Accelerating rates of spread in reaction-diffusion recolonization models

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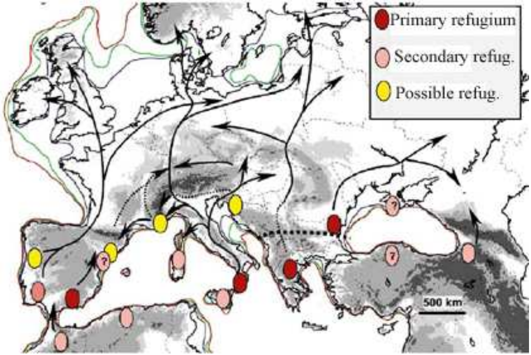
Biostatistique
BIO/Π
& Processus Spatiaux

Deterministic and stochastic front propagation

Banff, March 22, 2010

Reid's paradox of rapid plant migration

(*Reid, 1899*): Recolonization from Southern refugia at the end of the last glacial period ($\sim 10\,000$ years ago).
Current distribution of tree species in Europe and North America cannot be explained by diffusive dispersal.



$\rightarrow$ recolonization was faster than expected

Reid's paradox of rapid plant migration

Skellam's point of view (Skellam 1951)

1. INTRODUCTION

1·1. It is now fifty years since the publication of *The Origin of the British Flora* by Clement Reid (1899). In it is suggested an interesting numerical problem on the rate of dispersal of plants. Reid states: 'Though the post-glacial period counts its thousands of years, it was not indefinitely long, and few plants that merely scatter their seed could advance more than a yard in a year, for though the seed might be thrown further, it would be several seasons before an oak for instance, would be sufficiently grown to form a fresh starting point. 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.'

Of the population spread out after n generations, that proportion lying outside a circle of radius R is

$$p = \int_R^\infty \exp\left[-r^2/na^2\right] 2r\,dr/na^2 = \exp\{-R^2/na^2\}. \tag{4}$$

We then have $R/a < 300\sqrt{(\log 9{,}000{,}000)} = 1200$.

In the original form of the problem as stated by Reid, R is given as 600 miles. It then follows that a (the root mean square distance of daughter oaks about their parent) $> \frac{1}{2}$ mile. On these premises the conclusion which Reid reached appears inescapable—namely, that animals such as rooks must have played a major role as agents of dispersal.

Reid's paradox of rapid plant migration

The Long Distance Dispersal explanation

Nowadays, Reid's paradox = any recolonization faster than predicted on the basis of known dispersal capabilities.

The LDD explanation (*Skellam 1951, Clark et al., 1998*)

Interpretation: Rare, long distance dispersal events.
Models: Integro-difference or integro-differential equations:

$$N_{k+1}(x) = \int_{-\infty}^{+\infty} j(|x-y|)g(N_k(y))dy$$

or:

$$\frac{\partial u}{\partial t}(t,x) = \int_{-\infty}^{+\infty} j(|x-y|)u(t,y)dy - u + f(u)$$

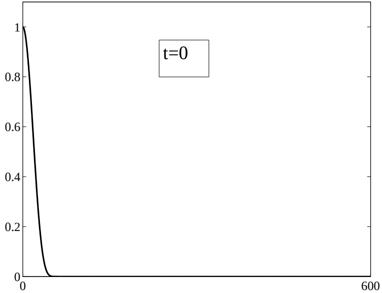
Results: Infinite spreading speed and accelerating rate of spread if the dispersal kernel j is "fat-tailed" (*Kot et al., 1996; Cabré and Roquejoffre 2009; Garnier 2010*).
(finite spreading speed if the kernel is exponentially bounded; Weinberger 1982)

Reid's paradox of rapid plant migration

Alternative explanation

Diffusion and growth from cryptic populations

Interpretation: Colonization-retraction events can lead to several profiles of initial condition: Colonization



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Mathematical results: Hamel, Roques, Fady, Fayard and Klein, 2010.

