Models for Spreading Populations

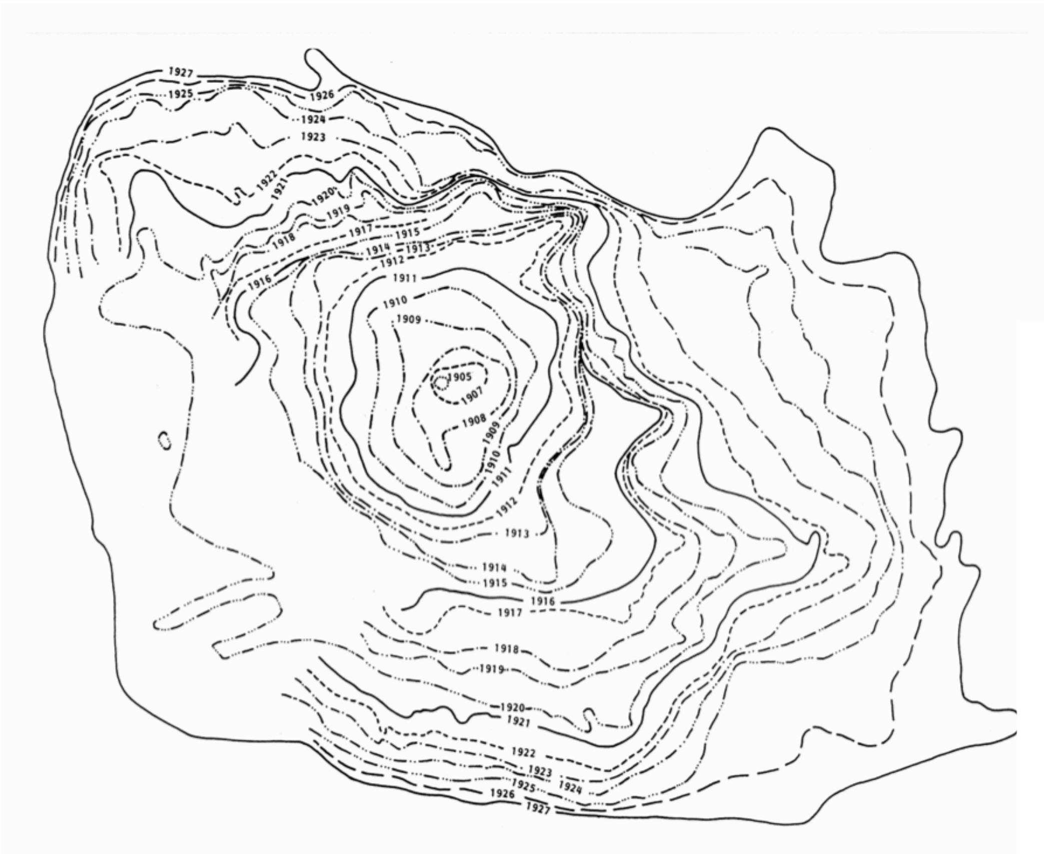
Mark Lewis

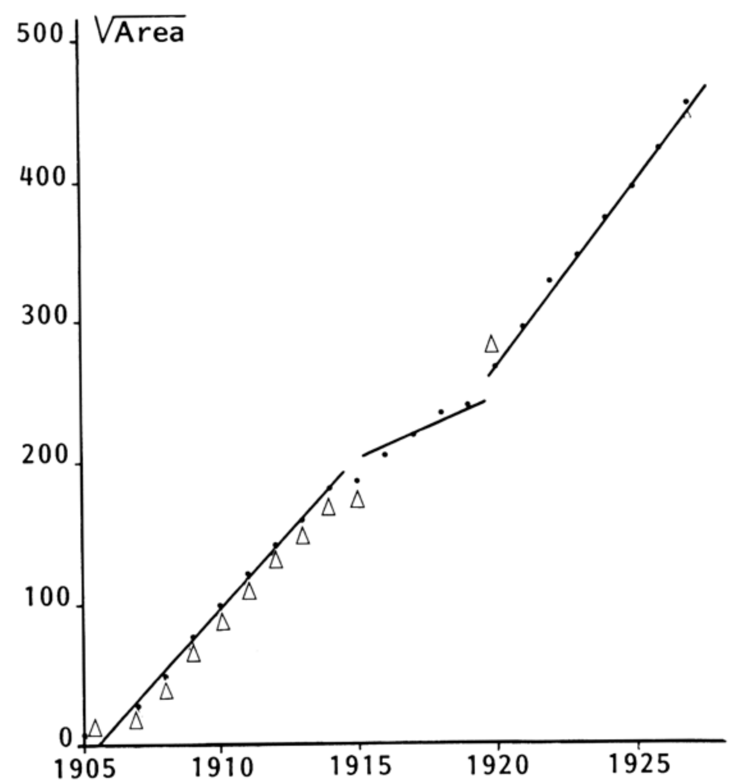
The Mathematics Behind Biological Invasions

Questions regarding potential invaders

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

Muskrat invasion of Europe





Skellam (1955)

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

$$
\begin{array}{rcl}
u(x,t) & = & \text{Population density} \\
r & = & \text{Intrinsic growth rate (units 1/time)} \\
D & = & \text{Diffusion coefficient (units space}^2\text{/time)} \\
f(u) & = & ru(1-u) \quad \text{nonlinear growth function}
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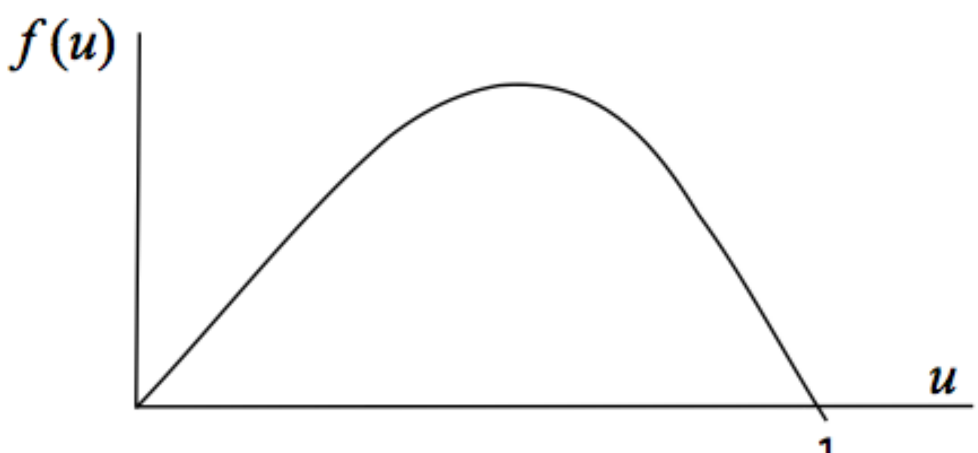
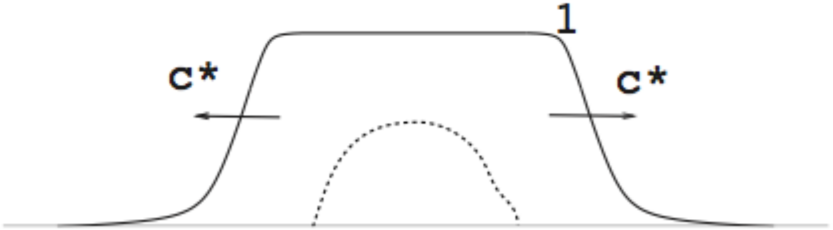


Spread with Fisher's model (1937)

- 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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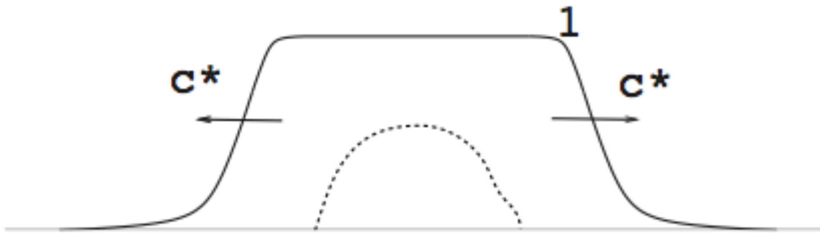
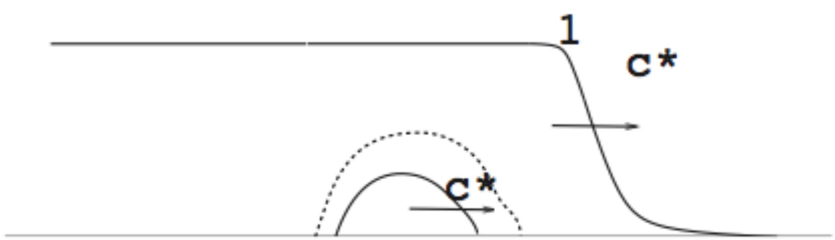


- Proof uses a comparison theorem (solutions that are initially ordered remain ordered for all time) plus super- and sub-solutions with speeds c^* as $t \to \infty$



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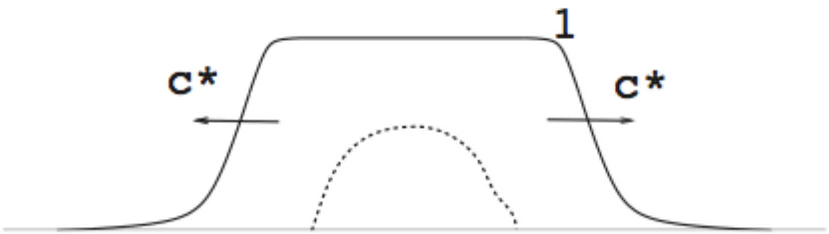

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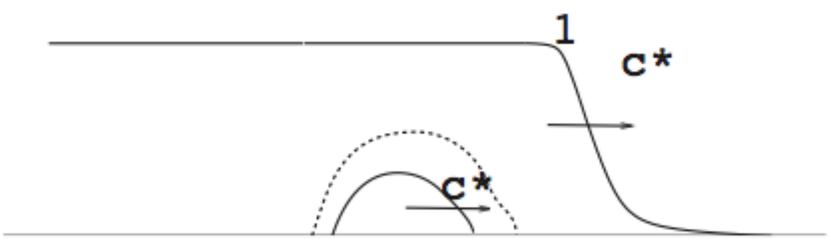

- Luther (1906) argued speed of a related chemical reaction was $c^* \propto \sqrt{rD}$ using dimensional arguments.

