Stochastic Models for Spreading Populations

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The Mathematics Behind Biological Invasions

Stochastic growth models

$N_{n+1} = \lambda_n N_n$ where λ_n is an iid random variable

Solution: $N_n = N_0 \prod_{i=0}^{n-1} \lambda_i$ with

average geometric growth rate $\bar{\lambda} = \left(\prod_{i=0}^{n-1} \lambda_i \right)^{1/n}$

average arithmetic growth rate $\bar{r}_n = \log\left(\bar{\lambda}\right) = \log\left(\prod_{i=0}^{n-1} \lambda_i \right)^{1/n} = \frac{1}{n} \sum_{i=0}^{n-1} \log\left(\lambda_i\right)$

The expected arithmetic growth rate is thus $\bar{r} = \mathrm{E}\left[\log\left(\lambda_n\right)\right]$

What is the growth rate for the expected number of individuals $\mathrm{E}\left[N_n\right]$?

Lewontin and Cohen (1969)

Stochastic growth models

What is the growth rate for the expected number of individuals $\mathrm{E}\left[N_n\right]$?

$\mathrm{E}\left[N_{n+1}\right]=\mathrm{E}\left[\lambda_n\right]\mathrm{E}\left[N_n\right]$ with solution $\mathrm{E}\left[N_n\right]=\mathrm{E}\left[N_0\right]\left(\mathrm{E}\left[\lambda_n\right]\right)^n$
and average geometric growth rate $\mathrm{E}\left[\lambda_n\right]$

The arithmetic growth rate in the expected number of individuals is thus $\tilde{r}=\log\left[\mathrm{E}\left(\lambda_i\right)\right]$

Which is bigger, the expected arithmetic growth rate ($\bar{r}$) or
the arithmetic growth rate in the expected number of individuals ($\tilde{r}$)?

$$\underbrace{\mathrm{E}\left[\log\left(\lambda_n\right)\right]}_{\bar{r}} \le \underbrace{\log\left[\mathrm{E}\left(\lambda_i\right)\right]}_{\tilde{r}} \qquad \text{so } \bar{r}\le\tilde{r}$$

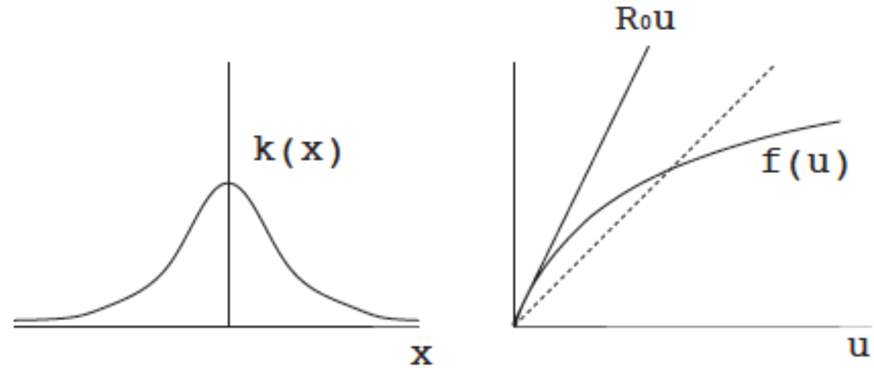
Jensen's Inequality: If X is a random variable and φ is a concave
function then $\mathrm{E}\left[\varphi\left(X\right)\right]\le\varphi\left(\mathrm{E}\left(X\right)\right)$

It is straightforward to find cases where $\bar{r}<0$ but $\tilde{r}>0$ (the expected growth rate
is negative but the growth rate in the expected number of individuals is positive)

Lewontin and Cohen (1969)

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

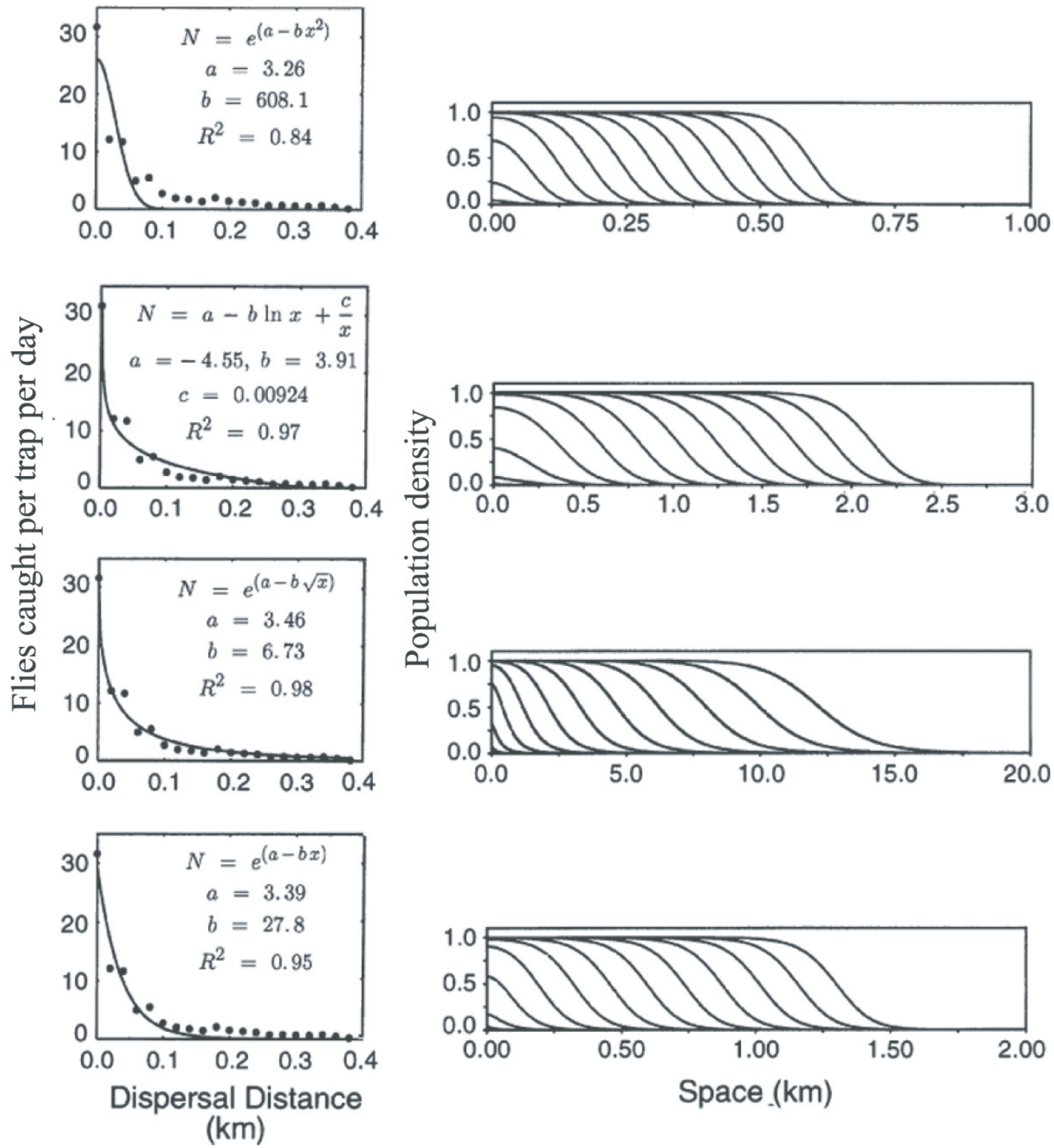
Ansatz $u_{n+1} = \alpha \exp(-s(x-nc))$ yields a dispersion relation between wave speed c and steepness s

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

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

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

Integrodifference model



Kot, Lewis and van den Driessche (1996)

Integrodifference model-stochastic environment

The population density $U_n(x)$ is a stochastic process satisfying

$$U_{n+1}(x) = \int_{-\infty}^{\infty} k_n(y-x) f\left(U_n(y), \lambda_n\right) dy$$

where k_n are chosen as iid random dispersal kernels and

λ_n are chosen as iid random variables independent from k_ts

At the leading edge $U_{n+1}(x) \approx \lambda_n \int_{-\infty}^{\infty} k_n(x-y) U_n(y)\, dy$

We start by looking at the rate of expansion of an *expectation wave*:

Taking expectations we have $\mathrm{E}\left[U_{n+1}(x)\right] = \mathrm{E}\left[\lambda_n\right] \int_{-\infty}^{\infty} \mathrm{E}\left[k_n(x-y)\right] \mathrm{E}\left[U_n(y)\right] dy$