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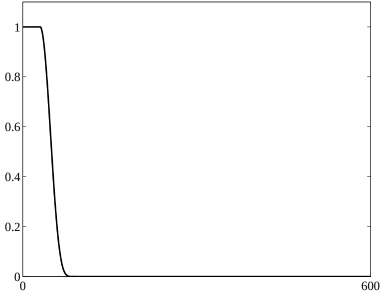

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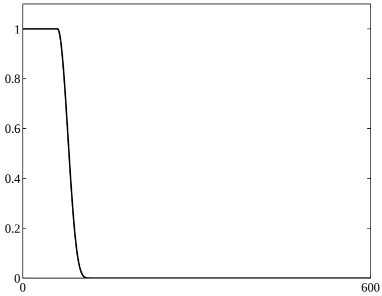

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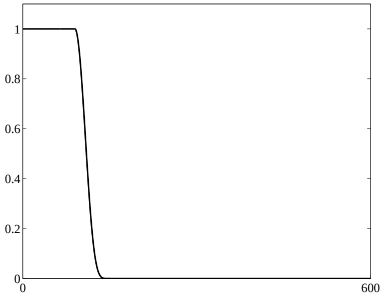

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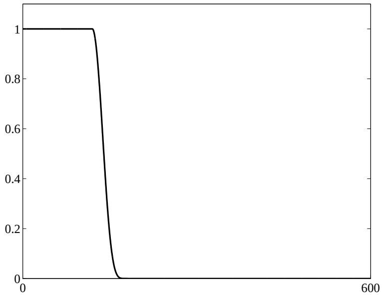

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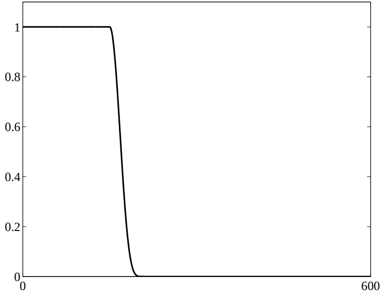

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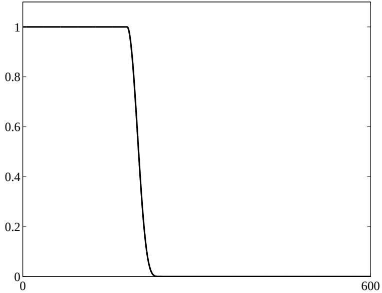

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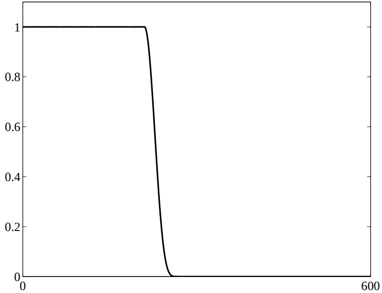

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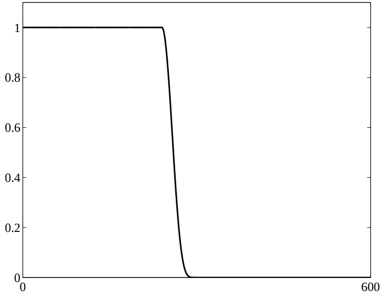

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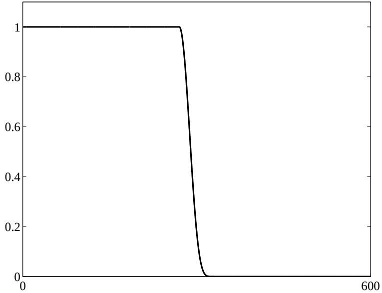

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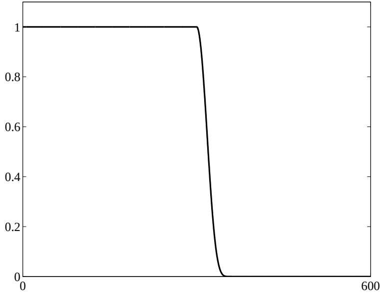

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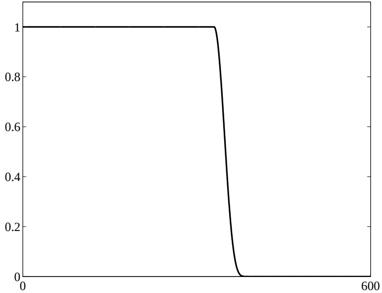

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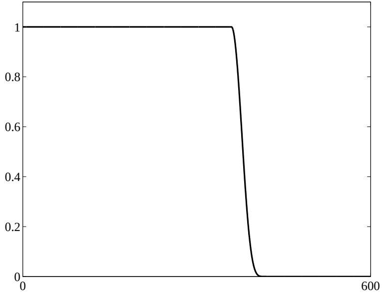

