Mathematics behind biological invasions

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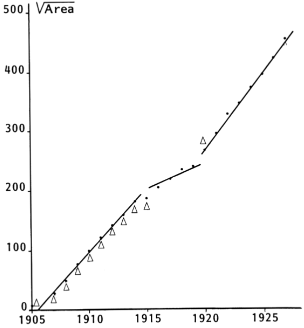
Muskrat Invasion of Europe

Skellam (1955)



Outline

① Fisher's spread model and linear predictability

② Nonlocal spread

③ Nonlinear stochastic effects

④ Population spread with multiple species

⑤ Discussion

Questions regarding potential invaders

- Can the invader establish itself in the new environment?
- Will the invading species spread and, if so, at what speed?
- What is the effect of the invading species on the communities it encounters?

Fisher's model (1937)

$$\begin{array}{ccccc} \text{Rate of change of density} & = & \text{Growth} & + & \text{Dispersal} \\ \frac{\partial u}{\partial t} & = & ru(1-u) & + & D\frac{\partial^2 u}{\partial x^2} \end{array}$$

where

$u(x,t)$ = Population density

r = Intrinsic growth rate (units 1/time)

D = Diffusion coefficient (units space^2/time)

$f(u)$ = $ru(1-u)$ nonlinear growth function

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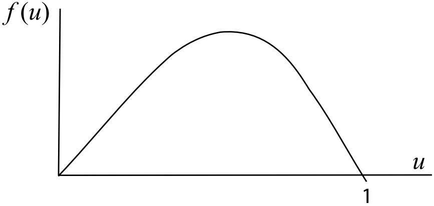
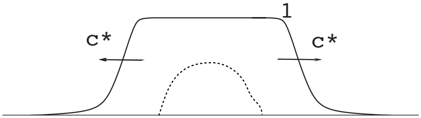


Spread with Fisher's model

- Step function initial data converges wave with speed $c^* = 2\sqrt{rD}$. (Kolmogorov, Petrovskii and Piskunov, 1937).
- Compact initial data $u_0(x)$ converges to a wave expanding at speed c^* (Aronson and Weinberger 1975, 1978).



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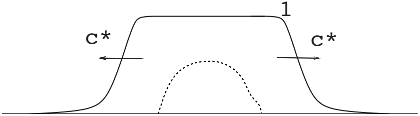
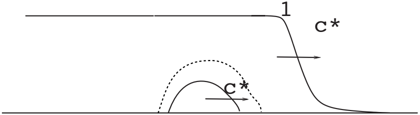


- Proof uses a comparison theorem (solutions that are initially ordered remain ordered for all time) plus super- and sub-solutions with speeds c^* as $t \to \infty$



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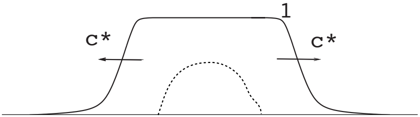

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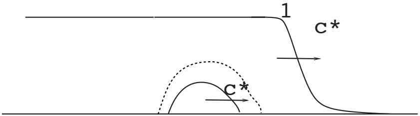

- Luther (1906) argued speed of a related chemical reaction was $c^* \propto \sqrt{rD}$ using dimensional arguments.

Definition of spread rate for Fisher's model

The model has **spread rate** c^* if, for any continuous initial function $u_0(x)$ with compact support, the solution $u(x,t)$ has the properties that for each $0 < \epsilon \ll 1$

$$\lim_{t\to\infty}\left[\sup_{|x|\geq t(c^*+\epsilon)} u(x,t)\right] = 0, \qquad \text{and} \qquad \lim_{t\to\infty}\left[\sup_{|x|\leq t(c^*-\epsilon)} |u(x,t)-1|\right] = 0.$$

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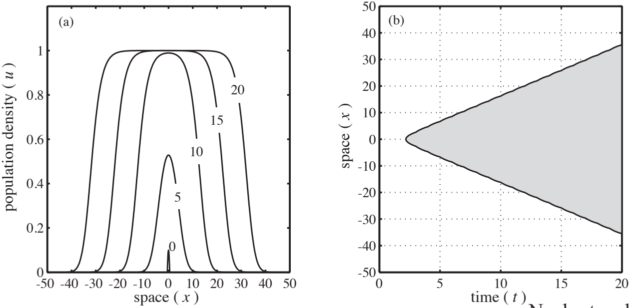

Neubert and Parker (2004)

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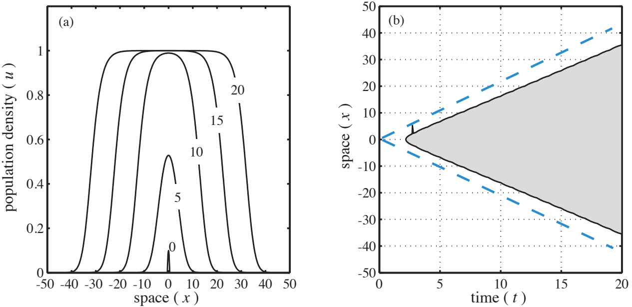

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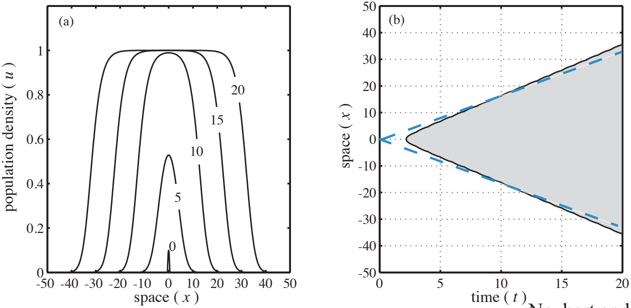

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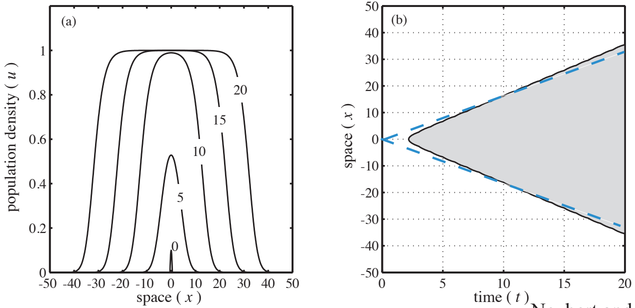

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From previous slide, Fisher's model has spread rate $c^* = 2\sqrt{rD}$.