$c^* = \min_{s>0} \frac{1}{s} \ln\left(\mathrm{E}\left[\lambda_n\right] \mathrm{E}\left[b_n(s)\right]\right)$ (rate at which $\mathrm{E}\left[U_n\right]$ expands)

Integrodifference model-stochastic environment

What if λ_n and k_n are correlated?

$$\tilde{c} = \min_{s>0} \frac{1}{s} \ln\left(\mathrm{E}\left[\lambda_n b_n(s) \right] \right)$$

versus

$$c^* = \min_{s>0} \frac{1}{s} \ln\left(\mathrm{E}\left[\lambda_n \right] \mathrm{E}\left[b_n(s) \right] \right)$$

positive correlations will tend to increase the rate of expansion

Integrodifference model-stochastic environment

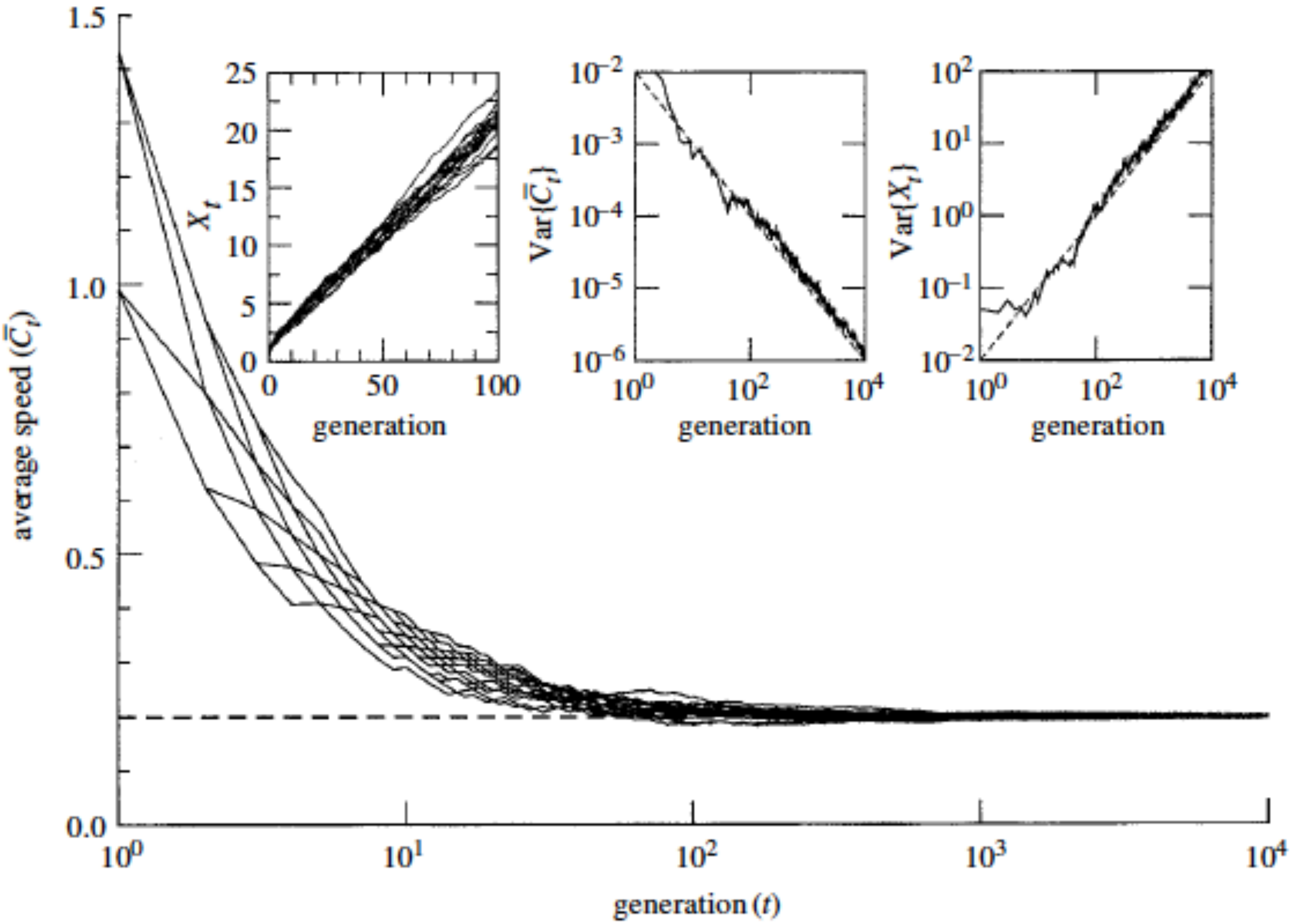
Previously we analyzed the rate of expansion of an *expectation wave*:

Now we consider the expected rate of expansion of the *stochastic wave*:

The rate of expansion itself will be a *stochastic process*, with a mean and variance

Suppose the population $U_n(x)$ has a random extent X_n defined to be the location farthest from the invasion's origin with $U_n(x) > u_{cr}$ and define the average speed to be $\bar{C}_n = (X_n - X_n)/n$

Integrodifference model-stochastic environment



Neubert Kot and Lewis (2000)

Integrodifference model-stochastic environment

Neubert et al (2000) showed that for a given wave steepness s

$$\bar{C}_n(s) = \frac{1}{n}\sum_{i=0}^{n-1}\frac{1}{s}\ln\left(\lambda_i b_i(s)\right)$$

This is the sum of n independent random variables, and so by the Central Limit Theorem $\bar{C}_n$ is asymptotically Normally distributed with mean μ and variance σ^2 given by

$$\mu = \min_{s>0} \mathrm{E}\left[\frac{1}{s}\ln\left(\lambda_n b_n(s)\right)\right] \text{ and } \sigma^2 = \frac{1}{n}\mathrm{Var}\left[\frac{1}{s^*}\ln\left(\lambda_n b_n(s^*)\right)\right]$$