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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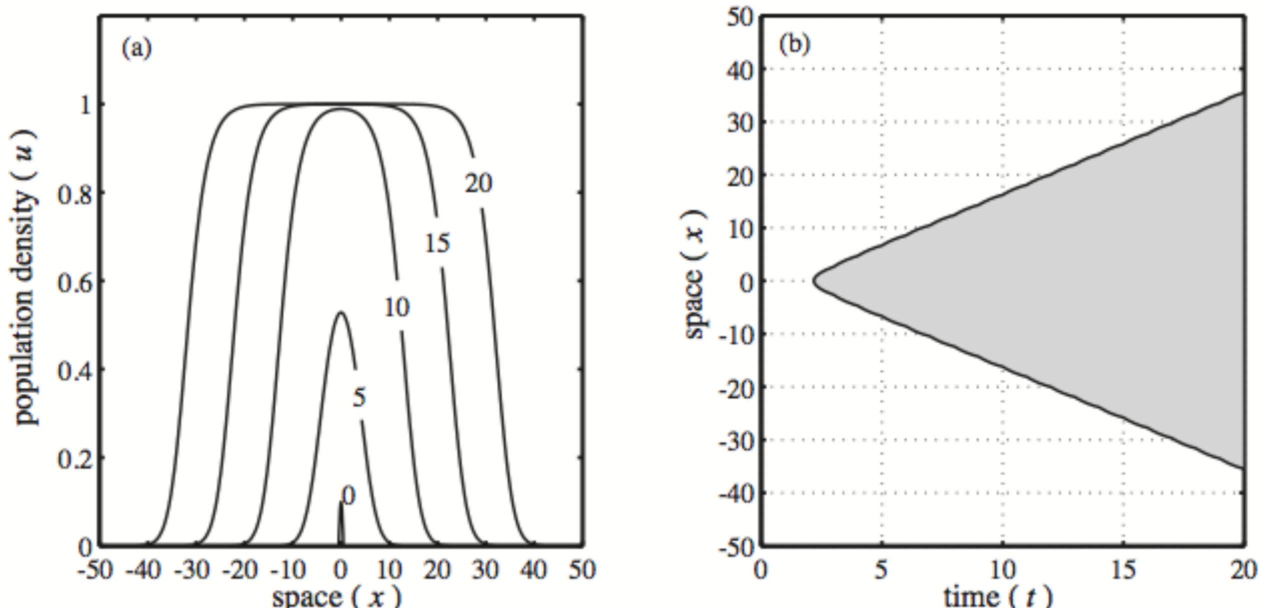

Neubert and Parker (2004)

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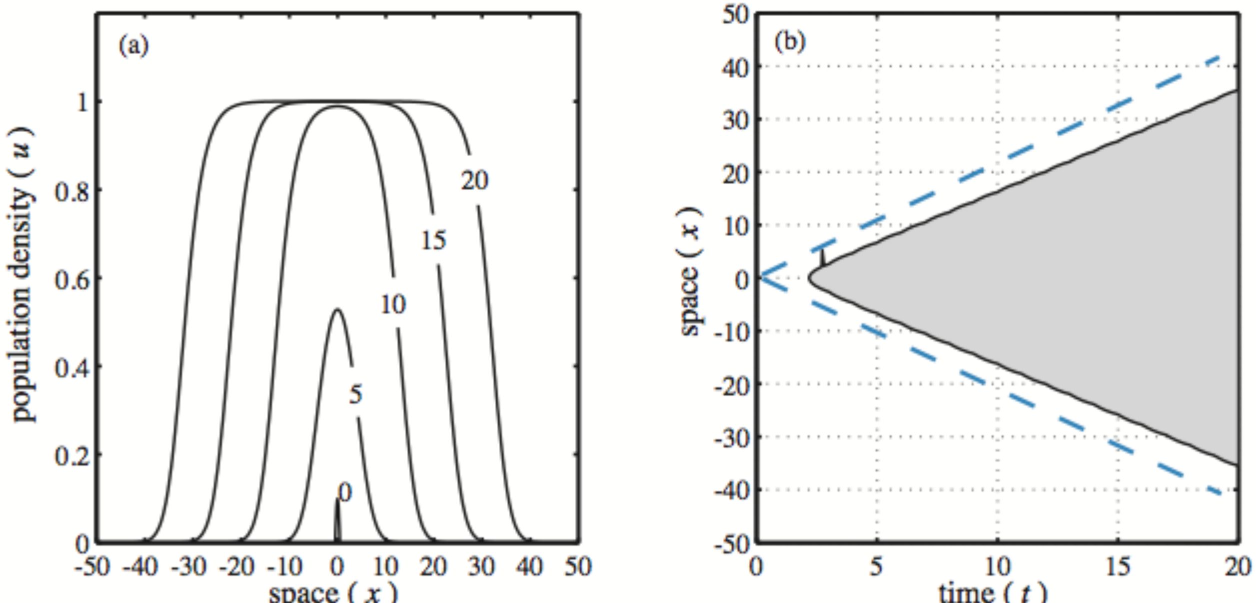

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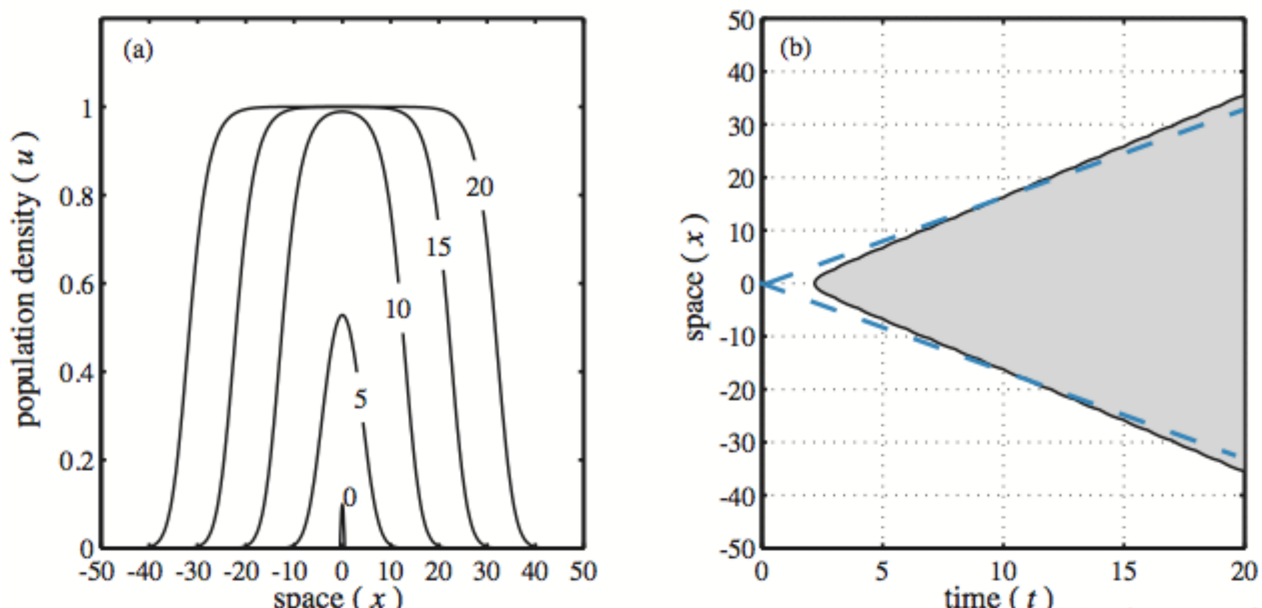

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Travelling wave

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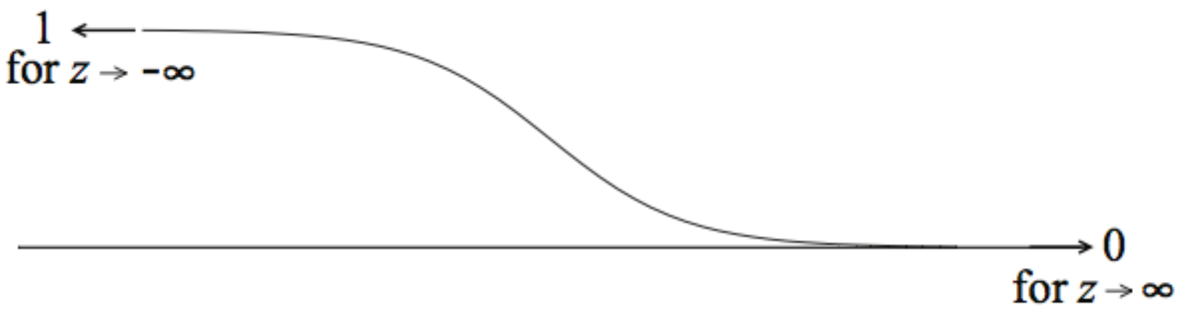