Travelling wave

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  $$u_t = f(u) + Du_{xx}$$

  where $f(0) = f(1) = 0$ and $f > 0$ for $0 < u < 1$.

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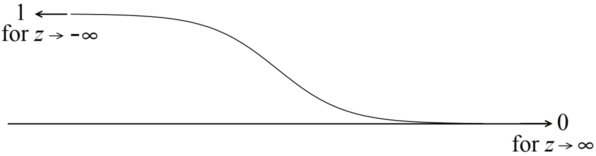

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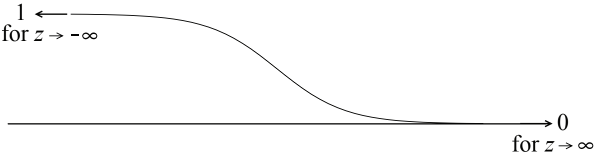
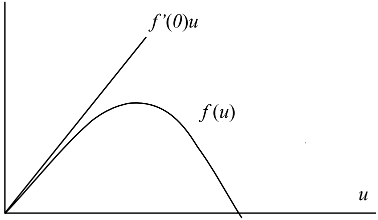


There is a family of travelling wave solutions. A solution exists for each $c \geq c^*$. Hence the spread rate coincides with the minimal travelling wave speed.

Linear determinacy

Nonlinear Model: $u_t = f(u) + Du_{xx}$
Linearized Model: $u_t = f'(0)u + Du_{xx}$



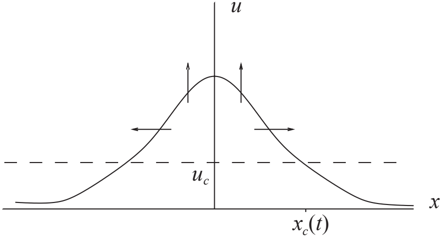
$$f(u) \leq f'(0)u$$

- The spread rate is **linearly determined** if spread rate of the nonlinear system equals spread rate of the linearized system.
- With Fisher's equation, the spread rate is linearly determined

Spread rate of linear equations

$$u_t = ru + Du_{xx}$$

Initial data: $\delta(x)$
Solution: $e^{rt}N(0, 2Dt)$
speed: $c^* = 2\sqrt{Dr}$.



$\lim_{t\to\infty} \dot{x}_c(t) = c^*$, independent of u_c.

Jump to integrodifference model

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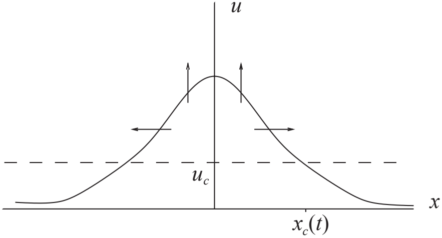

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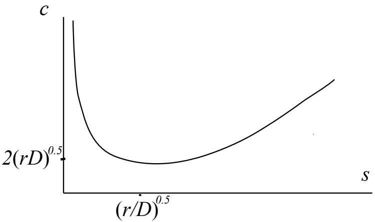
Jump to integrodifference model

Ansatz: $u = \alpha e^{-s(x-ct)}$
Dispersion relation:

$$\begin{aligned} cs &= r + Ds^2 \\ c &= r/s + Ds \end{aligned}$$

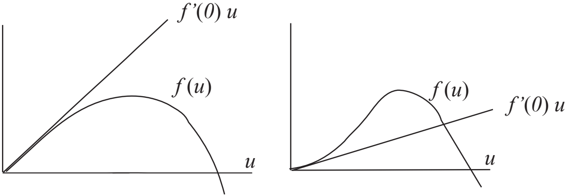
Speed: $c^* = \min_{s>0} c(s) = 2\sqrt{Dr}$.



Condition for Linear Determinacy

$$\begin{array}{cccccc} \text{Rate of change} & = & \text{Growth} & + & \text{Dispersal} \\ \text{of density} & & & & \end{array}$$

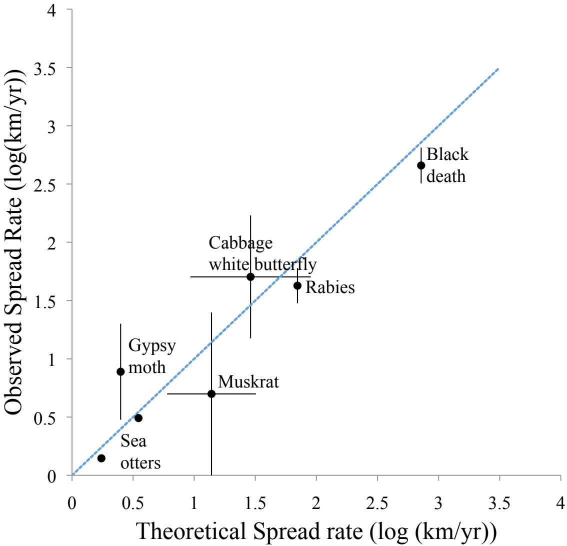
$$\frac{\partial u}{\partial t} = f(u) + D\frac{\partial^2 u}{\partial x^2}$$



- For the scalar model, $f(u) \leq f'(0)u$ is sufficient for linear determinacy (Aronson and Weinberger 1975).
- If this is violated (eg, reduced per capita growth at low density–Allee effect) spread may not be linearly determined (Hadeler and Rothe 1975).

