O(K^2)$ operations.)

Implementation of boundary conditions

- The integro-difference equations do not necessarily require boundary conditions.
- The absence of boundary conditions corresponds to a specific biological situation:
at every time step a certain fraction of the population leaves the computational domain Ω because of the dispersal.
- Since the space outside of domain Ω is not taken into account in the model, it means that this fraction never comes back and hence is lost forever ('free outflow' boundary conditions)

Implementation of boundary conditions

- The free outflow boundary conditions are intrusive.
- They are likely to hamper the population growth inside the domain, or even bring it down to extinction altogether.
- The free outflow boundary conditions will result in the population dynamics with different properties (the boundary forcing).

Implementation of boundary conditions

- We assume that the population dynamics will not be sensitive to the choice of the boundary condition over the time when the spreading populations remain sufficiently far from the domain boundary.
- Hence we require that a computational domain is sufficiently large.
- This requirement was confirmed by results of our numerical experiments.

Implementation of boundary conditions

- We assume that the population dynamics will not be sensitive to the choice of the boundary condition over the time when the spreading populations remain sufficiently far from the domain boundary.
- Hence we require that a computational domain is sufficiently large.
- This requirement was confirmed by results of our numerical experiments.
- What is 'a sufficiently large' domain?

Modelling nonlocal boundary conditions

- The normally distributed symmetric kernel:

$$k(x, y) = \frac{1}{\sqrt{2\pi\alpha^2}} \exp\left(-\frac{(x-y)^2}{2\alpha^2}\right).$$

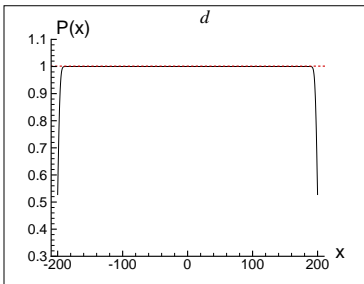
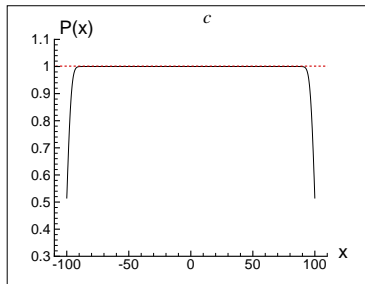
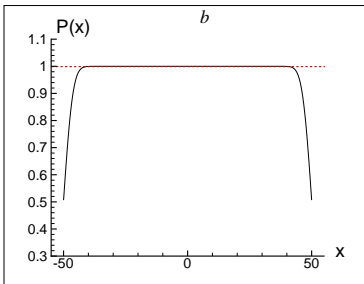
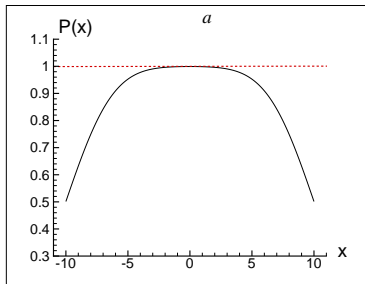
where $(x, y) \in \Omega$.

- The total probability is

$$P(x) = \int_{\Omega} k(x, y) dy \equiv 1.$$

- The boundary can only be regarded as non-intrusive when this condition holds at any point in the computational domain Ω .

Computation of the non-local kernel



Modelling nonlocal boundary conditions

We have to redefine the domain size in order to meet the condition $P(x) = 1$ at any point x of the new domain.

$$P = \int_{\Omega} k(y) dy = \int_{-L}^L k(y) dy = \frac{1}{2} \left[\operatorname{erf} \left(\frac{L-x}{\sqrt{2\alpha}} \right) + \operatorname{erf} \left(\frac{L+x}{\sqrt{2\alpha}} \right) \right],$$

where $\operatorname{erf}(x)$ is the error function with the following properties:

$\operatorname{erf}(-x) = -\operatorname{erf}(x)$, and $\operatorname{erf}(x)$ is a monotone function of x , and $\operatorname{erf}(x) \rightarrow 1$ as $x \rightarrow \infty$.

We require that

$$\operatorname{erf} \left(\frac{L-x}{\sqrt{2\alpha}} \right) = 1 \quad \text{and} \quad \operatorname{erf} \left(\frac{L+x}{\sqrt{2\alpha}} \right) = 1$$

with sufficient precision.

Modelling nonlocal boundary conditions

- Select tolerance x_τ : $\operatorname{erf}(x) \approx 1$ for $x \geq x_\tau$ (e.g. $\operatorname{erf}(3) = 0.99998$).
- Require that

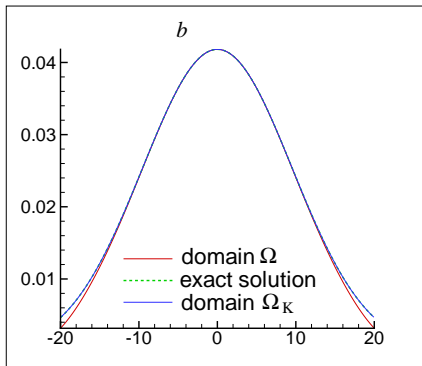
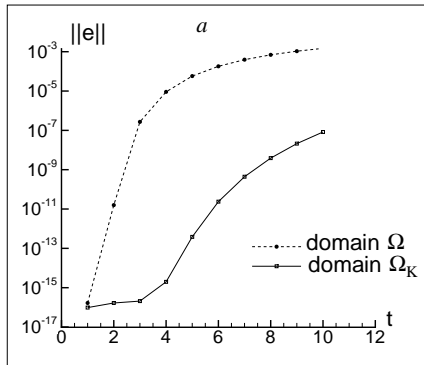
$$\frac{L-x}{\sqrt{2}\alpha} \geq x_\tau \quad \text{and} \quad \frac{L+x}{\sqrt{2}\alpha} \geq x_\tau$$

- Define Ω_K – the extended domain preserving the integral with sufficient accuracy in the original domain $\Omega = [-L, L]$.

$$\Omega_K = [-L - x_\tau\sqrt{2}\alpha, L + x_\tau\sqrt{2}\alpha].$$

Parameter α also gives us a rough estimate of the grid step size in the problem (the interval of the length α should contain at least one grid point)

Computation of the non-local kernel



Conclusions

- Interplay between the Allee effect and predation can turn continuous-front invasion into a patchy invasion. This appears to be a **generic property** of growth-dispersal systems (PDEs, IDEs).
- Long-distance dispersal preserves patchy invasion. Patchy invasion has been observed in a mathematical model with fat-tailed dispersal kernels.
- Integro-difference equations require careful choice of a numerical method.