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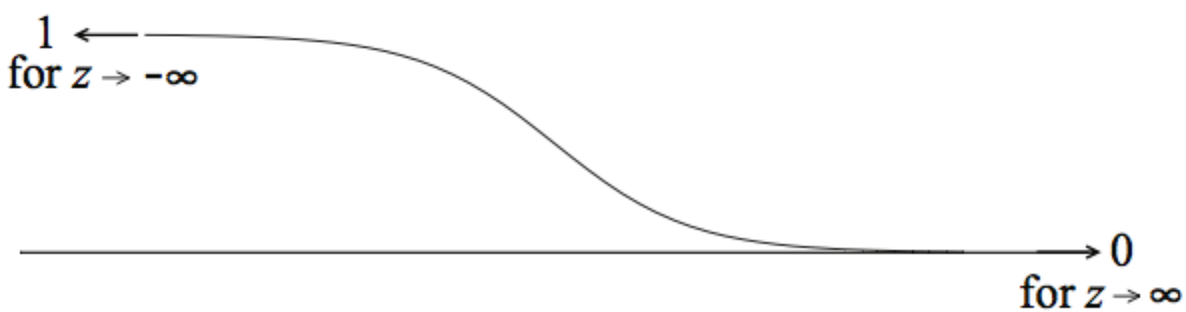
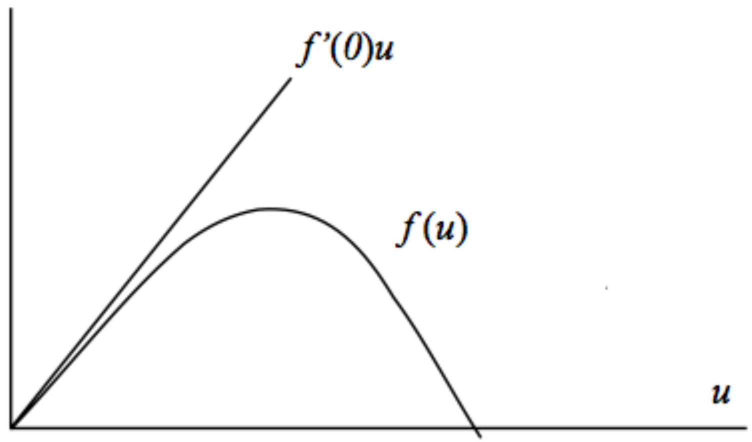


There is a family of travelling wave solutions. A solution exists for each $c \geq c^*$. Hence the spread rate coincides with the minimal travelling wave speed.

Linear determinacy

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



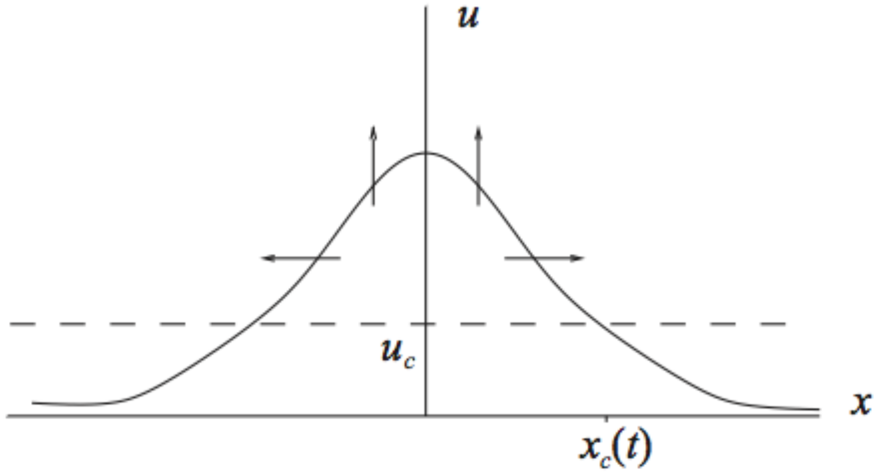
$$f(u) \leq f'(0)u$$

- 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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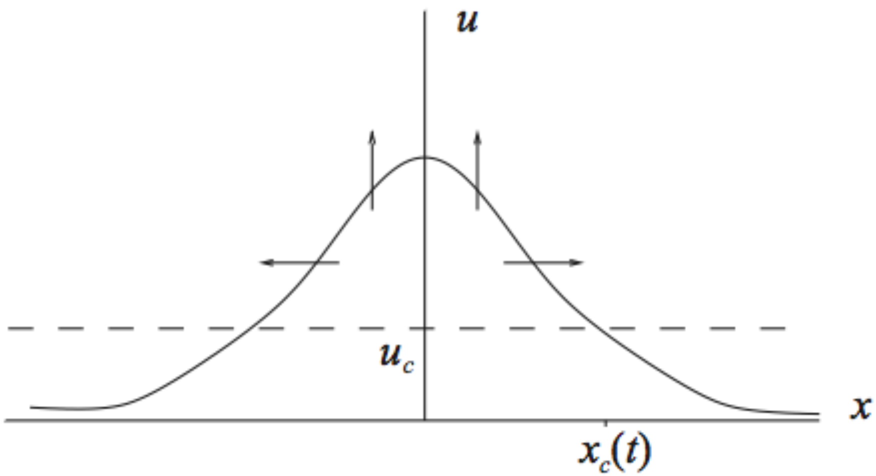

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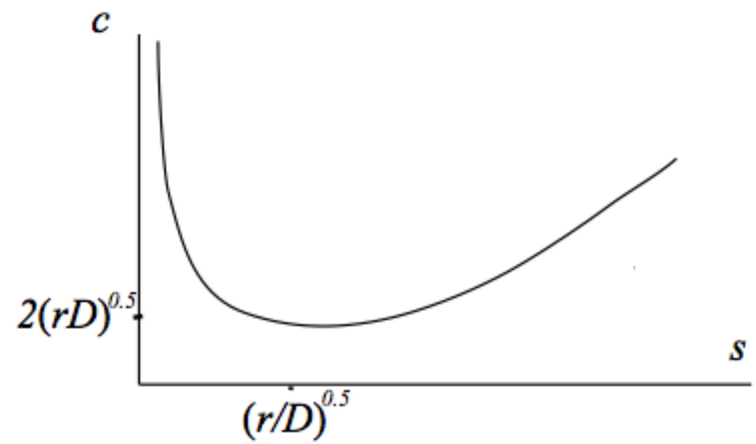
Jump to integrodifference model

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

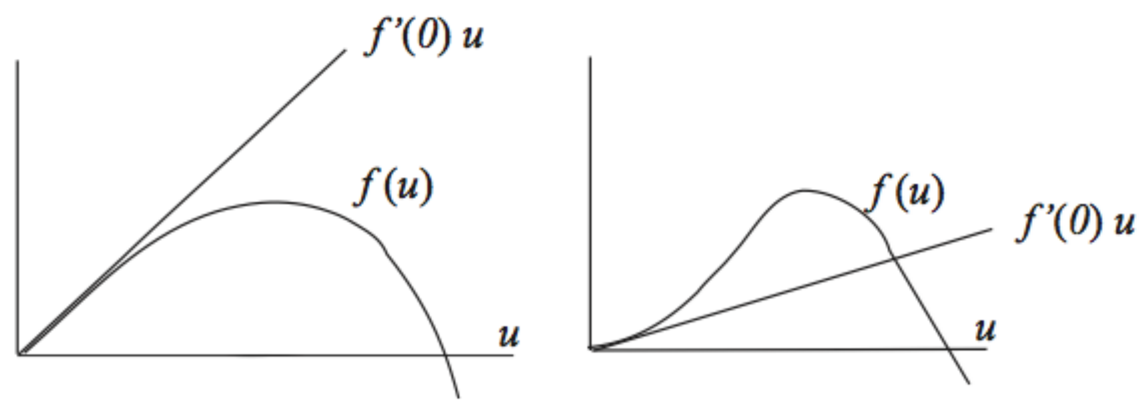
$$\begin{aligned} cs &= r + Ds^2 \\ c &= r/s + Ds \end{aligned}$$