Jump to competition induced Allee example

Comparison with data



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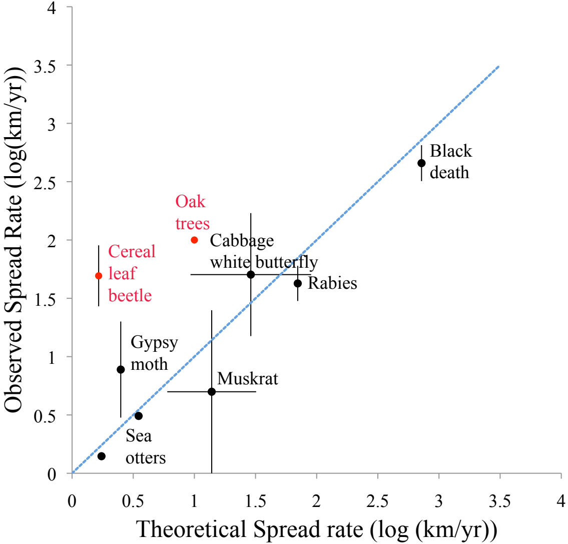

Outline

1. Fisher's spread model and linear predictability
2. Nonlocal spread
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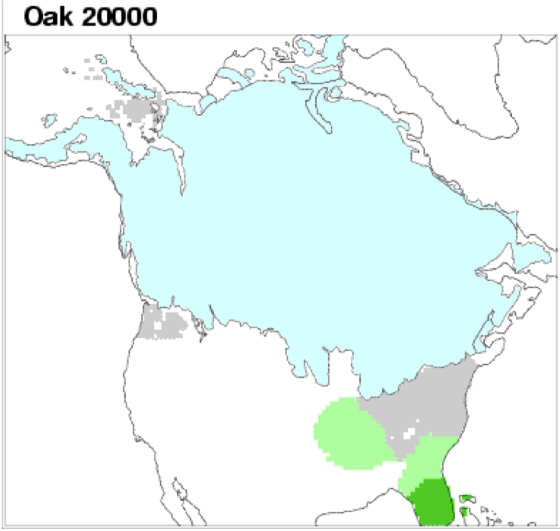
Spread of Oak in North America



North American Pollen Database

Spread of Oak in North America

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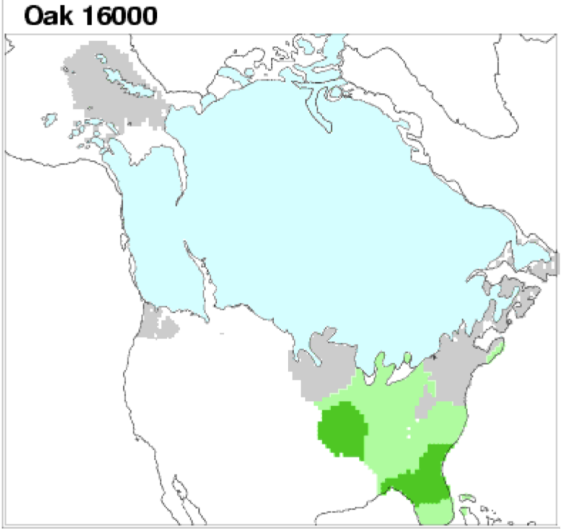
Percentages

- ⬜ 0 to 5
- 🟩 5 to 20
- 🟩 20 to 40
- ⬛ 40 to 100



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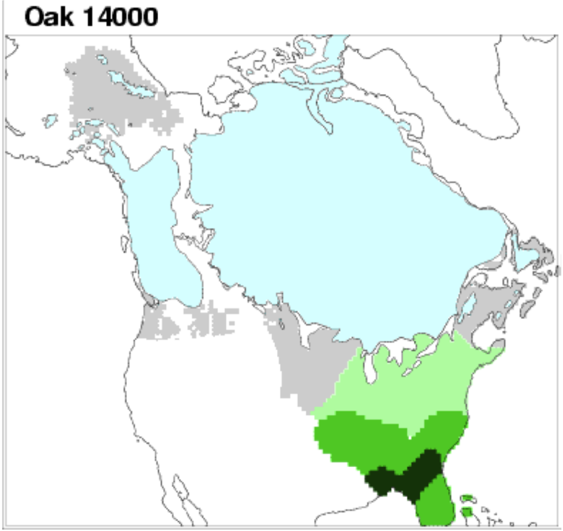

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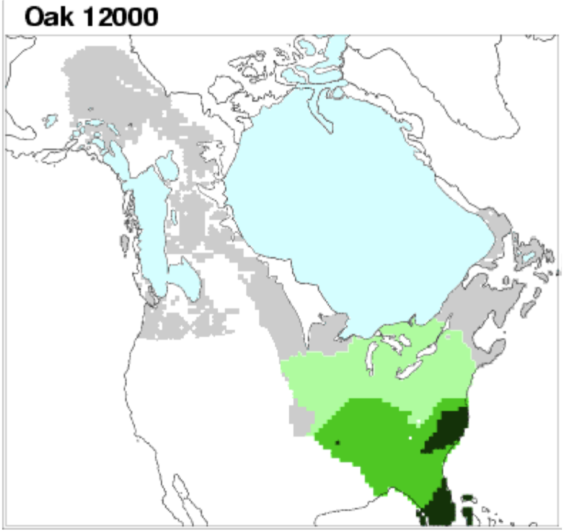