where s^* is the value of s that gives the minimum for μ

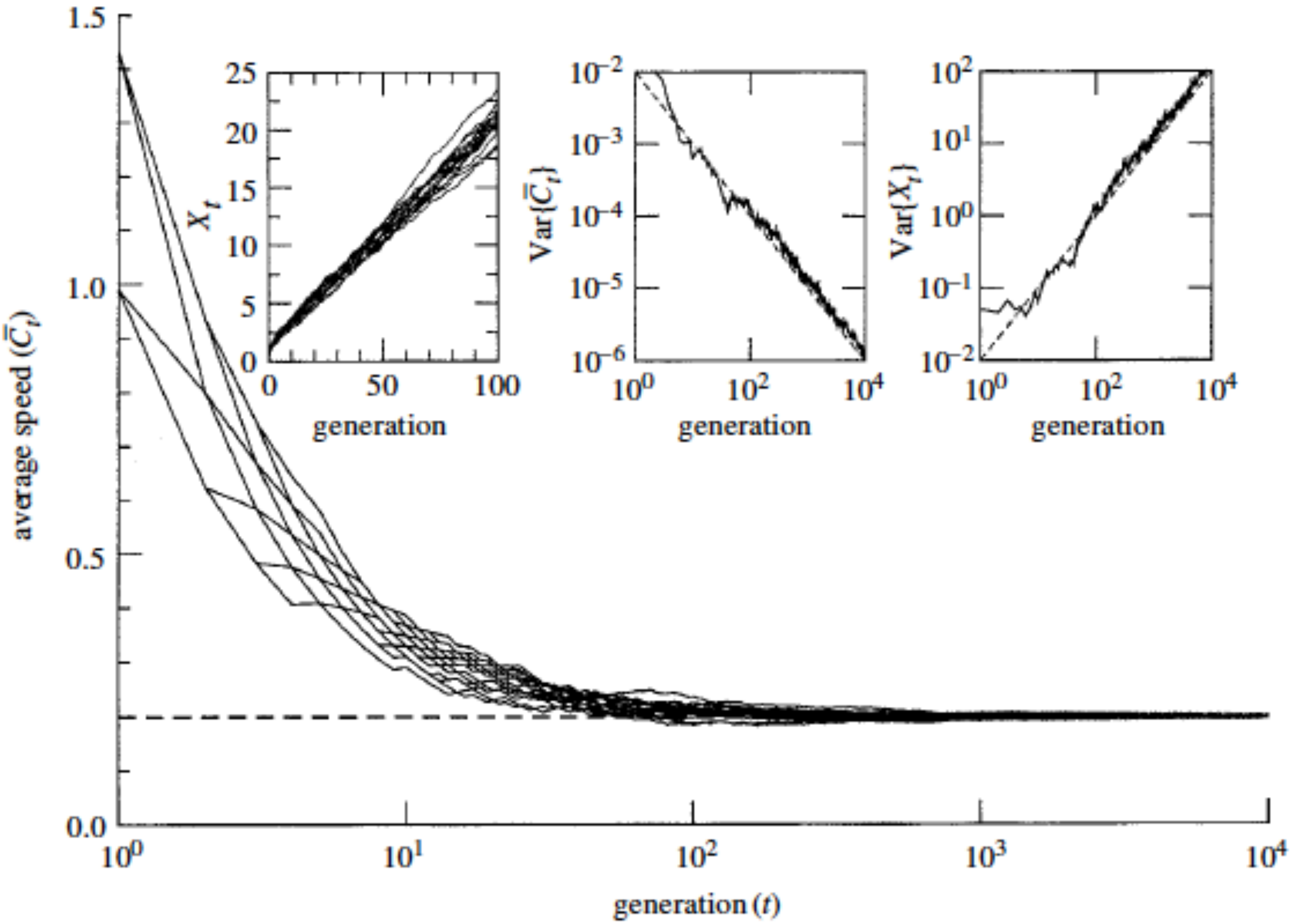
Central Limit Theorem

Suppose $X_0, X_1, \ldots$ are iid random variables with expectation μ, and variance $\sigma^2 < \infty$.

Define the sample average to be $S_n = \frac{1}{n}\sum_{i=0}^{n-1} X_n$.

Then an n approaches infinity, $\sqrt{n}\left(S_n - \mu\right)$ converges in distribution to $\mathrm{N}\left(0, \sigma^2\right)$.

Integrodifference model-stochastic environment



Neubert Kot and Lewis (2000)

Integrodifference model-stochastic environment

What happens to the average speed for large time?

As n $\to \infty$ the average speed $\bar{C}_n \to \min_{s>0} \mathrm{E}\left[\frac{1}{s}\ln\left(\lambda_n b_n(s)\right)\right] = \bar{c}$

How does this compare to the speed for the expectation wave?

$$\tilde{c} = \min_{s>0} \frac{1}{s}\ln\left(\mathrm{E}\left[\lambda_n b_n(s)\right]\right)$$

$\mathrm{E}\left[\ln\left(\lambda_n b_n(s)\right)\right] \le \ln\left(\mathrm{E}\left[\lambda_n b_n(s)\right]\right)$ so $\bar{c} \le \tilde{c}$

Jensen's Inequality: If X is a random variable and φ is a concave function then $\mathrm{E}\left[\varphi(X)\right] \le \varphi\left(\mathrm{E}(X)\right)$

Stage-structured Stochastic IDE Models

$$\mathbf{n}_{t+1} = \int_{-\infty}^{\infty} \left[\mathbf{K}_t \circ \mathbf{g}_t(\mathbf{n}_t(y))\right] \mathbf{n}_t(y)\, dy$$

$$\mathbf{g}_t(\mathbf{n}_t) = \begin{pmatrix} 0 & f_t \exp(-a n_t^{(2)}) \\ s_J & s_A \end{pmatrix}, \quad \mathbf{K}_t(y-x) = \begin{pmatrix} \delta(y-x) & \frac{1}{2b}\exp\left(-\frac{|y-x|}{b}\right) \\ \delta(y-x) & \delta(y-x) \end{pmatrix}$$

$$A_t = g_t(0) = \begin{pmatrix} 0 & f_t \\ s_J & s_A \end{pmatrix}$$ is the linearization of the growth matrix

$$\mathrm{B_t}(s) = \begin{pmatrix} 1 & \left(1 - s^2 b^2\right)^{-1} \\ 1 & 1 \end{pmatrix}$$ is the matrix of moment generating functions

$$\overline{C}_t \rightarrow \min_{s>0} \mathrm{E}\left[\frac{1}{s} \ln\left(\lambda_t \rho\left(A_t \circ B_t(s)\right)\right)\right] = \overline{c}$$

Schreiber and Ryan (2011)

Stage-structured Stochastic IDE Models

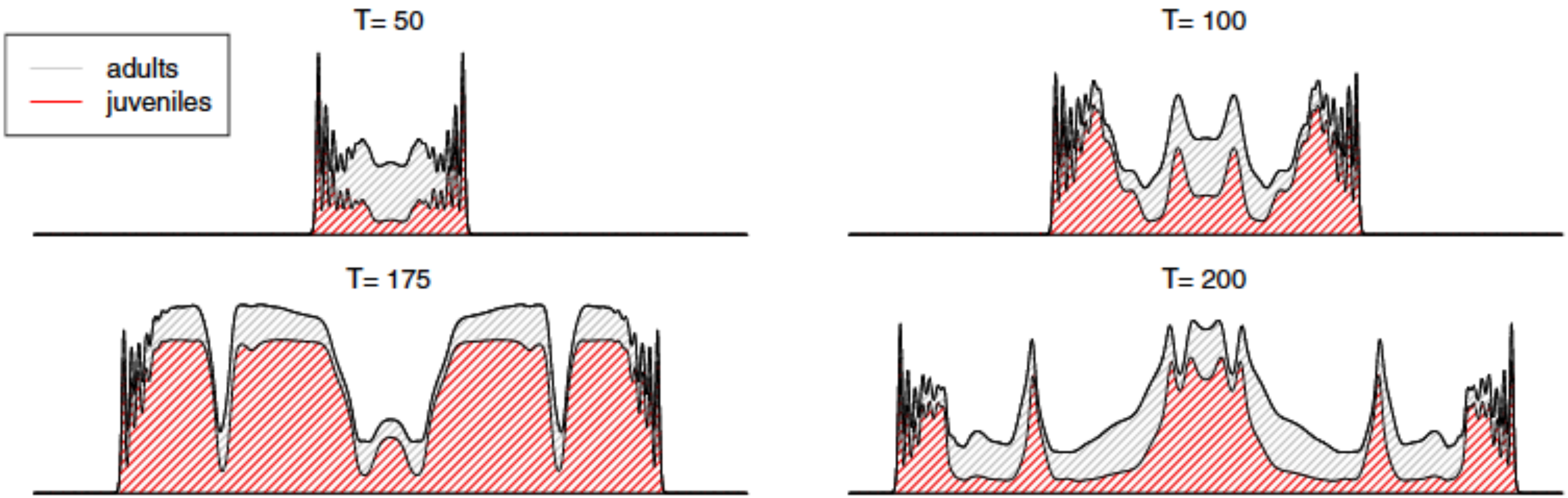
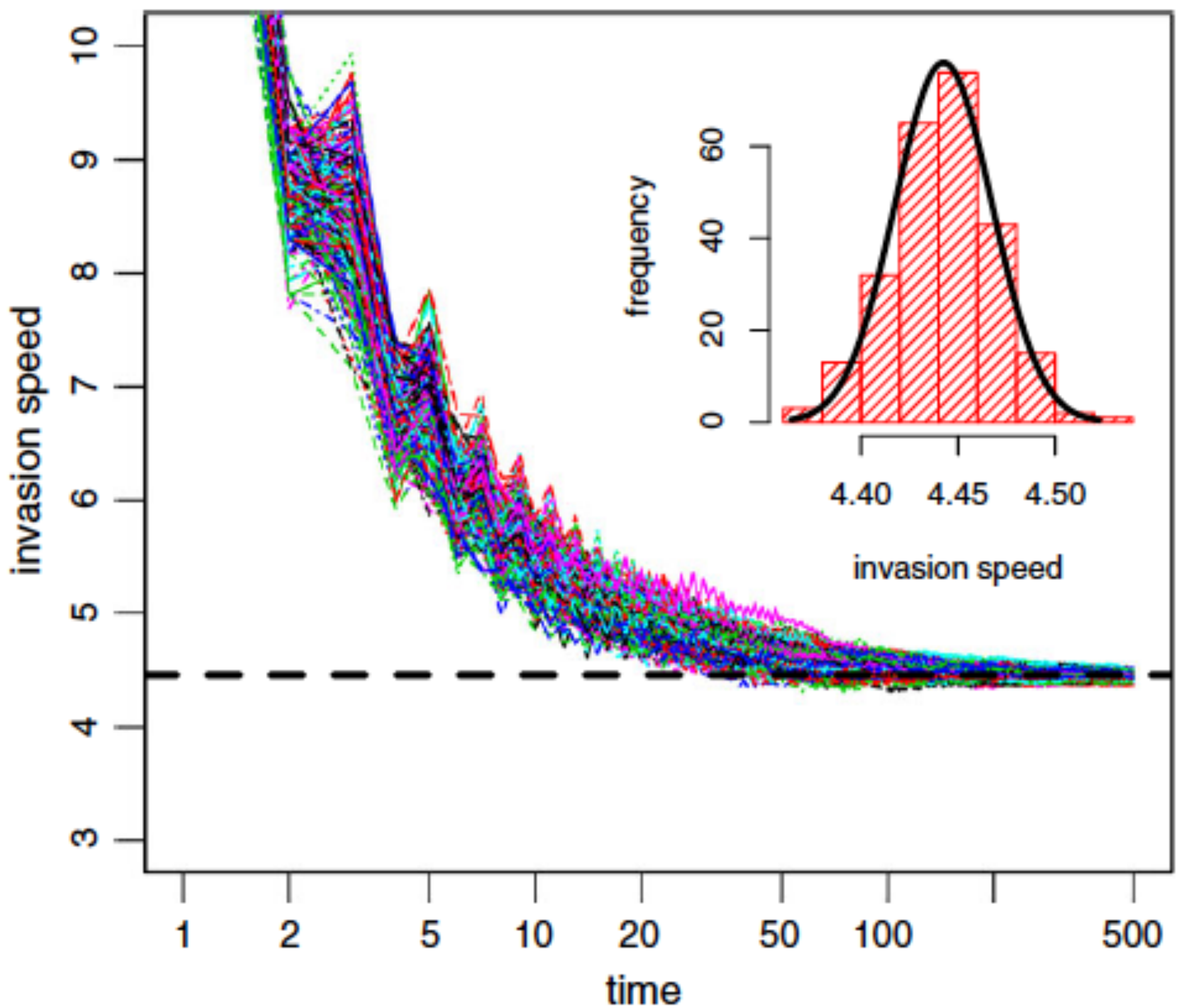