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



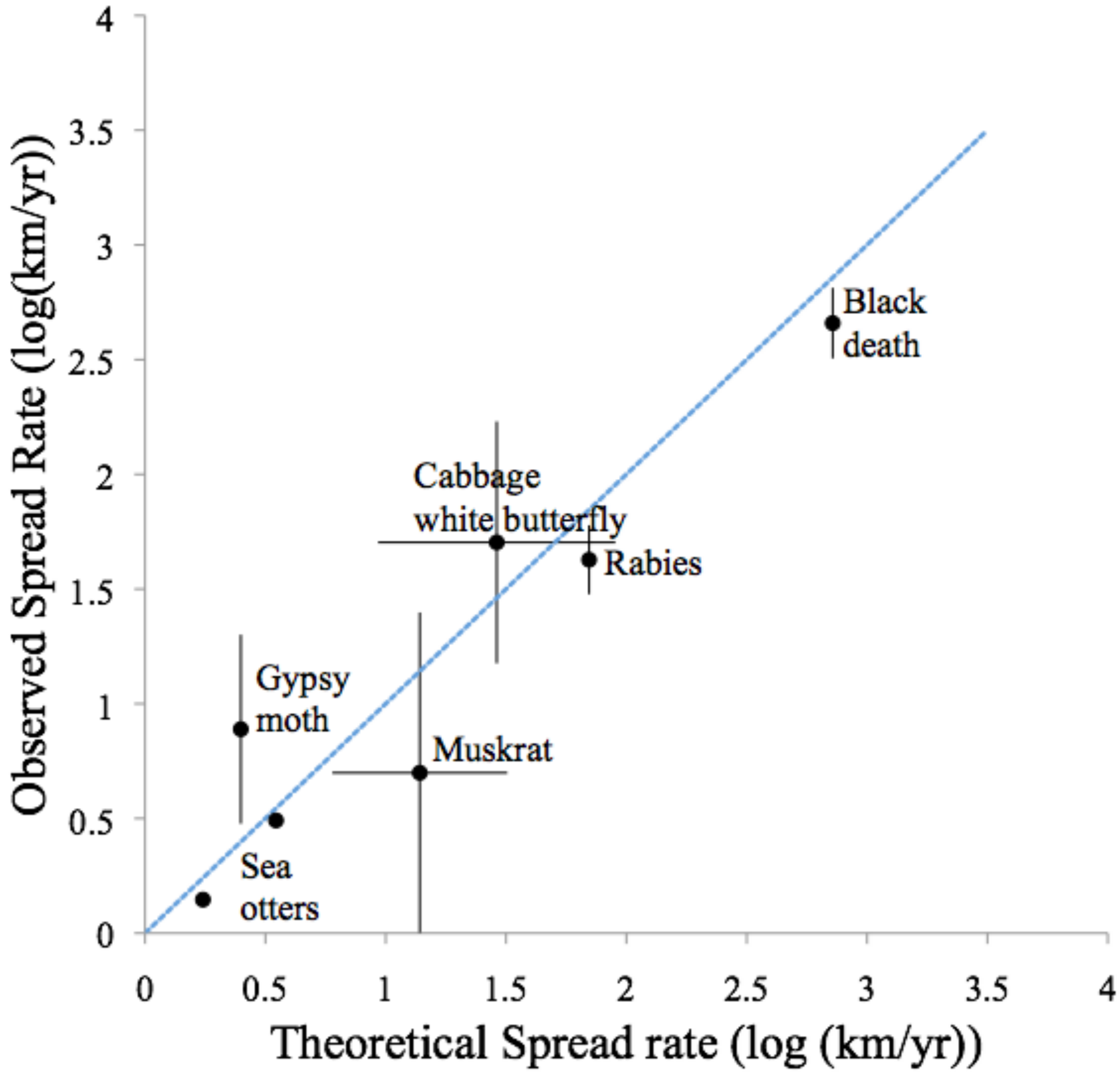
Conditions for linear determinacy

Rate of change of density	=	Growth	+	Dispersal
$\frac{\partial u}{\partial t}$	=	$f(u)$	+	$D\frac{\partial^2 u}{\partial x^2}$



- 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).

Conditions for linear determinacy



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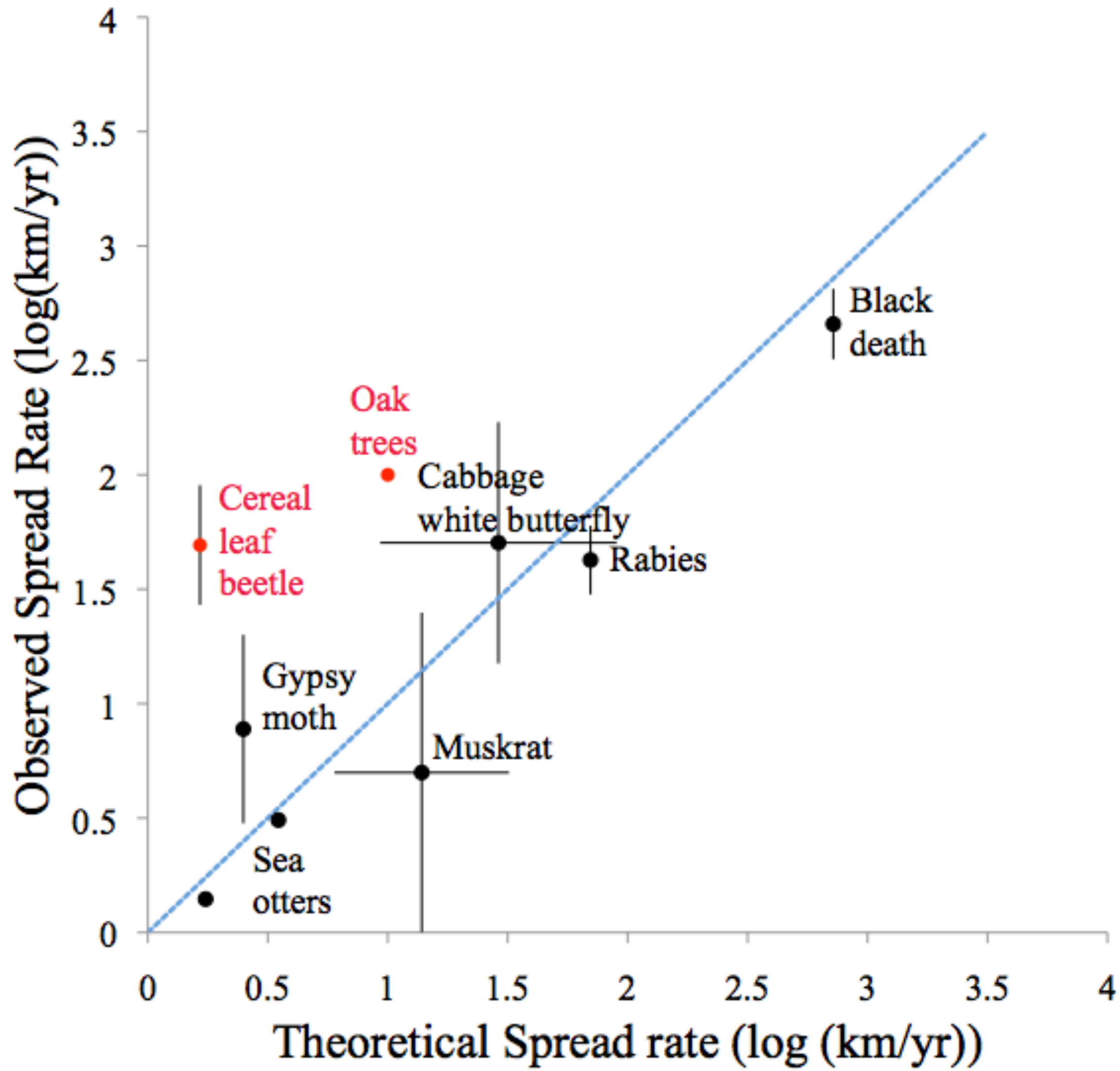
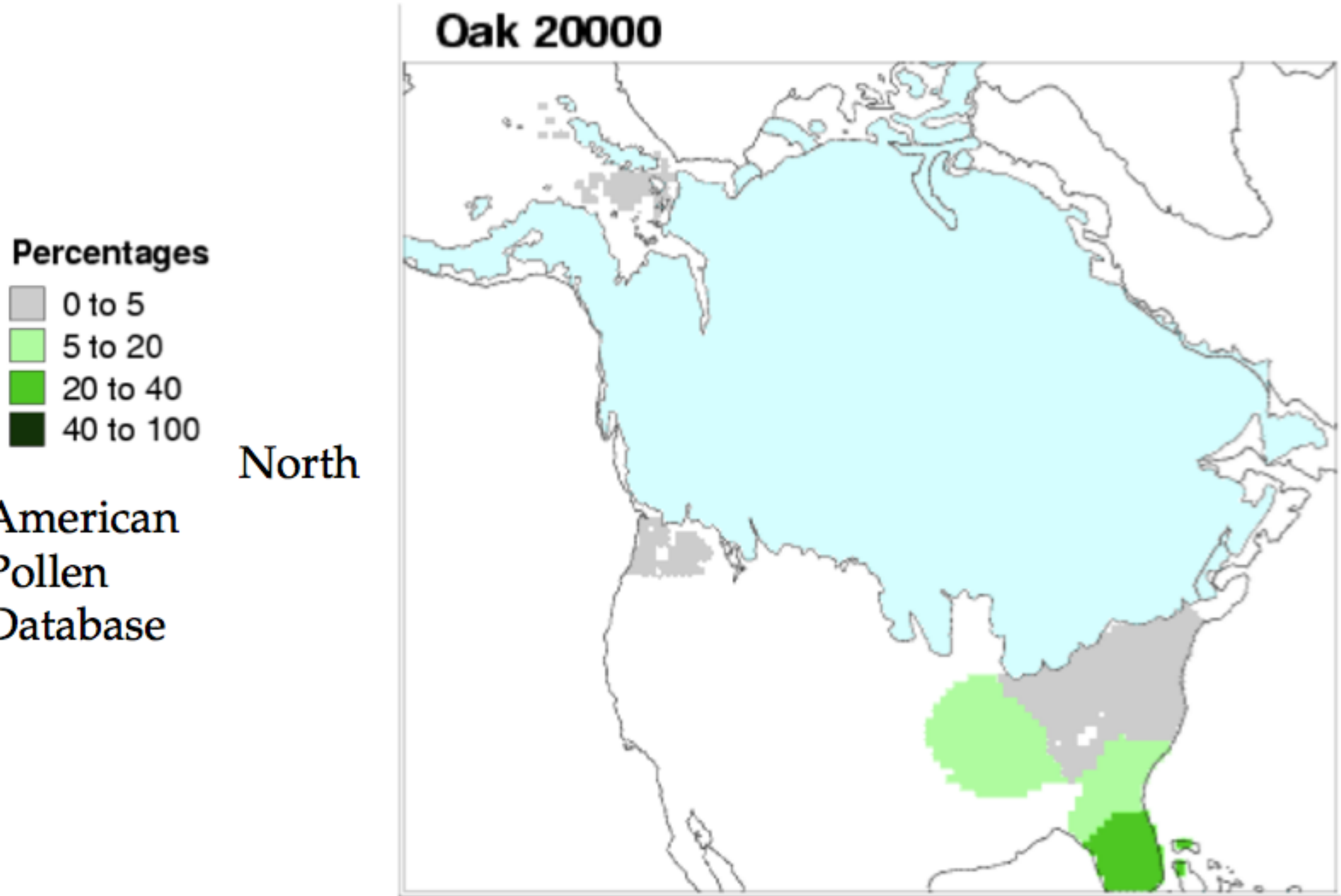