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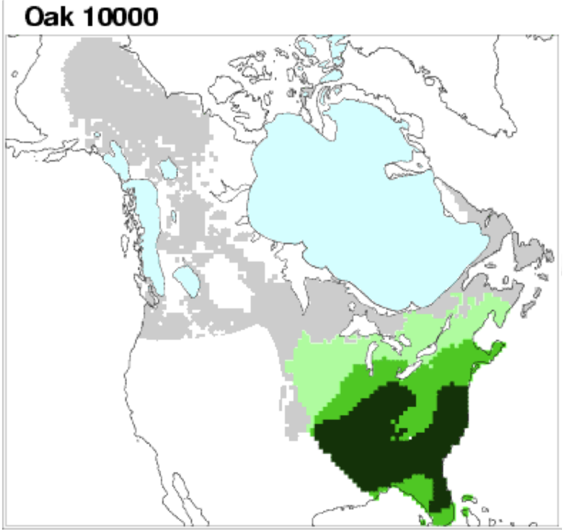


North American Pollen Database

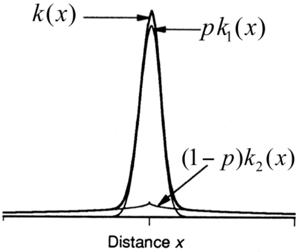
Modelling long-distance dispersal

- Implicit in the diffusion formulation is the assumption that, in a unit time interval, propagules disperse according to a Gaussian distribution $k(x) = N(0, 2D)$.
- Rare, long distance dispersal events typically change the shape from Gaussian to Leptokurtic. Eg.

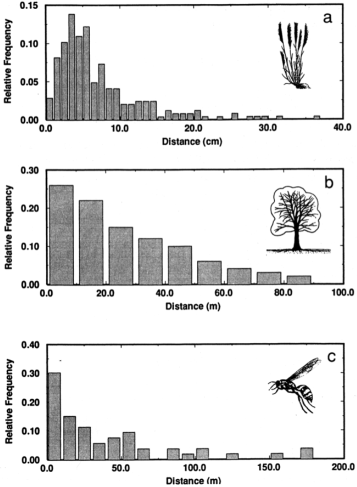
$$k(x) = pk_1(x) + (1-p)k_2(x)$$

where

$k(x)$ = Dispersal kernel
$k_1(x)$ = Local dispersal kernel
$k_2(x)$ = Long distance kernel
$1-p$ = Probability long-distance



Dispersal kernels can come directly from data

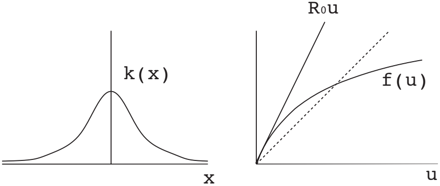


Neubert, Kot and Lewis (1995)

Integrodifference models

$$u_{n+1}(x) = Q(u_n)(x) = \int_{-\infty}^{+\infty} k(x-y) f(u_n(y))dy,$$

where k is the dispersal kernel and f is the growth function. $\int_{-\infty}^{+\infty} k(x)dx = 1$.



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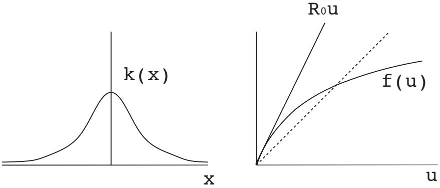

- At the leading edge $u_{n+1}(x) \approx R_0 \int_{-\infty}^{+\infty} k(x-y)u_n(y)dy = M(u_n)(x)$.

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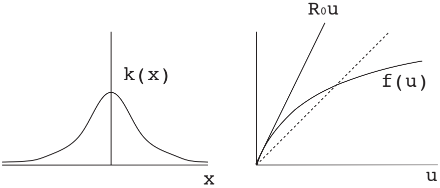

- At the leading edge $u_{n+1}(x) \approx R_0 \int_{-\infty}^{+\infty} k(x-y) u_n(y) dy = M(u_n)(x)$.
- Ansatz $u_n = \alpha e^{-s(x-nc)}$ yields a dispersion relation between wave speed c and steepness s

$$\begin{aligned} e^{sc} &= M(e^{-sx})|_{x=0} = R_0 \int_{-\infty}^{\infty} \exp(su) k(u)\, du = R_0 b(s) \\ c &= \frac{1}{s} \ln\left(R_0 b(s)\right) \end{aligned}$$

Jump to Fisher dispersion relation

Spread with integrodifference model

Theorem (Weinberger, 1982)

Assume f is monotonic and $f(u) \leq f'(0)u$. If the moment generating function $b(s)$ exists on an interval $[0, s^+)$ then the spread rate is linearly determined and given by

$$c^* = \min_{s>0} \frac{1}{s} \log(R_0 b(s)).$$

where

$$\begin{aligned} s &= \textit{wave steepness } (u_n(x) \propto \exp(-sx)) \\ R_0 &= f'(0) = \textit{Basic reproductive rate} \\ b(s) &= \textstyle\int_{-\infty}^{\infty} \exp(su)k(u)\,du \quad \textit{(MGF for kernel)} \end{aligned}$$

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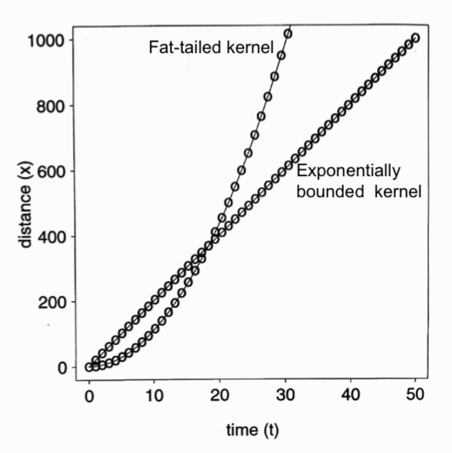
Proof uses a comparison theorem for the discrete-time recursion relation, plus construction of sub- and super-solutions, each of which spread asymptotically at speed c^*. ▸ Jump to spread with spatial correlations