Fig. 2 Spatiotemporal dynamics of range expansion for the juvenile–adult model. Spatial distribution and abundance of juveniles (in *shaded red*) and adults (in *shaded gray*) plotted at the indicated times. Parameters ($\rho = 0$, $\mu = \ln 40$, $\sigma = 0.1$, $a = 1$, $s_J = 0.3$, and $s_A = 0.4$) are such that local dynamics are chaotic

Schreiber and Ryan (2011)

Stage-structured Stochastic IDE Models

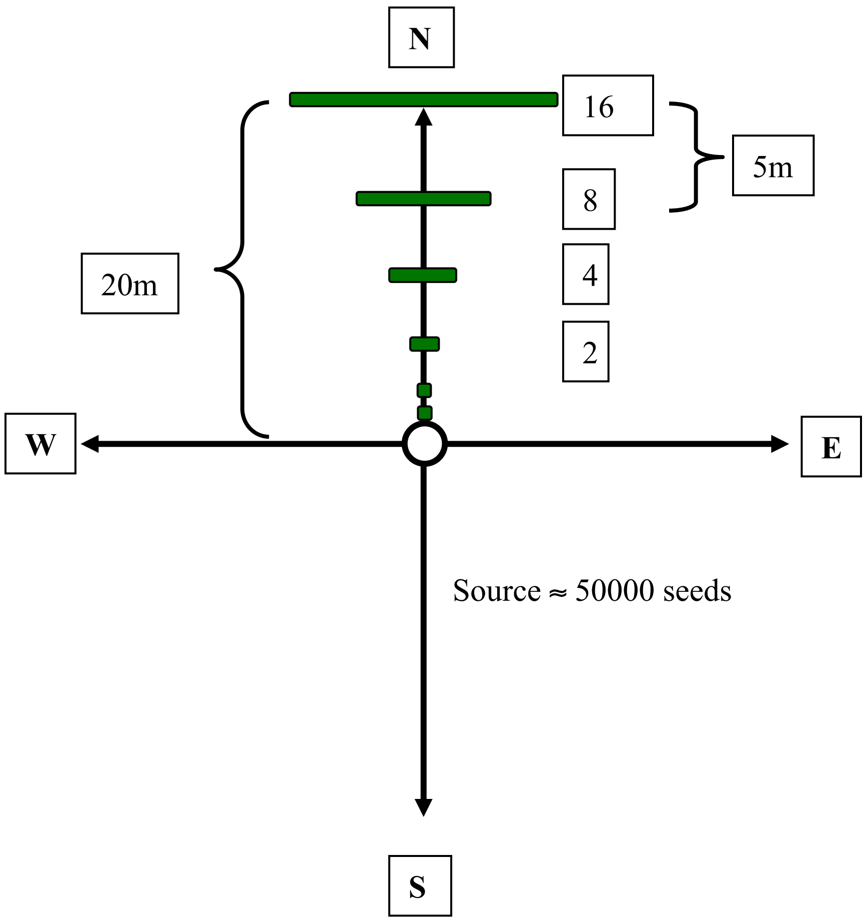
Fig. 1 The temporal dynamics of the wave speed $\frac{X_t - x_0}{t}$ for 250 simulations of the nonlinear juvenile–adult model. The front of the wave was determined by a threshold of $n_c = 0.001$ with equal weight on both stages, i.e., $\mathbf{w} = (1, 1)'$. The *dashed line* is the predicted asymptotic wave speed in Eq. 5. In the *inset*, a histogram of the waves speeds at $t = 500$ with the predicted normal approximation from the linearization. Parameter values are $\rho = 0$, $\mu = \ln 40$, $\sigma = 0.5$, $a = 1$, $s_J = 0.3$, and $s_A = 0.4$

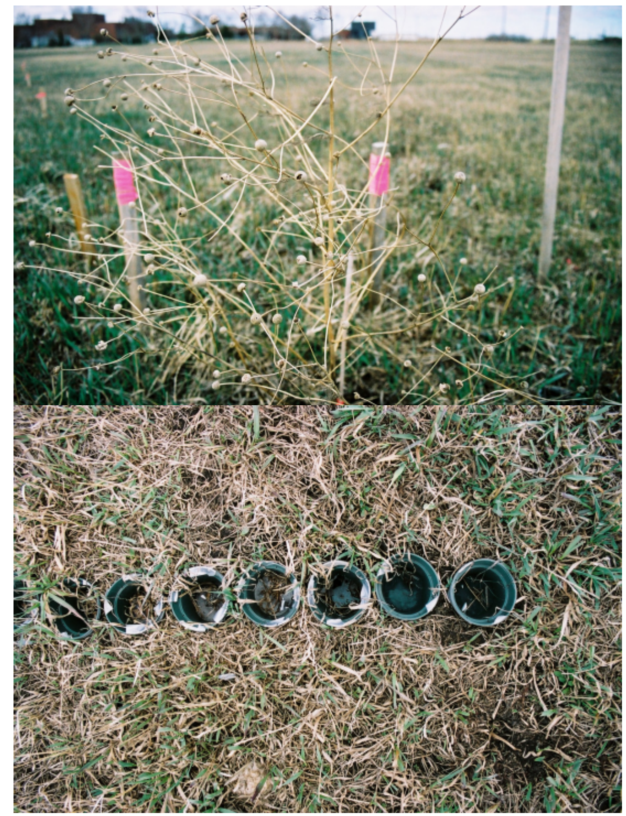


Schreiber and Ryan (2011)