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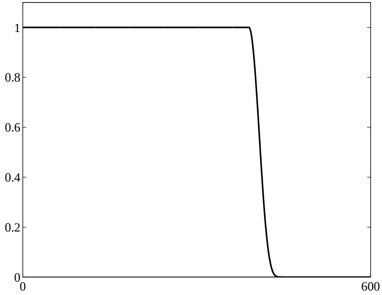

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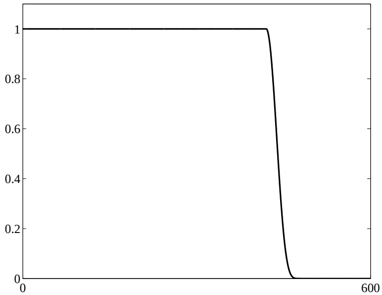

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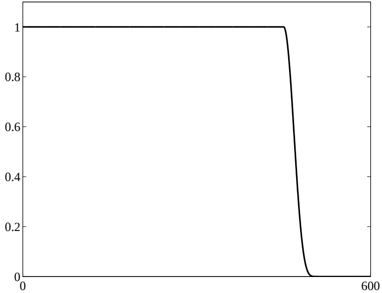

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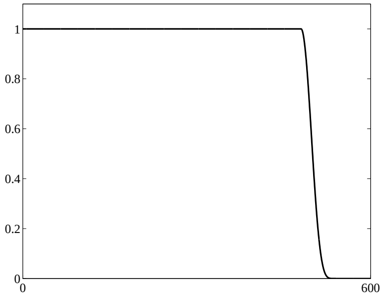

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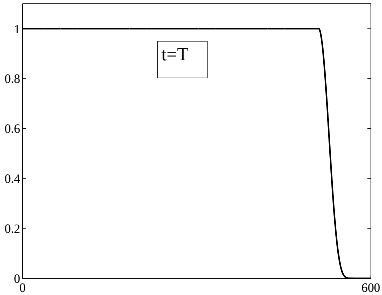

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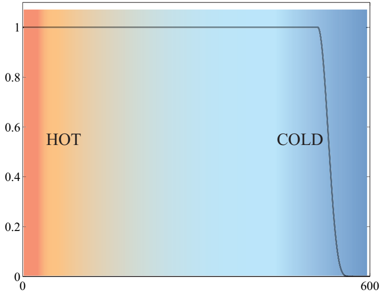
Interpretation: Colonization-retraction events can lead to several profiles of initial condition: External constraint



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Alternative explanation

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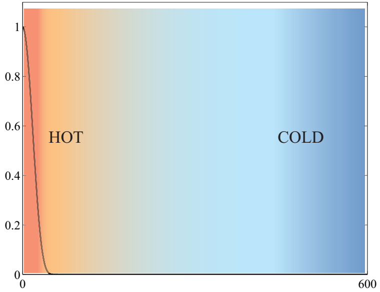
Interpretation: Colonization-retraction events can lead to several profiles of initial condition: Retraction



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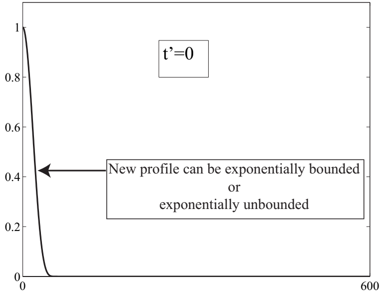
Interpretation: Colonization-retraction events can lead to several profiles of initial condition: Constraint is relaxed; recolonization



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Reaction-diffusion model, basic assumptions

The model:

$$\frac{\partial u}{\partial t}(t,x) = \frac{\partial^2 u}{\partial x^2} + f(u), \text{ for } t > 0 \text{ and } x \in (-\infty, +\infty).$$

Assumptions on f :

$$f > 0 \text{ in } (0,1), \ f(0) = f(1) = 0 \text{ and } f \text{ is concave on } [0,1]$$

Example: $f(u) = u\,(1-u)$.

In any cases $\rightarrow$ no Allee effect.

Basic assumptions on $u(0,x) = u_0(x)$:

$$u_0(x) = 1 \text{ for } x \leq 0, \ u_0' < 0 \text{ for } x > 0 \text{ and } u_0(+\infty) = 0.$$

Reaction-diffusion model, the initial condition (IC)

We either assume that u_0 is:
Exponentially bounded (EB),
or
Exponentially unbounded (EU).