Spread of Oak in North America



North American Pollen Database

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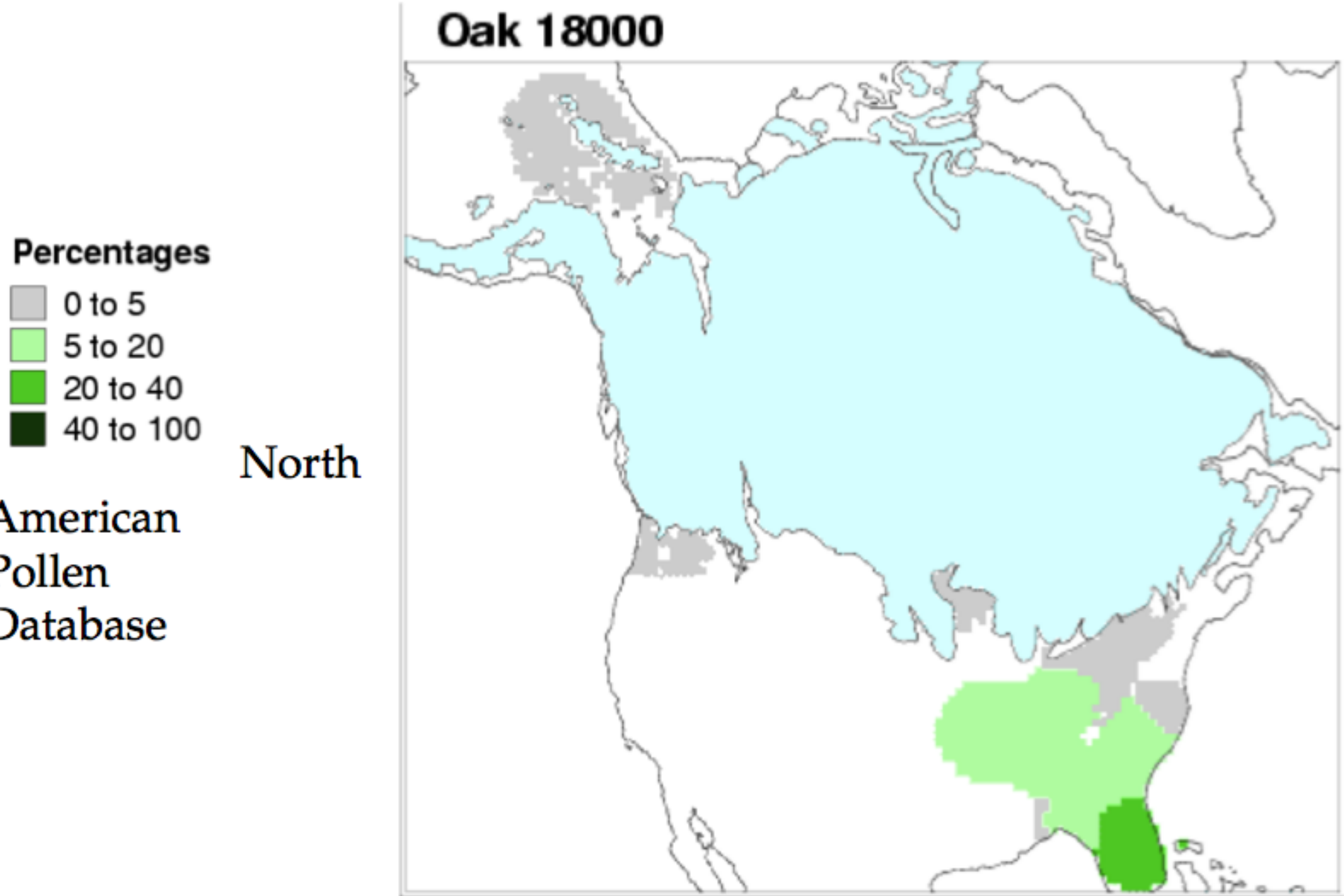

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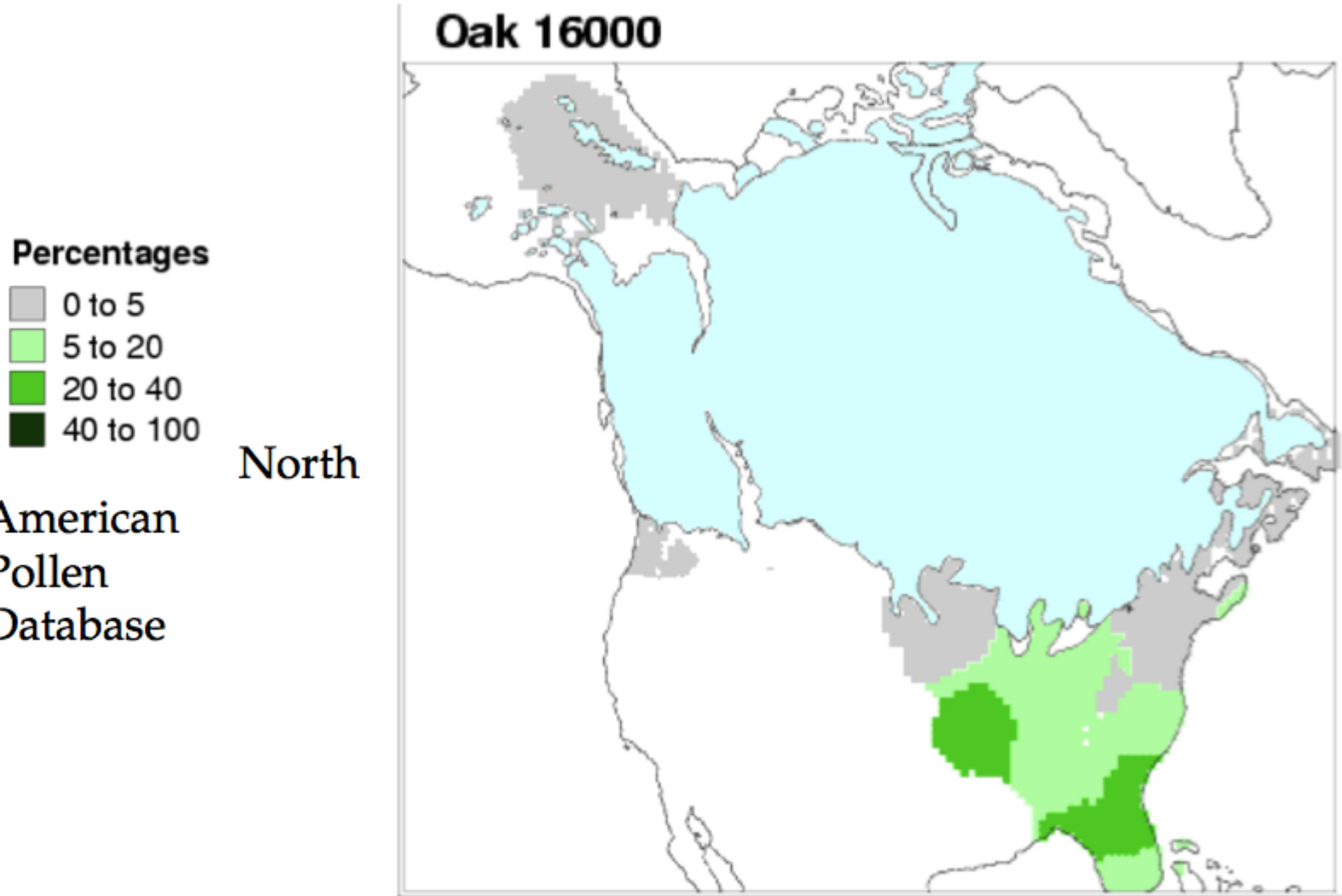