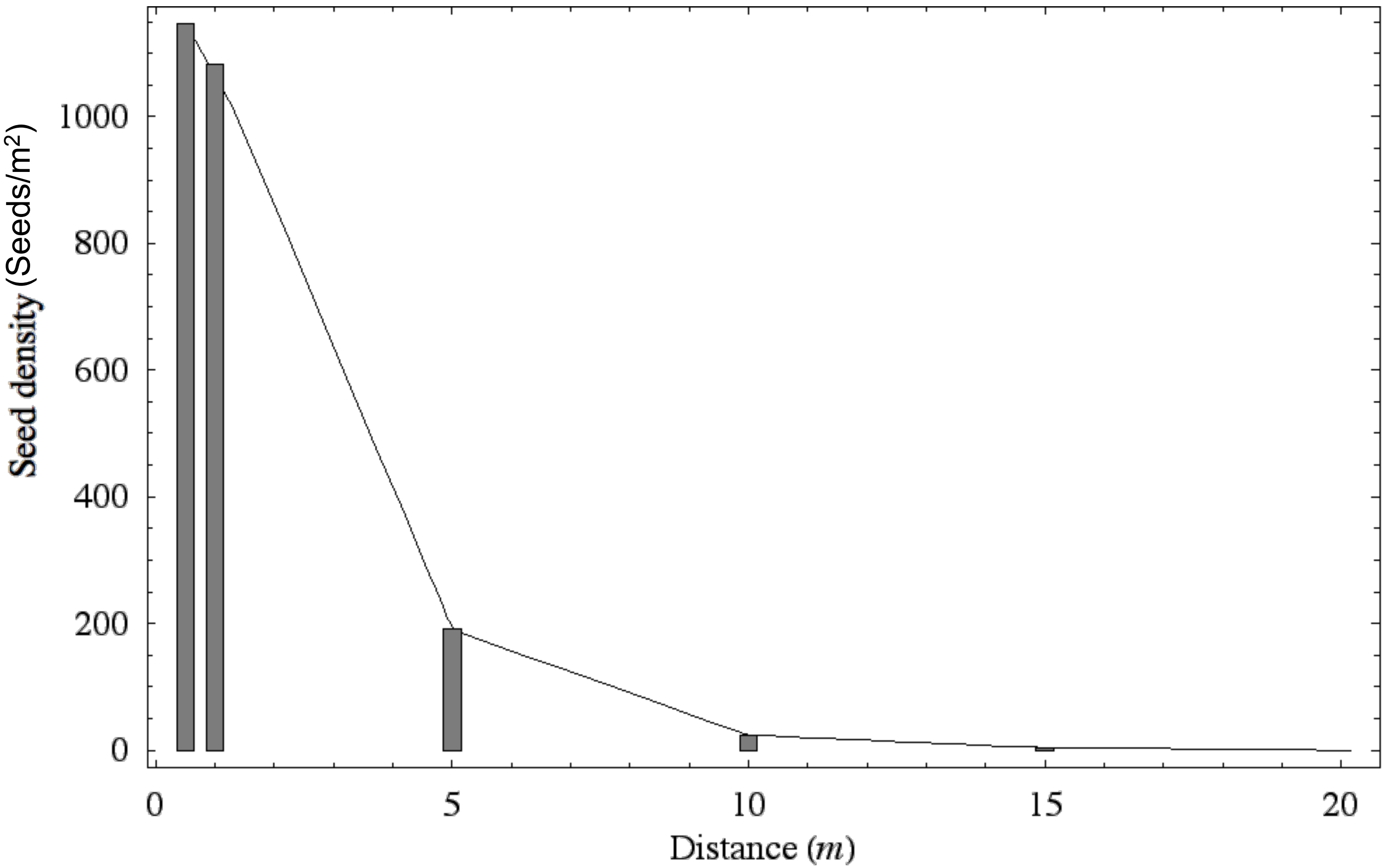
Scentless chamomile seed dispersal

Scentless chamomile:



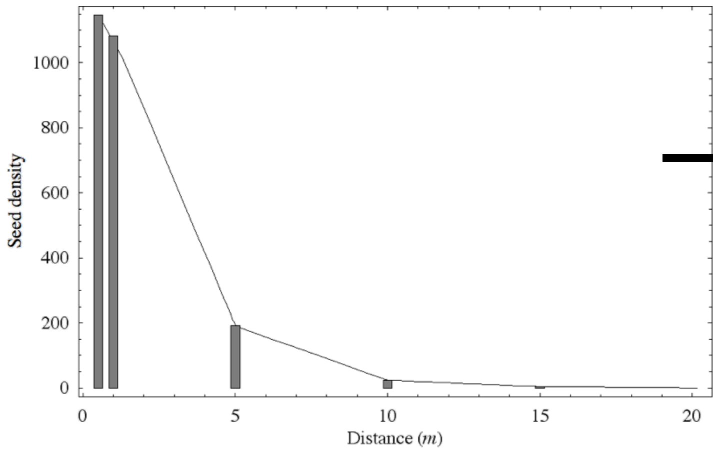


Scentless chamomile local dispersal data

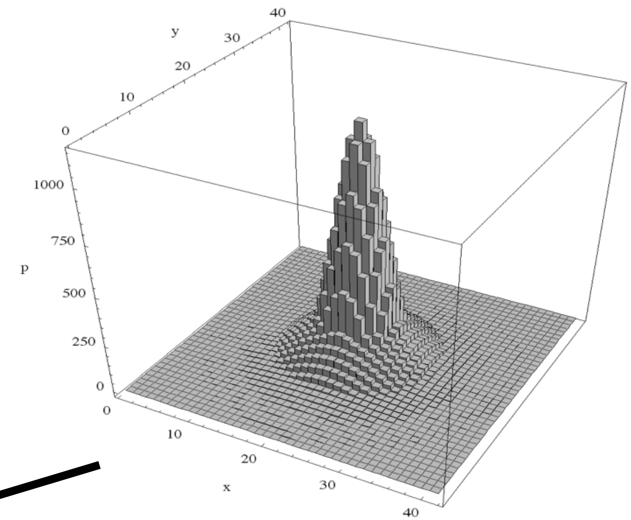


Scentless chamomile dispersal kernel

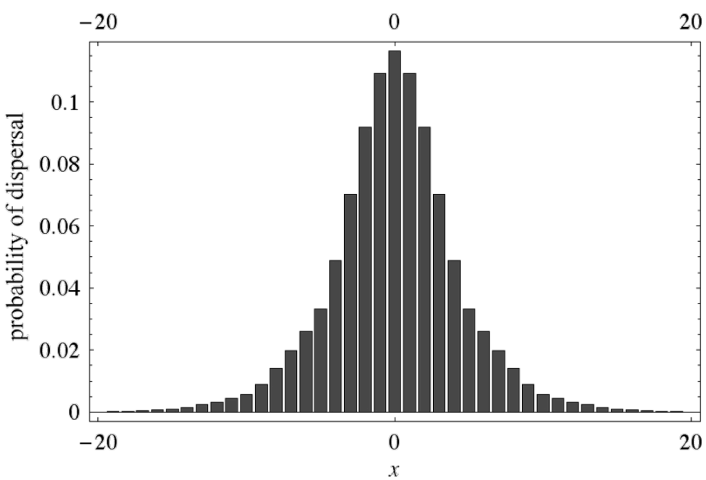
Scentless chamomile kernel:



Discretize



Marginalize



Scentless chamomile rate of spread

2004 (Year 1)

$$\mathbf{A} = \begin{bmatrix} 0.08 & 0 & 36376.45 \\ 0.27 & 0 & 517 \\ 0.04 & 0.45 & 297.85 \end{bmatrix}$$

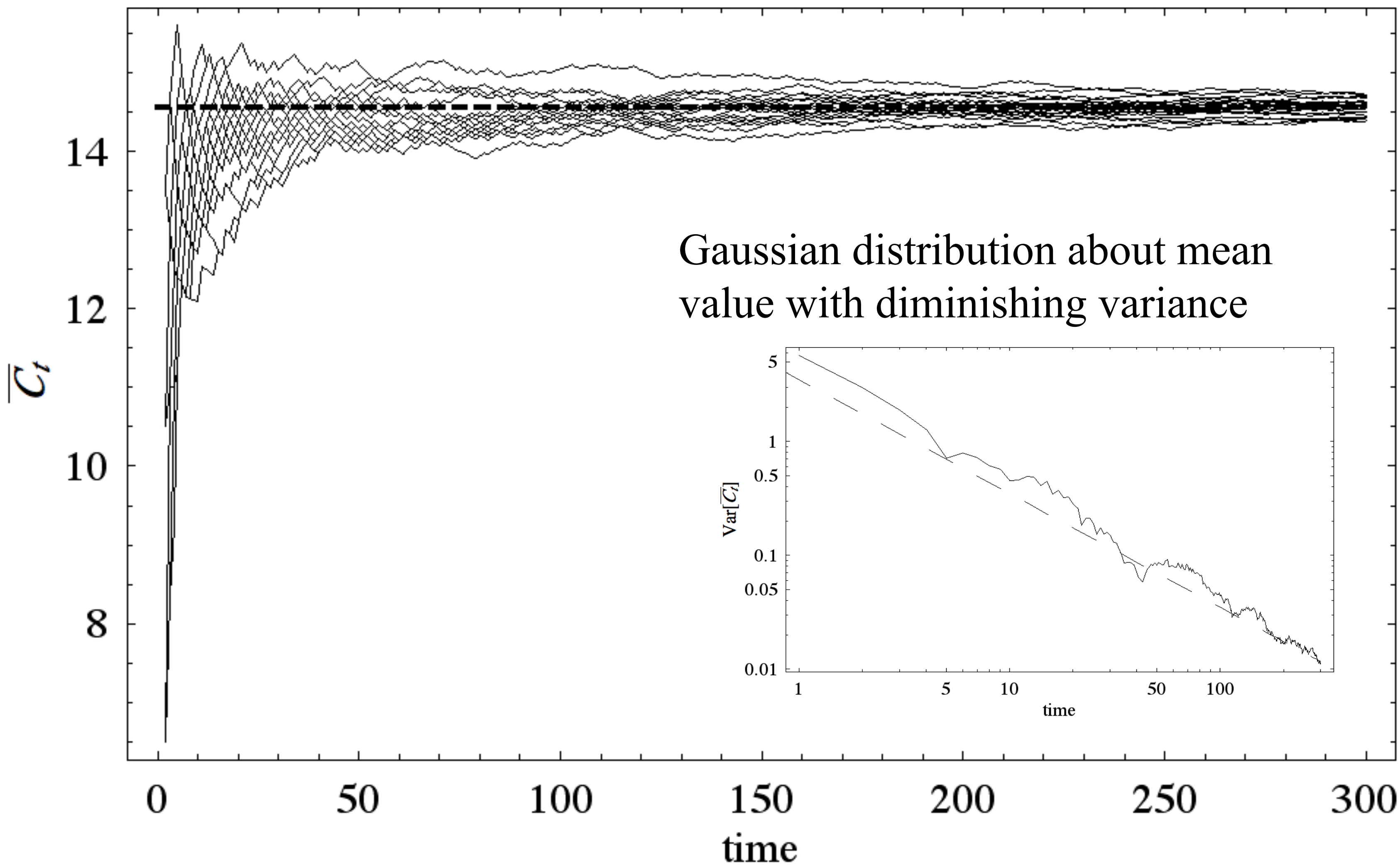
2005 (Year 2)