Definition

We say that u_0 is exponentially bounded (EB) if, for some $\alpha > 0$, we have $0 \leq u_0(x) \leq e^{-\alpha x}$, for large x.

Examples: compactly supported functions, solutions of KPP equations at time t, starting from compactly supported IC, ...

Definition

We say that u_0 is exponentially unbounded (EU) if $u_0(x)\, e^{\alpha x} \to +\infty$ as $x \to +\infty$ for all $\alpha > 0$.

Examples: $u_0(x) = e^{-\sqrt{x}}$, $u_0(x) = x^{-n}$, ... for large x.

Exponentially bounded IC: classical results

Let us define:
the population range, $x_\lambda(t) = \inf\{x > 0,\ u(t,x) < \lambda\}$,
the rate of spread, $v_\lambda(t) = \dfrac{x_\lambda(t)}{t}$,
the spreading speed c.

- If $u_0(x)$ decreases faster than $e^{-\sqrt{f'(0)}x}$ (eg compactly supported):
  (*KPP, 1937*) $\rightarrow$ spreading speed: $c = c^* = 2\sqrt{f'(0)}$.

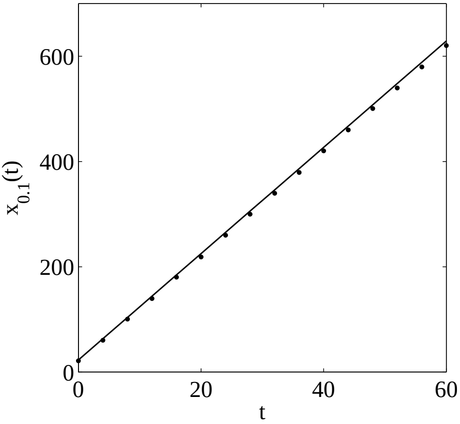
- If $u_0(x) \sim e^{-\alpha x}$, with $0 < \alpha < \sqrt{f'(0)}$:
  (*Bramson, 1983*) $\rightarrow$ the solution spreads faster:
  $c = c(\alpha) = \alpha + \frac{f'(0)}{\alpha} > c^*$.

In any cases, if u_0 is EB, the rate of spread remains bounded.

Exponentially bounded IC: numerical computations

$f(u) = u(1-u)$ and $u_0(x) = e^{-\frac{x}{10}}$ for $x \geq 0$.

Population range $x_{0.1}(t)$, and linear fit by $u_0^{-1}(0.1) + c(\alpha)\, t$:



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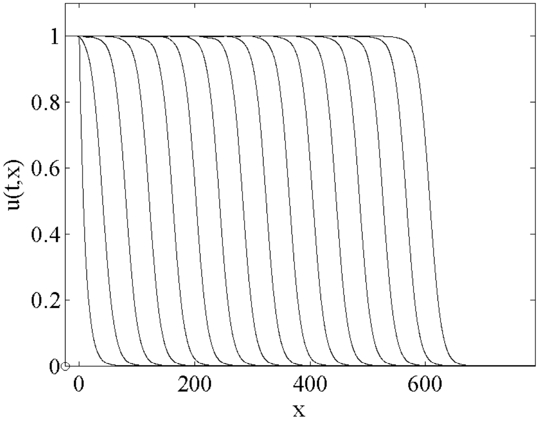
Convergence to a travelling wave with constant profile:



Exponentially unbounded IC: infinite spreading speed

Assumption:

For all $\alpha > 0$, $u_0(x)\, e^{\alpha x} \to +\infty$ as $x \to +\infty$ for all $\alpha > 0$.

$\to$ up to translation $u_0(x) \geq \varphi_\alpha(x)$: traveling wave with speed $c(\alpha) = \alpha + \frac{f'(0)}{\alpha}$.

Comparison principle $\to u(t,x) \geq \varphi_\alpha(x - c(\alpha)t)$.

Theorem

If u_0 is EU, the spreading speed of the solution $u(t,x)$ is infinite.