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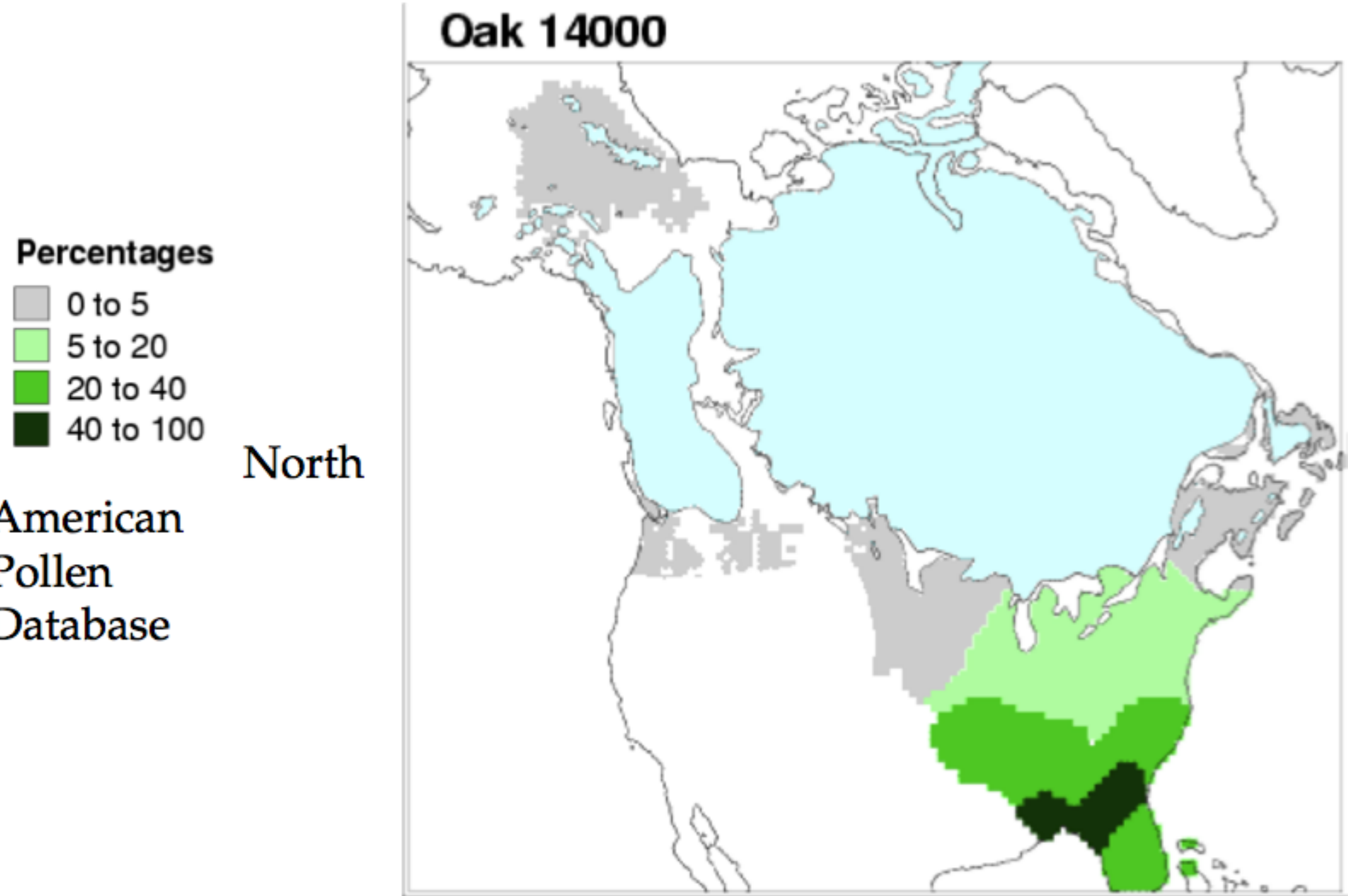

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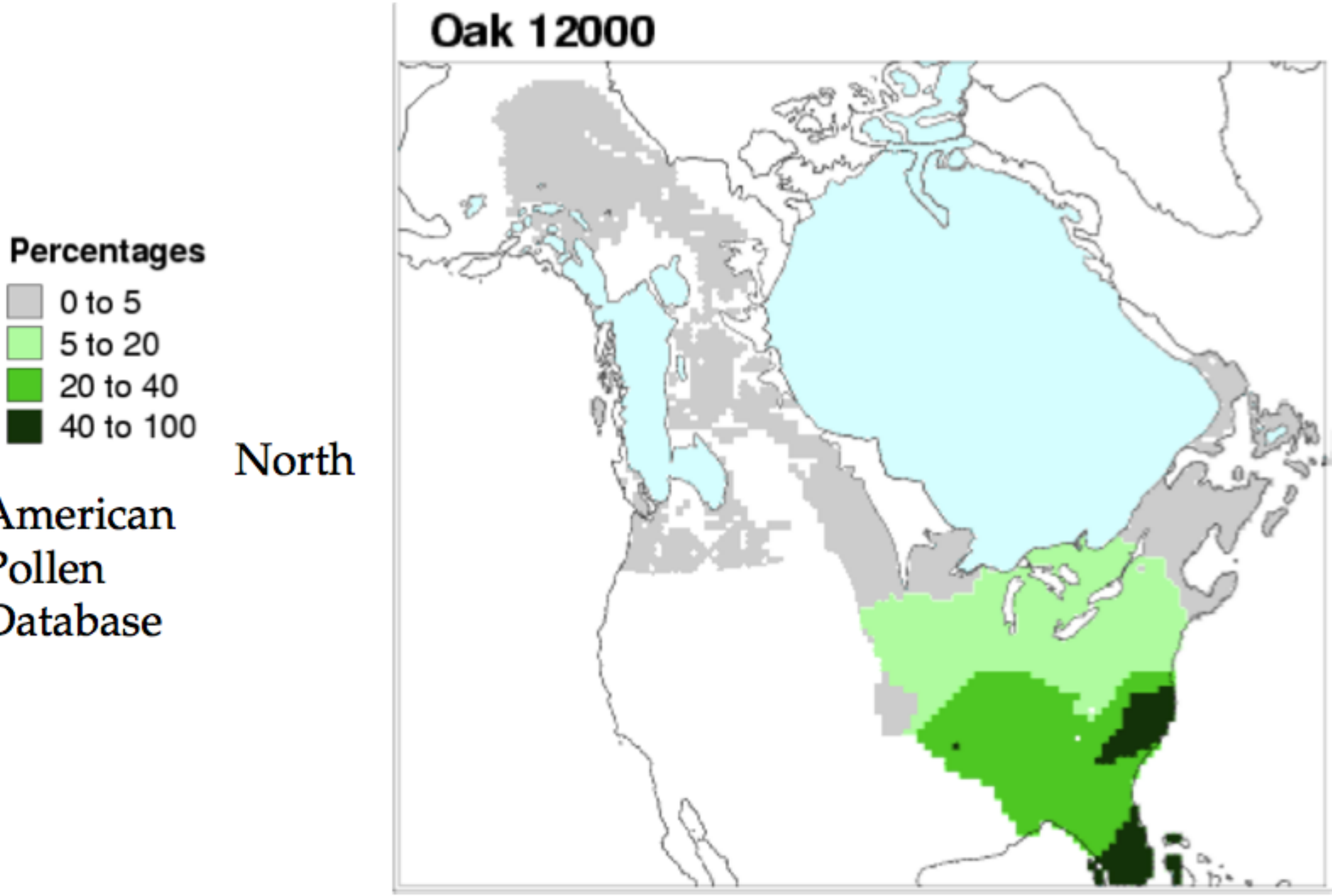

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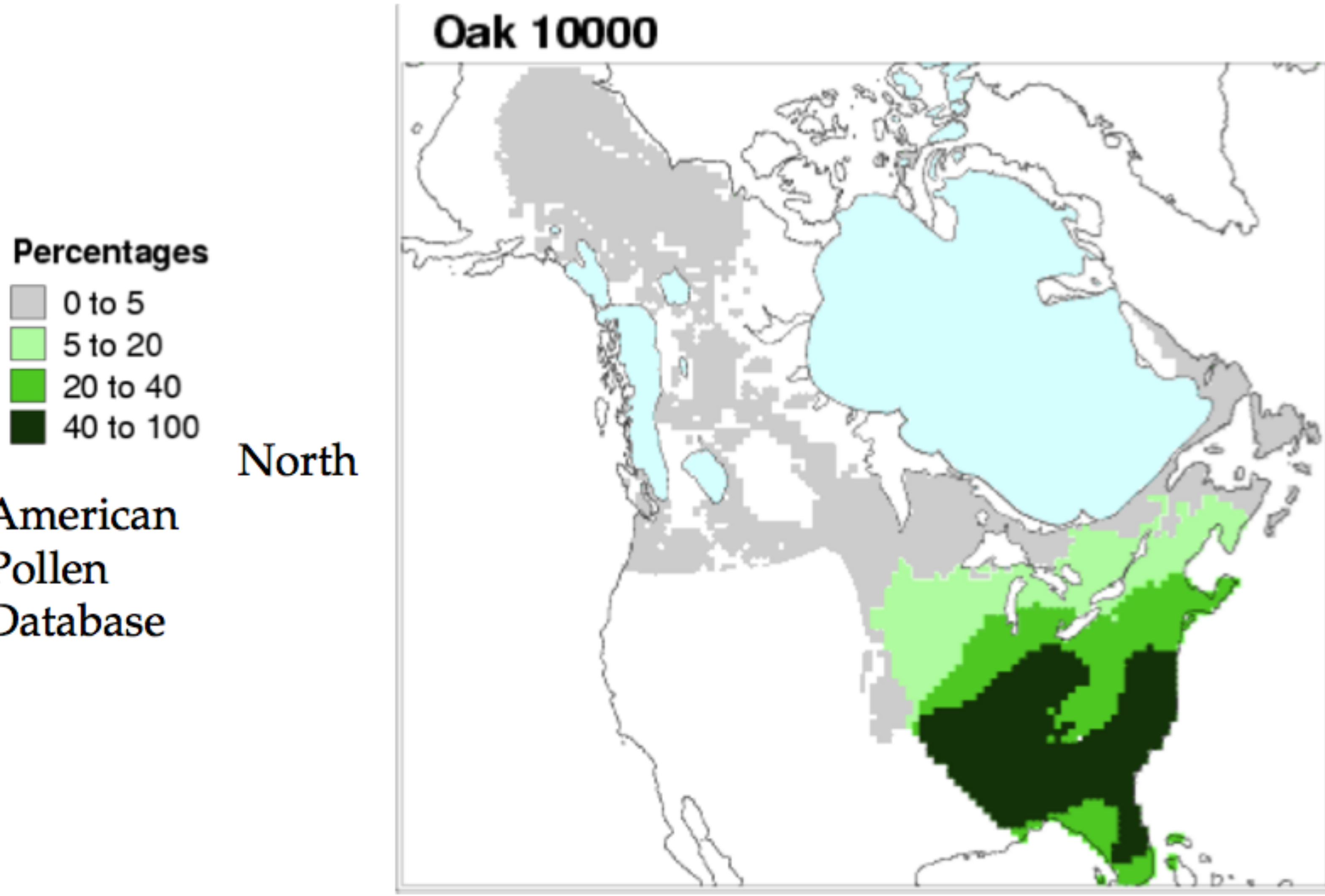


North American Pollen Database

Reid's Paradox

The oak, to gain its present most northerly position in north Britain after being driven out by the cold probably had to travel fully six hundred miles and this, without external aid, would take something like a million years (Reid, 1899).