$$\mathbf{A} = \begin{bmatrix} 0.08 & 0 & 1775.22 \\ 0.27 & 0 & 25.24 \\ 0.04 & 0.45 & 14.53 \end{bmatrix}$$

Method	c year 1	c year 2
Equation	$c^* = 16.55 m/yr$	$c^* = 11.32 m/yr$
Simulation in 1D	$c^* \approx 16.55 m/yr$	$c^* \approx 11.32 m/yr$
Bootstrap 90% CI	$\{16.43, 16.67\}$	$\{10.33, 12.10\}$

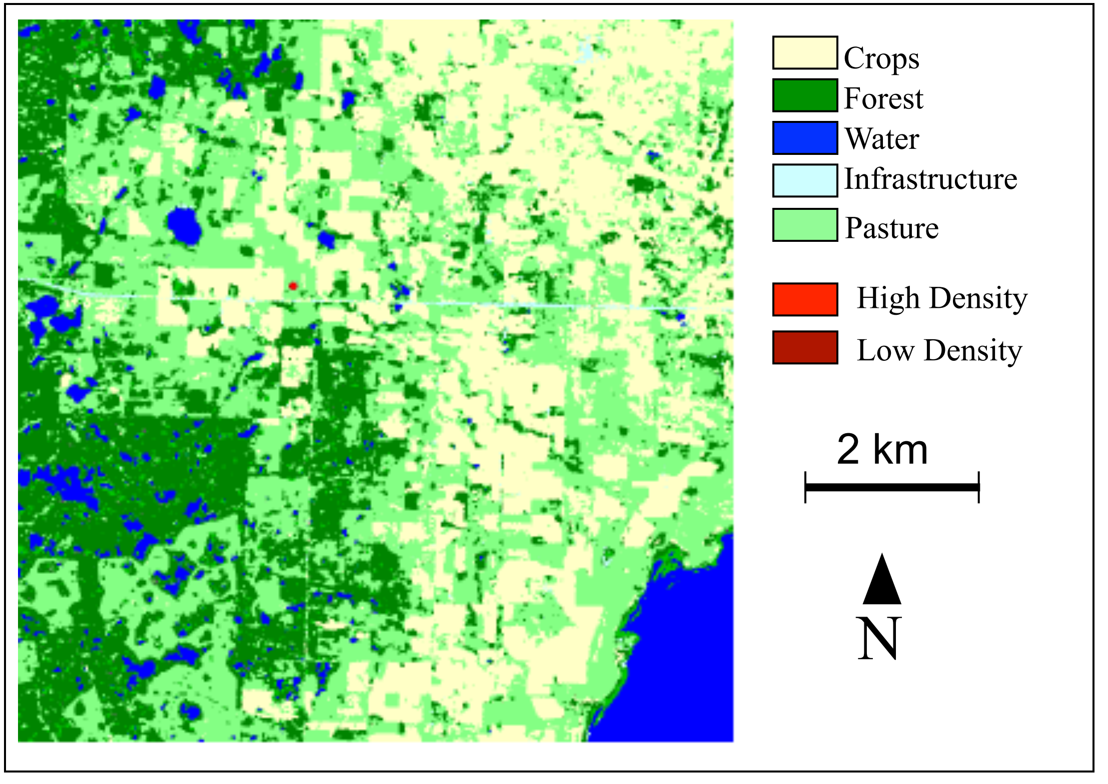
Scentless chamomile dispersal kernel

Stochastic Environments: year 1, year 2 $\overline{C}_t = \frac{x_t}{t}$



Scentless chamomile simulation model

$$\mathbf{n}_{t+1}(\mathbf{x}_i) = \mathbf{P}(\mathbf{x}_i) \circ \sum_{x_j \in \Omega} [\mathbf{K}(\mathbf{x}_j - \mathbf{x}_i) \circ \mathbf{A}] \, \mathbf{n}_t(\mathbf{x}_j)$$



Spread is approx 14 m per year

Furthest forward velocity

Consider simple branching process with Brownian motion:

•At time $t = 0$ a single particle commences standard Brownian motion, with mean squared displacement per unit time D, starting from $x = 0$ and continuing for a random length of time T given by an exponential random variable with mean $1/r$.

•At this point in time the particle splits in two and the new particles continue with independent Brownian paths starting from $x(T)$

•These particles are subject to the same splitting and movement rules, as are their offspring.

•After an elapsed period of time t, there are n particles located t $x_1(t)\ldots x_n(t)$.

•Denote $u(x,t) = \Pr\left[\max_{i \le n} x_i(t) < x\right]$

•Then

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + ru(1-u), \qquad u(x,0) = 1 - H(x)$$

McKean (1975)

Furthest forward velocity

What if the the stochastic process is nonlinear?

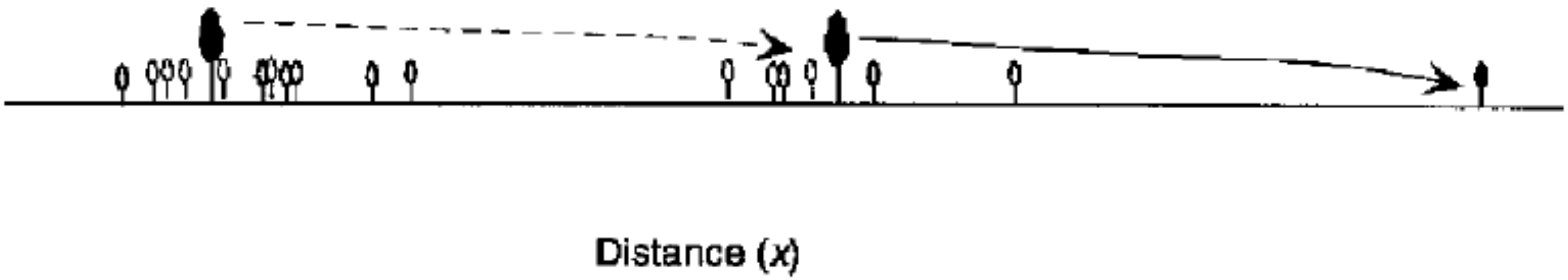
Let $p(x;N)\ dx$ be the probability that the furthest dispersing individual from a group of N evenly spaced parents settles on the interval $\left[x, x+dx\right]$. Then p is the probability density function for the furthest dispersing individual.

Let $P(x;N)\ dx$ be the probability that the furthest dispersing individual from a group of N evenly spaced parents lies to the left of the point x. Then P is the cumulative density function for the furthest dispersing individual.

Let $k(x)$ be the dispersal kernel for a single disperser and $K(x) = \int_{-\infty}^{x} k(y)\ dy$ be the cumulative density function for dispersal.