Spread with the integrodifference model

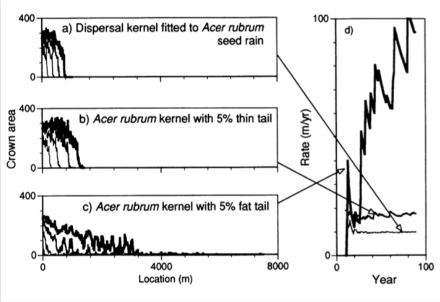
- A Gaussian kernel gives Fisher's wave speed $c^* = 2\sqrt{rD}$ where the variance of the dispersal kernel is $2D$ and the arithmetic growth rate is $r = \log R_0$.
- Kernels that are exponentially bounded but are leptokurtic can give much higher spread rates c^*.
- "Fat-tailed kernels" that drop off slower than exponentially give constantly accelerating invasions
- For kernels with moments of all order, this rate of acceleration can be explicitly calculated.



Kot, Lewis and van den Driessche (1996)

A resolution to Reid's paradox

Stochastic simulation for Red Maple (*Acer rubrum*)



Fat-tailed dispersal kernels are consistent with measured seed rain data and also with some observations of long-distance dispersal.

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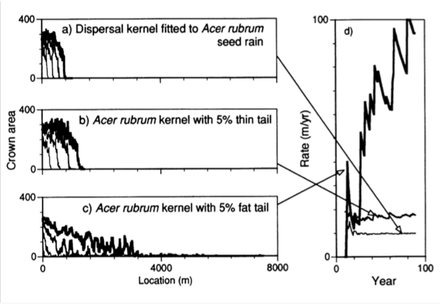

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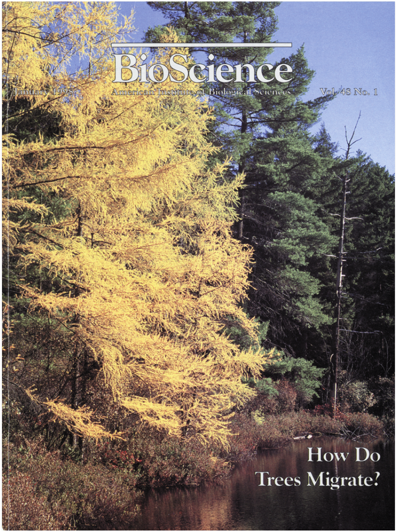
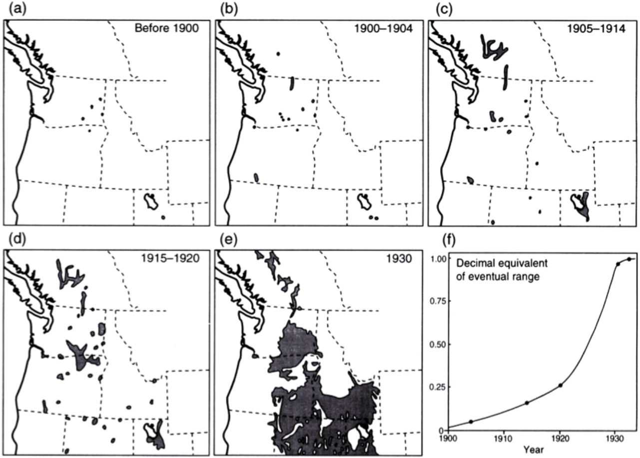
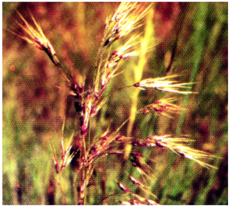


Clark et al. (1998)

Cheatgrass Invasion of North America





Mack (1981)

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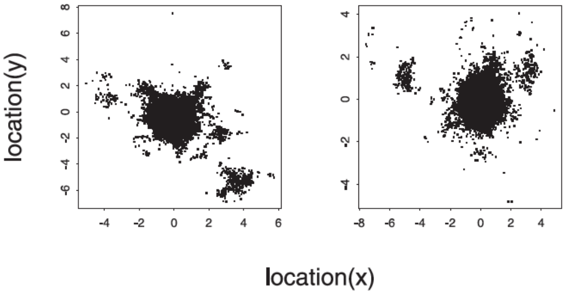
An individual-based approach

- When observing invasions it is typical to see a series of invaded patches which spread coalesce and spawn new patches.
- Monte-Carlo simulations of invasion processes produce similar results.
- In a homogeneous environment spatial correlations can give rise nonlinear interactions at the leading edge of the spreading population



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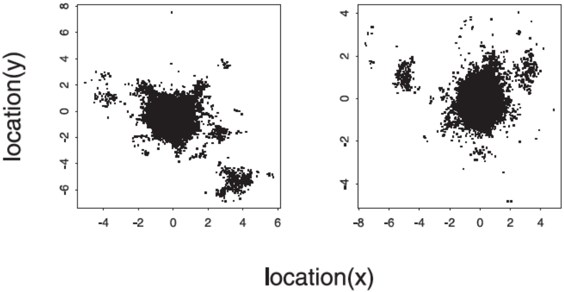

How does this relate to the mean field models we have already considered?