Skellam's Analysis (1951)

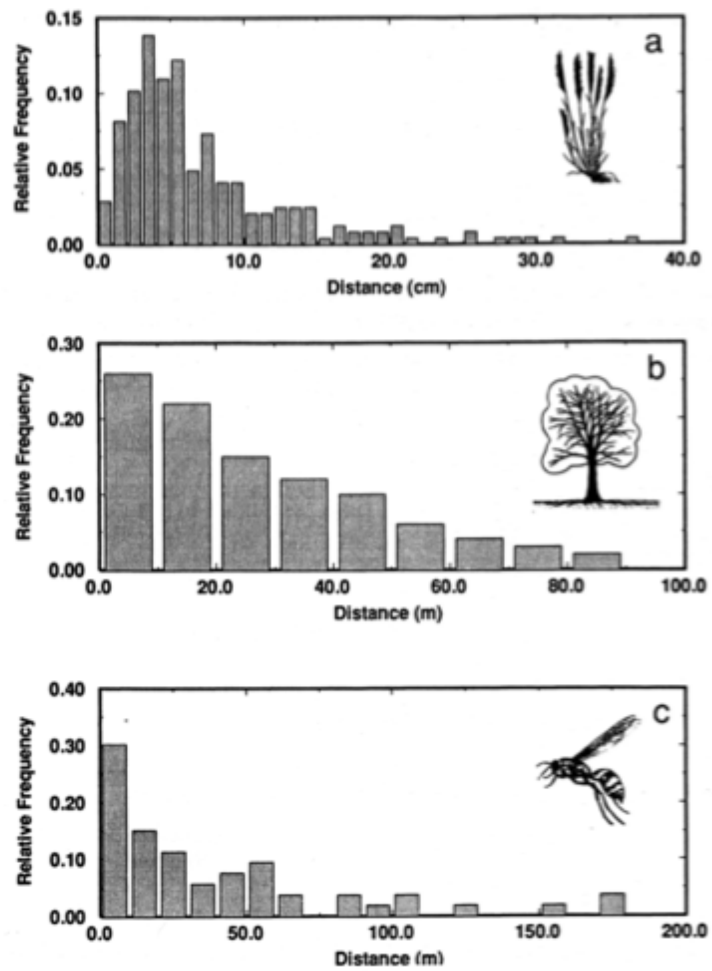
Using $c^* = 2\sqrt{rD}$, what average dispersal distance σ, $(\sigma^2 = 4D)$ must seeds disperse to explain the spread of 1000 km in 300 generations of oak trees?

$\sigma = 0.83$ km. **Reid's Paradox!**

Accelerating Invasions

- Rapid spread through rare-long distance dispersal events appears to be widespread with weeds and other invaders
- We believe that this is the case for scentless chamomile
- Williamson (2005) found that 36 out of 70 data sets for weeds showed evidence of accelerating invasions.

Dispersal kernels can come directly from data



Neubert, Kot and Lewis (1995)

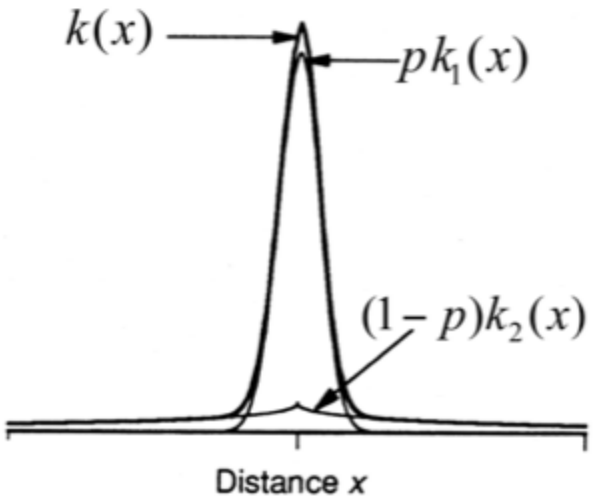
Modelling long-distance dispersal

- 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.

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

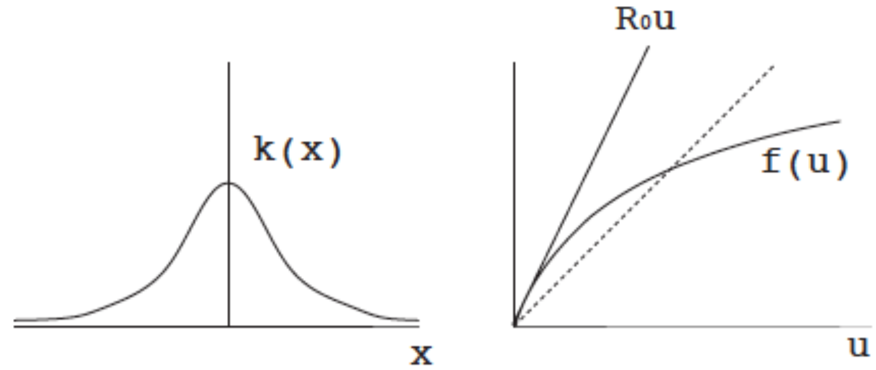
where

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



Integrodifference model

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



At the leading edge $u_{n+1}(x) \approx \lambda \int_{-\infty}^{\infty} k(x-y) u_n\left(y\right)\, dy$

Ansatz $u_{n+1}(x) = \alpha \exp(-s(x-nc))$ yields a dispersion relation between wave speed c and steepness s

$$\exp(sc) = \lambda \underbrace{\int_{-\infty}^{\infty} \exp(su) k(u)\, du}_{b(s)} = R_0 b(s)$$

$$c = \frac{1}{s} \ln\left(\lambda b(s)\right)$$

$$c^* = \min_{s>0} \frac{1}{s} \ln\left(\lambda b(s)\right) \text{ (Weinberger, 1982)}$$

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

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

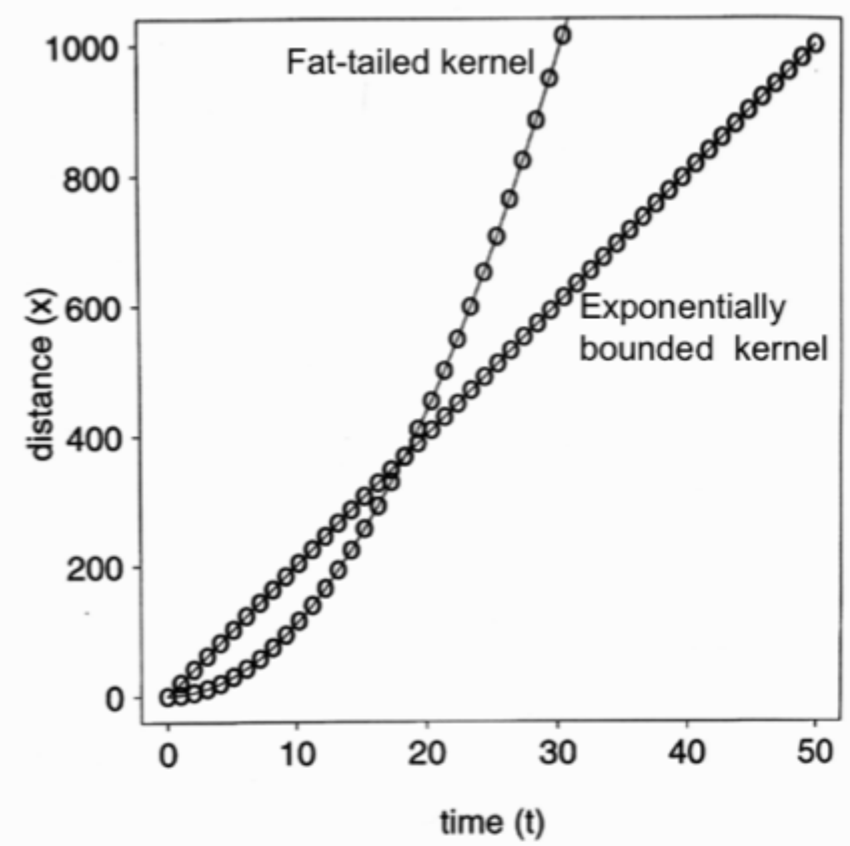
where

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

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^*.