Furthest forward velocity

Consider "spread by extremes," where the furthest forward individual in the population produces the furthest forward individual in the next generation



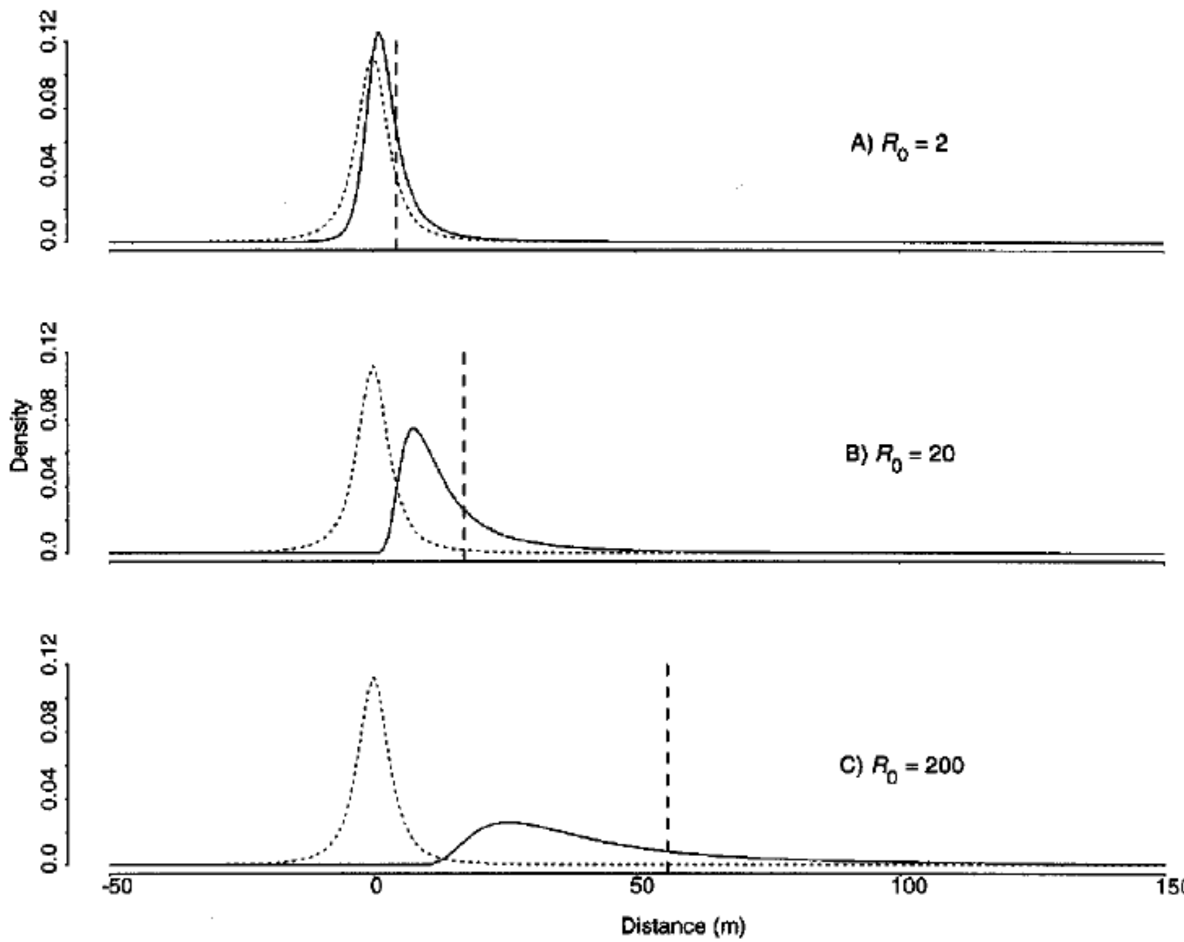
Then if each individual produces R_0 offspring, and offspring disperse independently

$$P(x;1) = \left[K(x)\right]^{R_0} \text{ and } p(x;1) = \frac{d}{dx}P(x;1) = R_0 k(x)\left[K(x)\right]^{R_0-1}$$

Clark Lewis and Horvath (2001)

Furthest forward velocity

$$p(x;1) = \frac{d}{dx}P(x;1) = R_0 k(x)\left[K(x)\right]^{R_0 - 1}$$

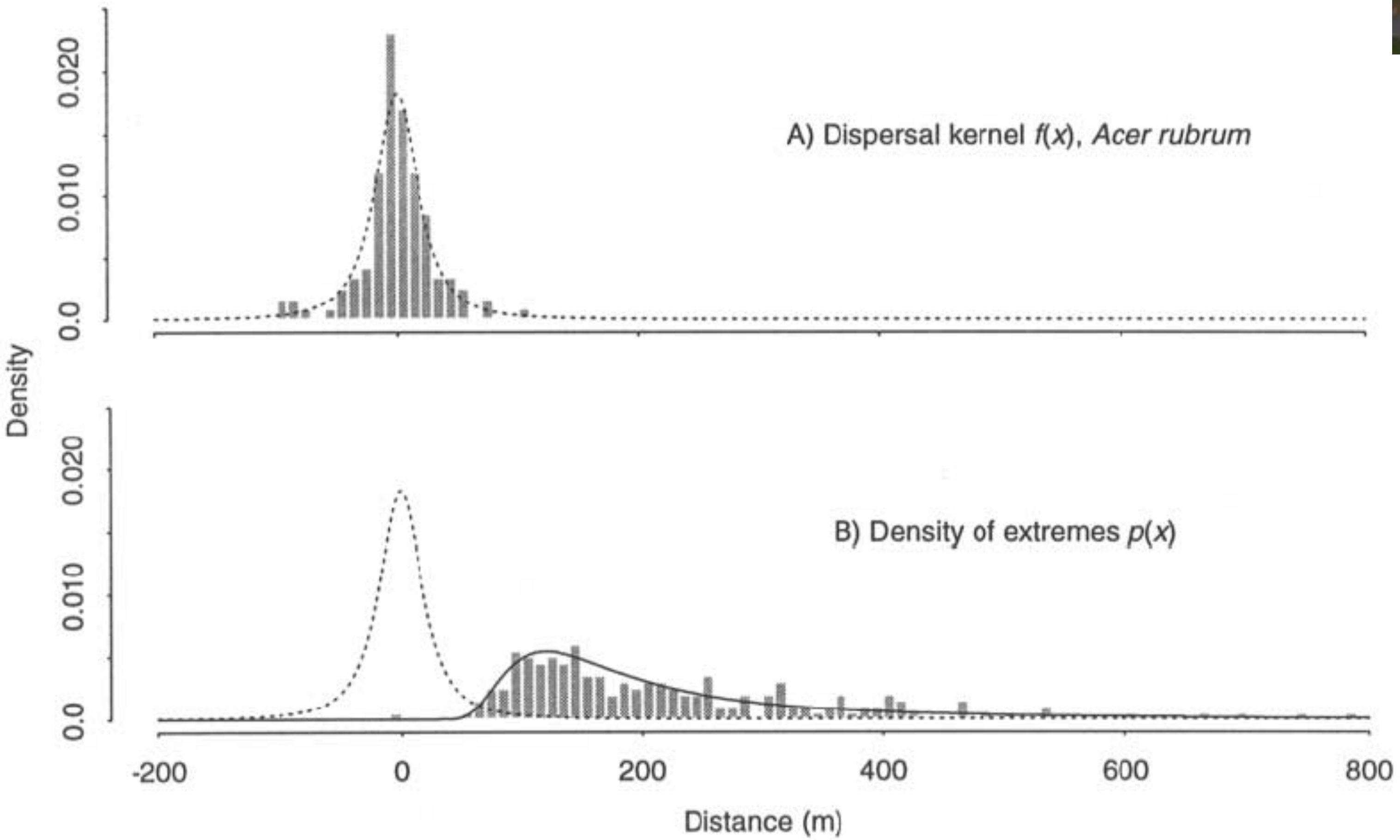


Clark Lewis and Horvath (2001)