Thus, for any $\lambda \in (0,1)$, the rate of spread verifies

$$v_\lambda(t) \to \infty \text{ as } t \to \infty.$$

Exponentially unbounded IC: population range

supersolution = solution of the ODE model without diffusion:

$$\begin{cases} \dfrac{\mathrm{d}\overline{u}(t;x)}{\mathrm{d}t} & = & (f'(0)+\varepsilon)\overline{u}(t;x), \\ \overline{u}(0;x) & = & C_\varepsilon u_0(x), \end{cases}$$

subsolution = “flattening pulse":

$$\underline{u}(t,x) = \max\left(u_0(x)e^{(f'(0)-\varepsilon)t} - M_\varepsilon(u_0(x)e^{(f'(0)-\varepsilon)t})^2, 0\right).$$

Theorem

If u_0 is EU, and if $u_0''(x)/u_0(x) \to 0$ as $x \to \infty$, for any $\lambda \in (0,1)$ and $\varepsilon > 0$,

$$u_0^{-1}\left(\lambda e^{-(f'(0)-\varepsilon)t}\right) \leq x_\lambda(t) \leq u_0^{-1}\left(\lambda e^{-(f'(0)+\varepsilon)t}\right),$$

for large t.

Exponentially unbounded IC: some examples

- If u_0 is logarithmically sublinear for large x:

  $u_0(x) = e^{-x^\alpha}$ for large x, with $0 < \alpha < 1$.
  $\rightarrow x_\lambda(t)$ is asymptotically algebraic and superlinear:

  $$x_\lambda(t) \sim (f'(0)\, t)^{1/\alpha}.$$

- If $u_0(x)$ decays algebraically for large x:

  $u_0(x) = x^{-\alpha}$ with $\alpha > 0$.
  $\rightarrow x_\lambda(t)$ increases exponentially fast:

  $$\ln(x_\lambda(t)) \sim \frac{f'(0)}{\alpha}\, t.$$

Exponentially unbounded IC: profile of the solutions

Convergence to accelerating travelling waves ?
Answer = No: the solutions become uniformly flat as time increases.

Theorem

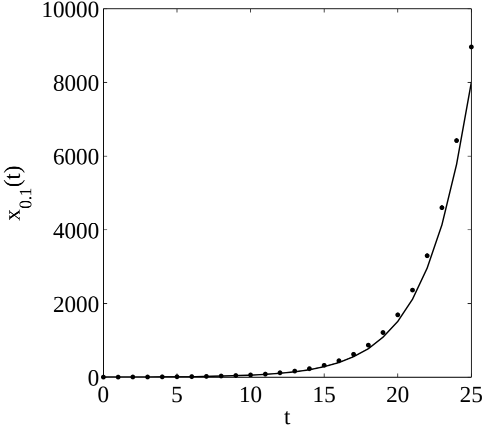
If u_0 is EU, and if $\int_{-\infty}^{+\infty} |u_0'/u_0|^p dx < \infty$ for some $p > 1$, we have

$$\max_{x \in (-\infty, +\infty)} \left| \frac{\partial u}{\partial x}(t,x) \right| \to 0 \text{ as } t \to +\infty.$$

Exponentially unbounded IC: numerical computations

$f(u) = u(1-u)$ and $u_0(x) = 1/(1+x^3)$ for $x \geq 0$.

Population range $x_{0.1}(t)$, and its approximation by
$u_0^{-1}\left(\lambda e^{-f'(0)t}\right) = \left(10e^t - 1\right)^{1/3}$:



Exponentially unbounded IC: numerical computations

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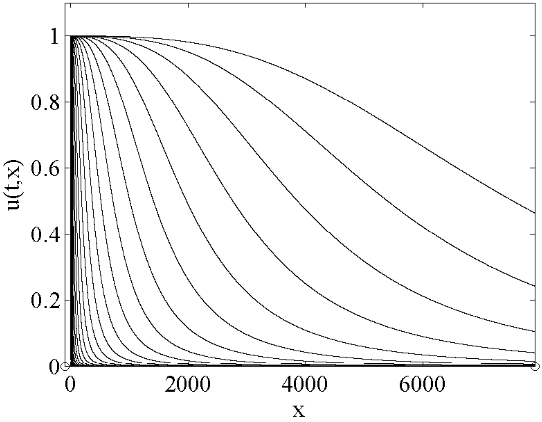
Uniform flattening of the profile:



Exponentially unbounded IC: further results

Conclusion and further results

Main conclusions:

- RD + EU IC $\rightarrow$ accelerating rates of spread
- RD + EU IC $\rightarrow$ flattening profiles
- RD + EU IC $\rightarrow$ similar to integro-differential eqs with EU kernels

For more precise results and assumptions, please refer to:

- Roques, Hamel, Fayard, Fady and Klein. Recolonisation by diffusion can generate increasing rates of spread. *Theoretical Population Biology.* In Press,

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