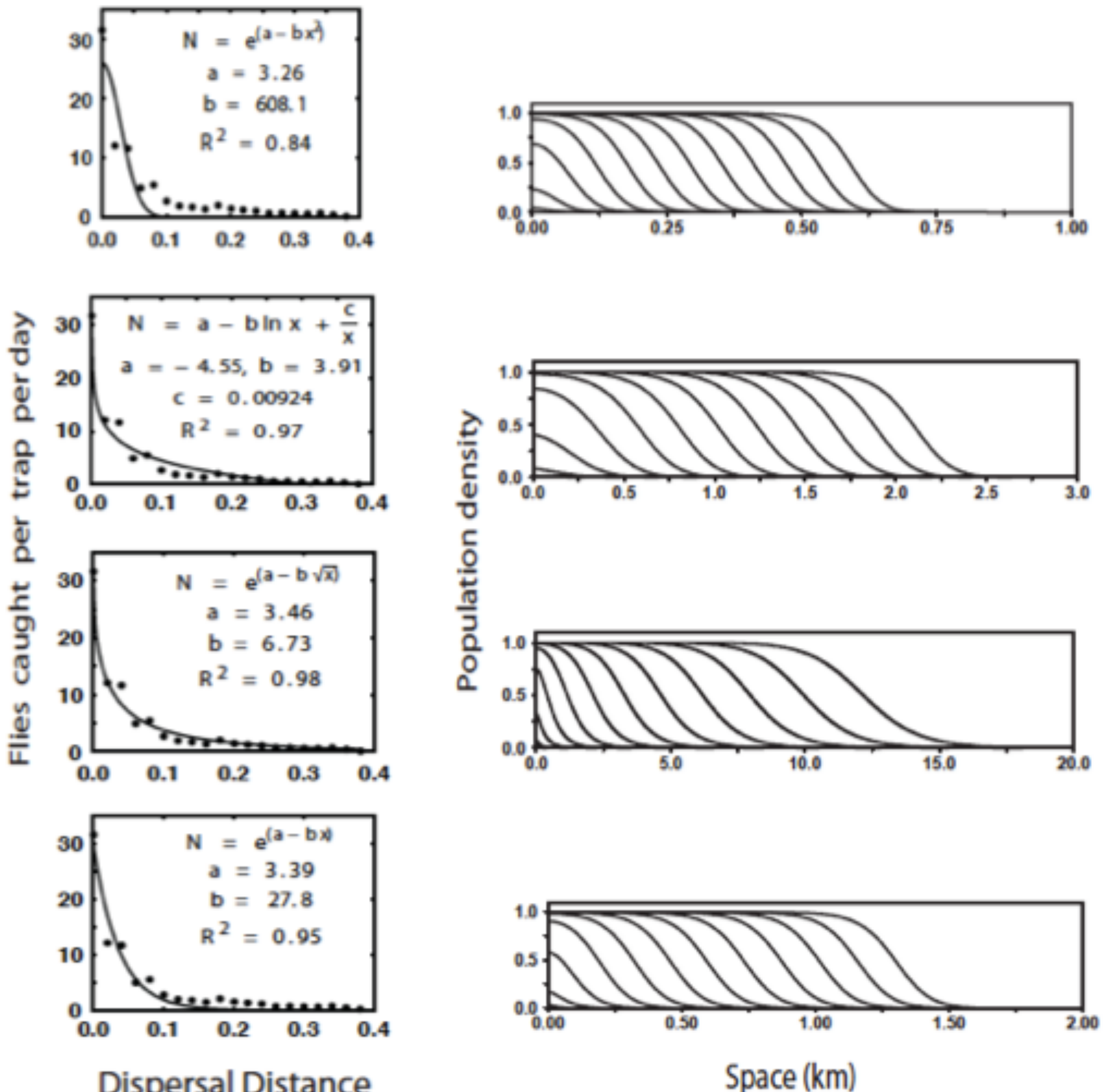
Spread with the integrodifference model

- 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)

Numerical solutions of integrodifference model



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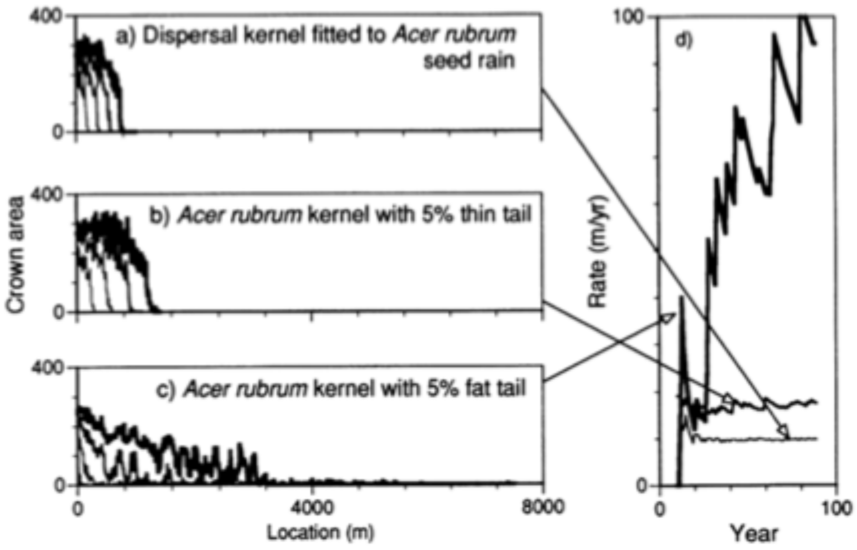
A resolution to Reid's paradox

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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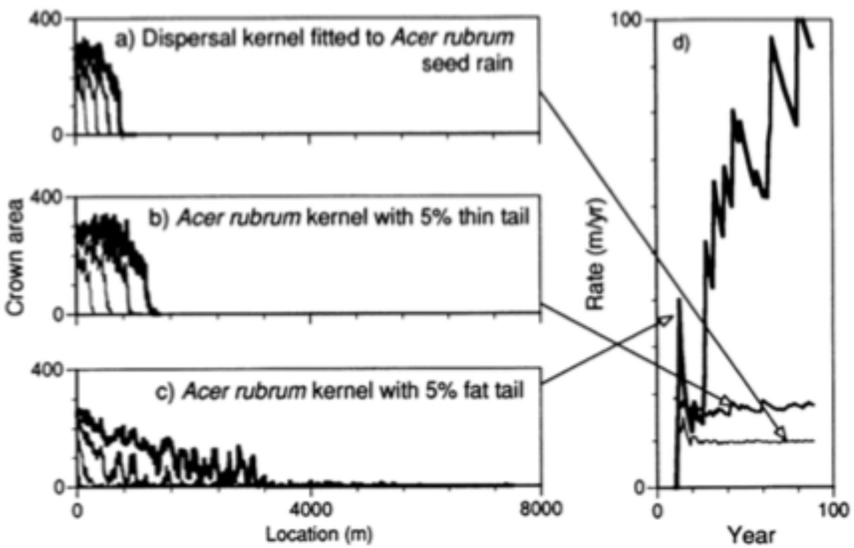

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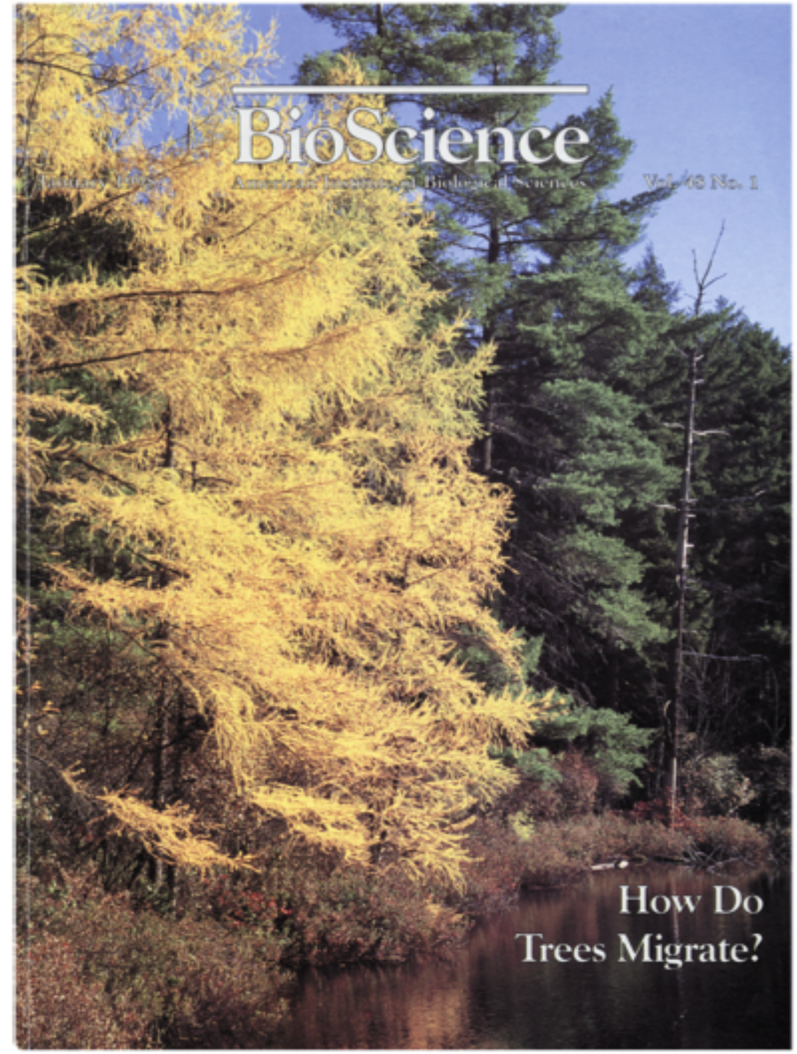

Clark et al. (1998)

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