Furthest forward velocity

$$p(x;1) = \frac{d}{dx}P(x;1) = R_0 k(x)\left[K(x)\right]^{R_0 - 1}$$

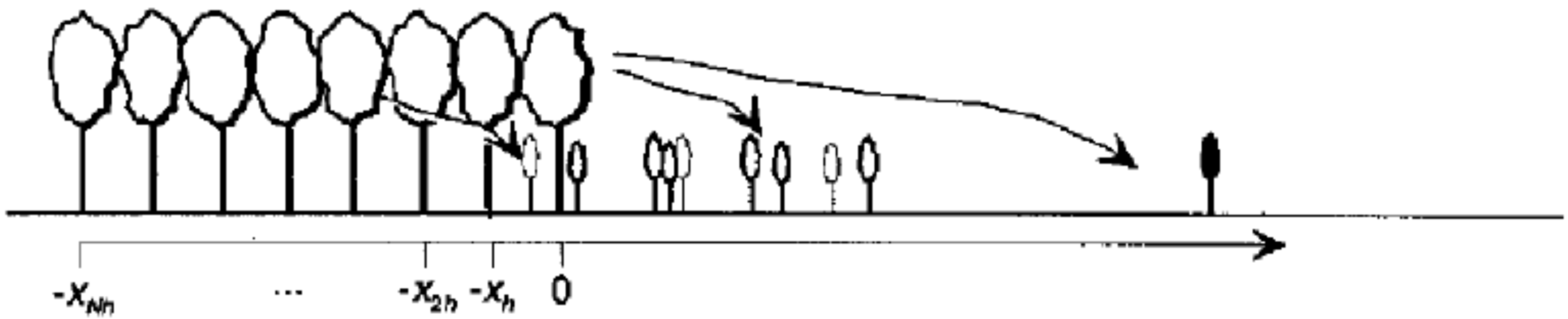
Red maple



Clark Lewis and Horvath (2001)

Furthest forward velocity

Consider "initial expansion from a population frontier," where trees are packed at spacing h, and the furthest forward individual in the population can come from any tree



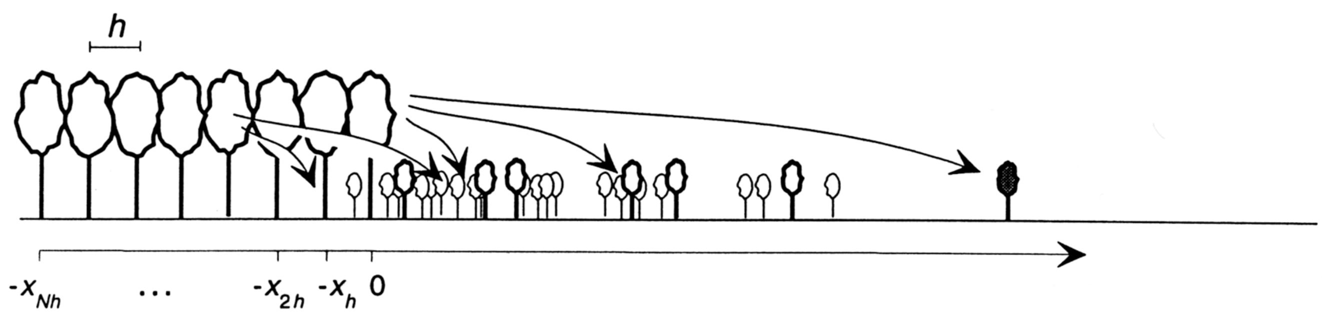
Then if each individual produces R_0 offspring, and offspring disperse independently

$$P(x;N) = \prod_{k=0}^{N} \left[K(x + x_{hk})\right]^{R_0} \text{ and } p(x;N) = \frac{d}{dx} P(x;N)$$

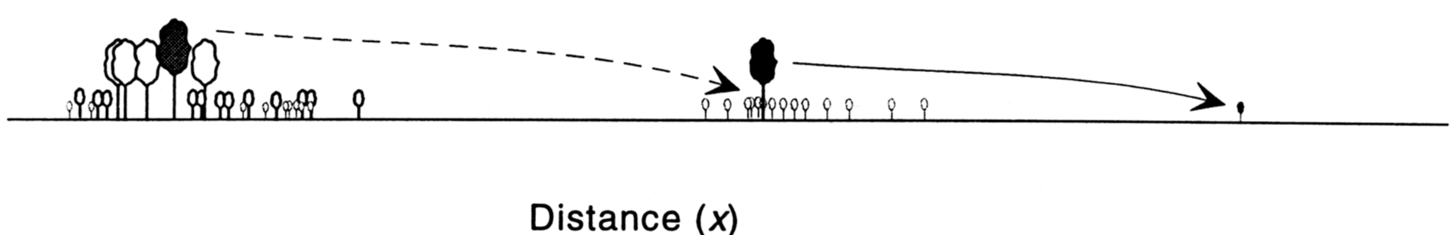
Clark Lewis and Horvath (2001)

Approach

- An upper bound on the speed comes from assuming that forest 'fills in' immediately behind the furthest forward tree.



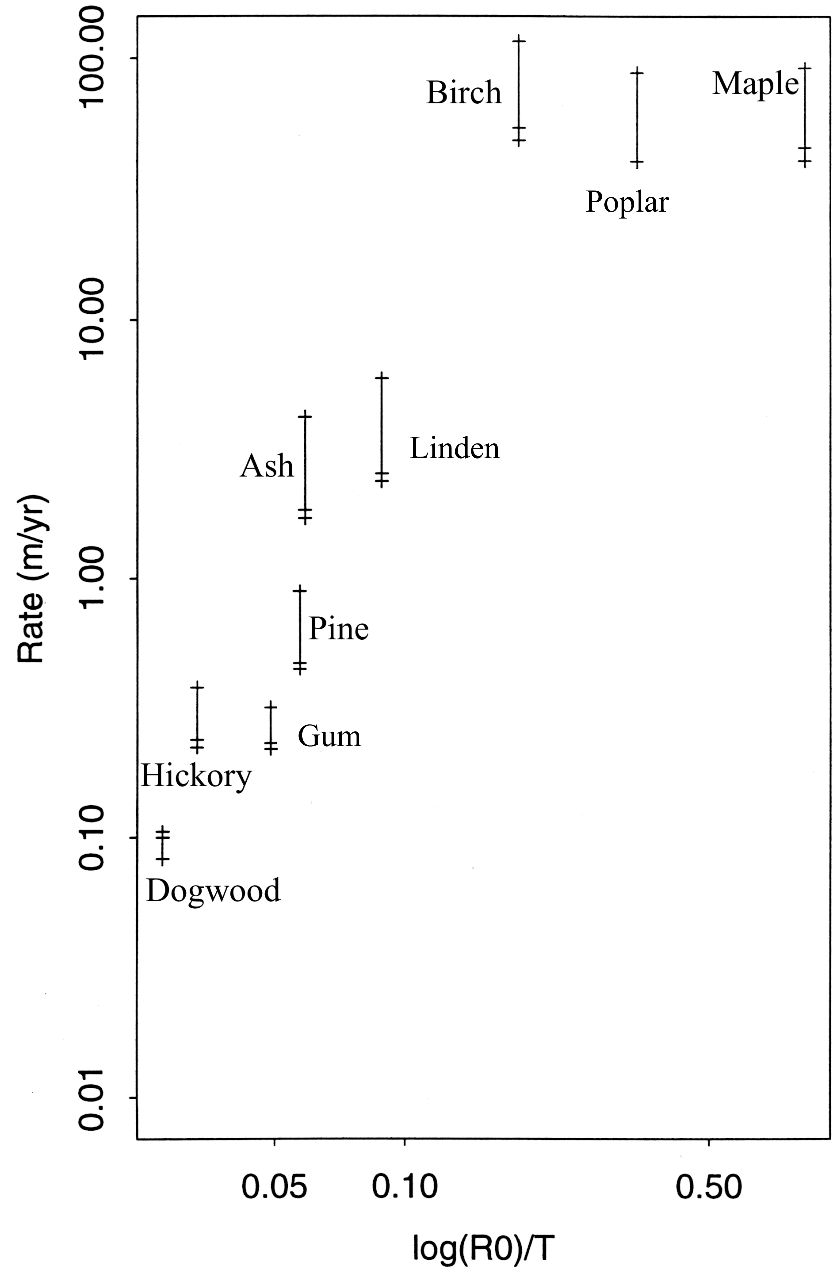
- A lower bound on the speed comes from assuming that the furthest-forward tree remains isolated and produces the furthest-forward tree in the next generation.



Clark Lewis and Horvath (2001)

Results

- Both bounds generally lie **above** the theoretical predictions of Fisher's model and **below** theoretical predictions using integrodifference model.
- The upper bound typically lies **below** historical spread rates of 100-1000 m per year.
- Kernels with fat tails no longer produce asymptotically infinite spread rates.



(Clark, Lewis and Horvath 2001)

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