Keeping track of correlations

Expected density of individuals: $n(x)$
Expected joint density of individuals: $n^{(2)}(x,y)$
Spatial covariance density function: $c(x,y) = n^{(2)}(x,y) - n(x)n(y), \quad x \neq y$
Local spatial covariance $c(x,x) = \lim_{y \to x} c(x,y)$

$$n_{t+1}(x) \quad = \quad \int_{-\infty}^{\infty} R_0 \, k(z-x) \, n_t(z) \, dz$$

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$$\begin{aligned} n_{t+1}(x) &= \int_{-\infty}^{\infty} R_0\, k(z-x)\, n_t(z)\, dz \\ c_{t+1}(x,y) &= \int_{-\infty}^{\infty} \left\{R_0(R_0-1)+\sigma^2\right\}\, n_t(z)\, k(z-x)\, k(z-y)\, dz \end{aligned}$$

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Thus an expanding wave in density is accompanied by an expanding wave in covariance.

Including weak nonlinear interactions

- Assume that each individual inspects an ϵ-neighborhood for other individuals.
- If there are others in this neighborhood the individual does not reproduce and dies.
- If there are no others in this neighborhood the individual has a Poisson number of offspring with mean R_0 and dies.
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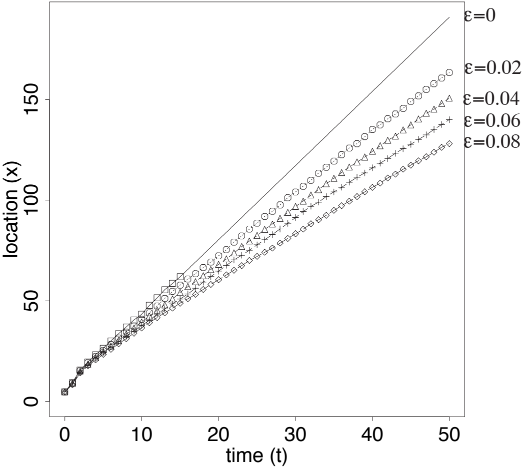
The equivalent mean field model

$$n_{t+1}(x) = \int_{-\infty}^{\infty} R_0\, k(z-x)\, \left(n_t(z) - \epsilon n_t^2(z)\right)\, dz$$

is linearly determined (Li, Lewis and Weinberger, 2008), ie., the nonlinear interactions have no effect. However...

Effect of nonlinear interactions on expectation speed



The plot shows location of the n_eth furthest forward individual, averaged over many realizations of the stochastic process.

Including spatial correlations

$$\begin{aligned} n_{t+1}(x) &= \int_\Omega R\,k(z-x)\,\left(n_t(z)-\epsilon\left(n_t^2(z)+c_t(z,z)\right)\right)\,dz \\ c_{t+1}(x,y) &= \dots \end{aligned}$$

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Theorem (Lewis, 2000)

The expectation speed for this problem is bounded above by

$$c_\epsilon^* = \min_{s>0} \frac{1}{s} \log(R_0 b_1(s,\epsilon)).$$

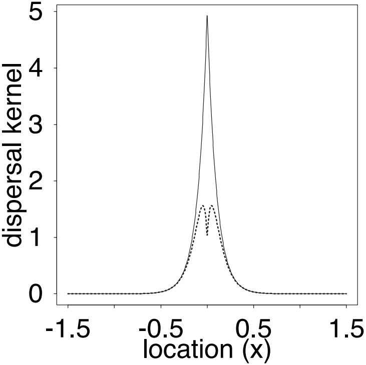
where

$$b_1(s,\epsilon) = \int_{-\infty}^{\infty} \exp(su)\left(k(u) - \epsilon R_0 k^2(u)\right)\,du$$

▸ Jump to case with no correlations

Including spatial correlations

- This is as for the linearly determined speed c_0^*, but with the dispersal kernel $k(u)$ replaced by $k(u) - \epsilon R_0 k^2(u)$. Hence $c_\epsilon^* < c_0^* = c^*$.
- The proof involves moment closure methods coupled to comparison theorem methods.



Outline

1. Fisher's spread model and linear predictability
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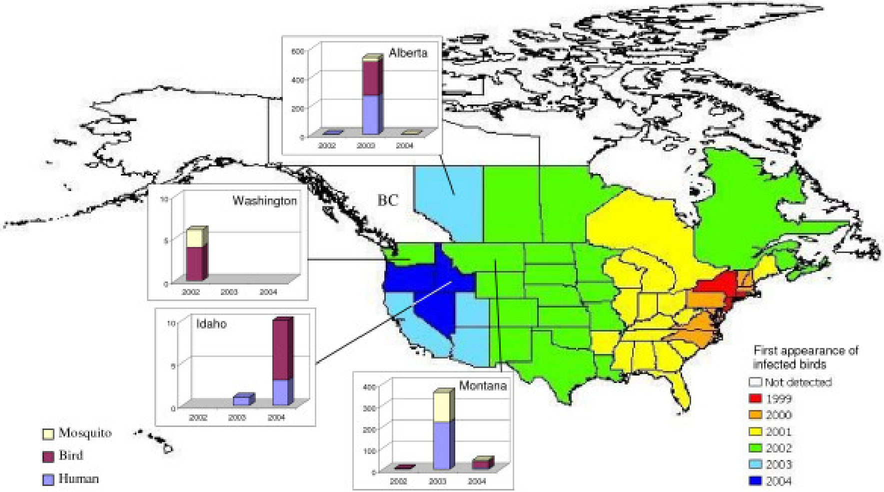
3. Nonlinear stochastic effects
4. Population spread with multiple species
5. Discussion

Grey Squirrel Invasion of the United Kingdom

The Mammal Society (2008)

West Nile Virus Invasion of North America



Tachiiri et al. (2006)

Spread with cooperative recursions

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- It has been developed further by Thieme, Zhao and many others.

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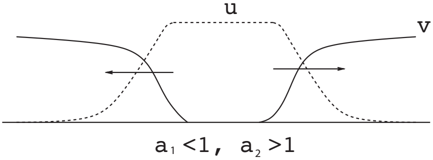
- How can results from the theory of discrete-time recursions be translated to partial differential equations?
- What is the connection to travelling waves?

Spread of grey squirrels into red squirrel populations

$$\begin{aligned}\frac{\partial u}{\partial t} &= r_1 u(1-u-a_1 v) + d_1 \frac{\partial^2 u}{\partial x^2}\\ \frac{\partial v}{\partial t} &= r_2 v(1-v-a_2 u) + d_2 \frac{\partial^2 v}{\partial x^2}\end{aligned}$$

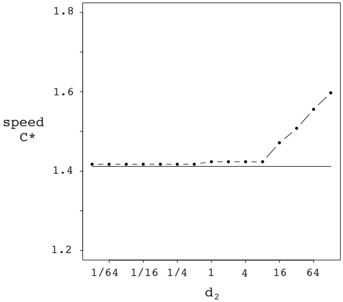


Theory versus numerical experiments

At the wave front of the invading species, $u \approx 0$, $v \approx 1$ and the linear approximation for the u equation is

$$u_t = r_1(1 - a_1)u + d_1 u_{xx}.$$

This predicts a spread rate for u of $c^* = 2\sqrt{r_1 d_1 (1 - a_1)}$.



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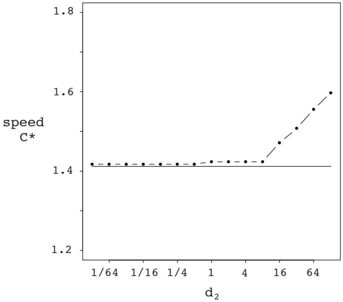
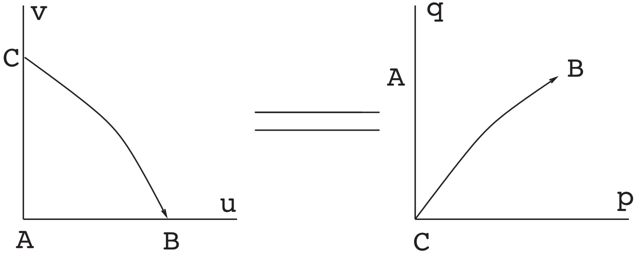


The speed is linearly determined for some parameters, but not for others (Hosono, 1998). ▸ Jump to Lotka Volterra Theorem

Two species cooperative model

Introduce the new variables $p = u$ and $q = 1 - v$ which converts the *competitive* system into a *cooperative* system.



Recursions

The Lotka-Volterra model becomes a recursion by letting $Q_\tau = (Q_\tau^1, Q_\tau^2)$ be its time τ map

$$p_{n+1}(x) = Q_\tau^1(p_n, q_n)(x)$$

$$q_{n+1}(x) = Q_\tau^2(p_n, q_n)(x).$$

or

$$\vec{u}_{n+1}(x) = Q_\tau(\vec{u}_n)(x)$$

Q_τ is order-preserving nonlinear spatial operator.

Spreading speed of the Lotka-Volterra model

Theorem (Lewis, Li, and Weinberger, 2002)

Suppose that grey squirrel is the better competitor ($a_1 < 1$), and that growth rate r_1 of the grey squirrel is sufficiently large and the diffusion coefficient d_2 of the red squirrel is sufficiently small ($\mathbf{r_1}(2d_1 - \mathbf{d_2})(1 - a_1) \geq \max\{d_1 r_2(a_1 a_2 - 1), 0\}$). Then both components spread at the linearly predicted speed $c^* = \sqrt{d_1 r_1 (1 - a_1)}$.

▸ Compare with Lotka Volterra Numerical

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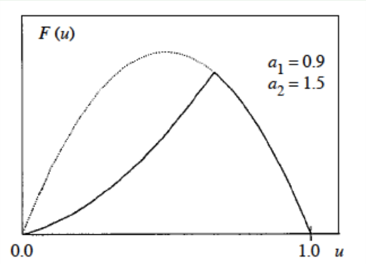
Example

A singular perturbation approach can be used to connect to the scalar problem. Hosono (1998) considered $d_2 \to 0, r_2 \to \infty$ and $a_1 a_2 > 1$. This yields

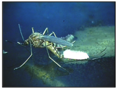
$$u_t = d_1 u_{xx} + F(u)$$

Which exhibits a weak Allee effect.

▸ Go to Allee slide



Spread of West Nile virus



$$\text{Larvae} \quad \frac{\partial L_V}{\partial t} = b_V(S_V + E_V + I_V) - m_V L_V - d_L L_V$$

$$\text{Susceptible} \quad \frac{\partial S_V}{\partial t} = -\alpha_V \beta_R \frac{I_R}{N_R} S_V + m_V L_V - d_V S_V + \epsilon \frac{\partial^2 S_V}{\partial x^2}$$

$$\text{Exposed} \quad \frac{\partial E_V}{\partial t} = \alpha_V \beta_R \frac{I_R}{N_R} S_V - (\kappa_V + d_V) E_V + \epsilon \frac{\partial^2 E_V}{\partial x^2}$$

$$\text{Infected} \quad \frac{\partial I_V}{\partial t} = \kappa_V E_V - d_V I_V + \epsilon \frac{\partial^2 I_V}{\partial x^2}$$

$$\text{Susceptible} \quad \frac{\partial S_R}{\partial t} = -\alpha_R \beta_R \frac{S_R}{N_R} I_V + \eta_R R_R + D \frac{\partial^2 S_R}{\partial x^2}$$

$$\text{Infected} \quad \frac{\partial I_R}{\partial t} = \alpha_R \beta_R \frac{S_R}{N_R} I_V - (\delta_R + \gamma_R) I_R + D \frac{\partial^2 I_R}{\partial x^2}$$

Simplified West Nile virus model

- The model can be simplified and studied on an stable invariant manifold. On this manifold, the model involves infected mosquitoes and birds.
- This simplified model is cooperative and lies below its linearization at the leading edge of the wave.
- A unique spreading speed can be calculated from the linearized operator, and the existence of a family of travelling waves can be proved with the spread rate as the lowest wave speed.
- This spread rate for the simplified model depends on the bird movement rate D, but for our best parameter estimates is approximately 1000 km/yr.
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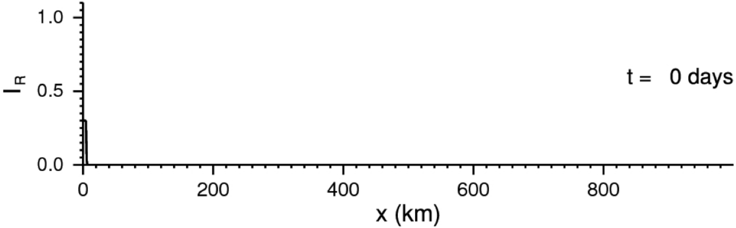

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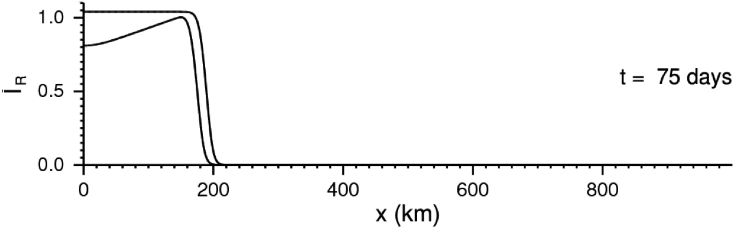

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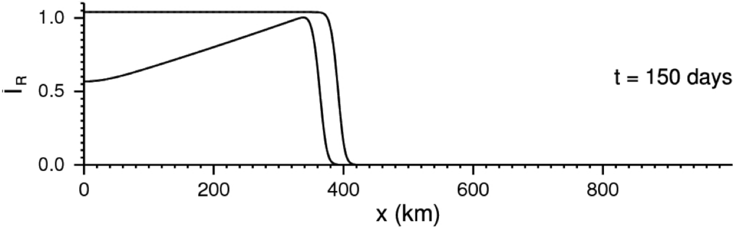

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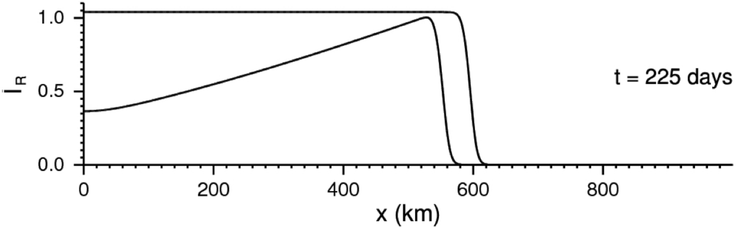

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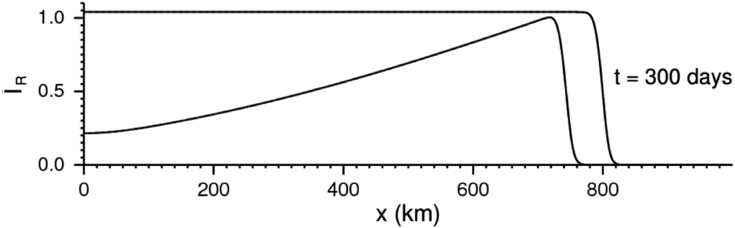

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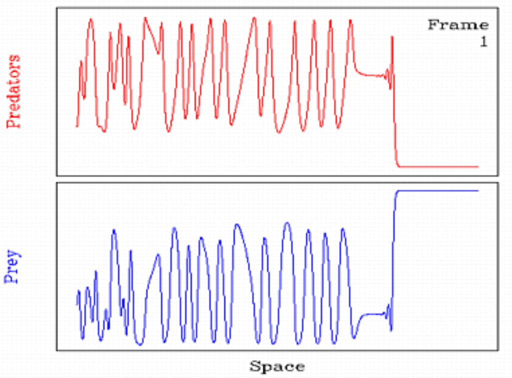
- However, when such events are included as fat-tailed dispersal kernels, spread rates can increase by an order of magnitude.
- A more realistic model of an invasion is a stochastic process. Here, correlations between individuals can be proved to slow population spread, but there are many open questions.
- Linear predictability is not well-understood for multispecies models and is a subject of ongoing research. When models are cooperative it is possible to derive general results, but it is an open problem for non-cooperative systems (eg., predator-prey).

Predator-prey invasion



If a group of predators is introduced into a spatially uniform population of prey, they invade the prey. Irregular spatiotemporal oscillations appear behind the invasion front (animation courtesy of J. Sherratt).

Sherratt, Lewis and Fowler (1995)

Thanks

- Linear predictability for non-cooperative systems (B. Li and others).
- Analysis of systems that are not linearly predictable (M. Kot, M.A. Lewis, R. Lui and others).
- Spread in epidemic models (M.A. Lewis, R. Liu, J. Wu, H. Zhu and others).
- Spread in spatially and temporally varying environments (H. Berestycki, H. Caswell, X. Liang, S. Schreiber, N. Shigesada, H.F Weinberger and others).
- Spread models with time delay (J. So, H Theime, X. Zhao, X. Zou and others).
- Spread in stage-structured populations (H. Caswell, R. Lui, M. Neubert and others).
- Analysis of accelerating waves and asymptotically infinite spreading speeds (X. Zhao, H.F. Weinberger and others).
- Spreading speeds and persistence in river environments with unidirectional flow (M.A. Lewis, F. Lutscher, E. McCauley, R. Nisbet and others).