The time-evolution of small populations

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A few hundred rabbits share a patch of land, less than a hundred share the same warren. They are not sane, the virus of the mixomatosis has taken part of the population. How will the population evolve? Will the illness become endemic? Which strain of virus will be the prevalent one? The problem has been posed for about 50 years, the standard (deterministic) models give clear answers to these questions, but Nature does not behaves according to them. What is wrong with our models?

At a can-making factory the manager goes berserk! Once again the process is out of control and one complete roll of steel will have to be re-processed. Why our nosy-deterministic models cannot account for this situation? Why we have been unable to solve this problem so far?

We will discuss these and related problems of small populations where stochasticity is not just a correction to the deterministic dynamics but a fundamental element of the dynamics.

(Sad) Rabbit tales

Some known facts about the spread of mixomatosis in exotic populations of *Orictolagus Cunniculus*

- Rabbits are social animals, live in warrens around 80 individuals, share dusting places with other warrens, warrens are often located close to rivers.

- Mixomatosis is an infection by a virus proper of the *Silvilagus Brasilensis* transmitted by vector (fleas or mosquitoes mainly), is used as a biological control of the European Rabbit in France, Great Britain, Australia, New Zealand, Chile, Argentina, ...

- The mixoma virus is a POX virus (stable)
- Several early attempts to establish the virus in Australia failled
- Once established, the illness traveled following the rivers
- Co-evolution of the virus and the hosts has been observed
- *The un-expected diversity of virus strains in the field apparently contradict the principle of competitive exclusion*
- Genetic variability cannot explain virus diversity

Susceptible **I**nfected **R**ecovered model (SIR) with n viral strains

$$\begin{aligned}
\frac{dS}{dt} &= a \quad (S+R)(1-\frac{(S+R)}{M}) - bS - S\sum_i^n \beta_i I_i, \\
\frac{dI_j}{dt} &= S\beta_j I_j - (b+c_j+d_j)I_j, \qquad 1 \le j \le n \\
\frac{dR}{dt} &= \sum_i^n c_i I_i - bR
\end{aligned}$$

$$I_j^{\beta_j}/I_k^{\beta_k} = \exp((\frac{b+c_j+d_j}{\beta_j} - \frac{b+c_k+d_k}{\beta_k})t)$$

$R0_k = \left(\frac{b+c_k+d_k}{\beta_k}\right)^{-1}$ is the basic reproductive number. The strain with larger $R0$ is prevalent.

Stochastic SIR model (back to the basic)

Event	Effect	Transition rate
Birth	$S \to S + 1$	$a(S+R)(1 - \frac{S+R}{K})$
Death S	$S \to S - 1$	bS
Death I	$I \to I - 1$	$(b+d)I$
Death R	$R \to R - 1$	bR
Recovering	$I \to I - 1$, $R \to R + 1$	cI
Contagion	$S \to S - 1$, $I \to I + 1$	βSI

Time between events is exponentially distributed with mean

$$\tau = \{a(S+R)(1 - \frac{S+R}{K}) + bS + (b+d)I + bR + cI + \beta SI\}^{-1}$$

The dynamics in an isolated warren results in the extinction of the illness for realistic population numbers.

The stochastic model is extended to a model for a linear array of colonies allowing for a few more events:

- migration of viruses to adjacent colonies

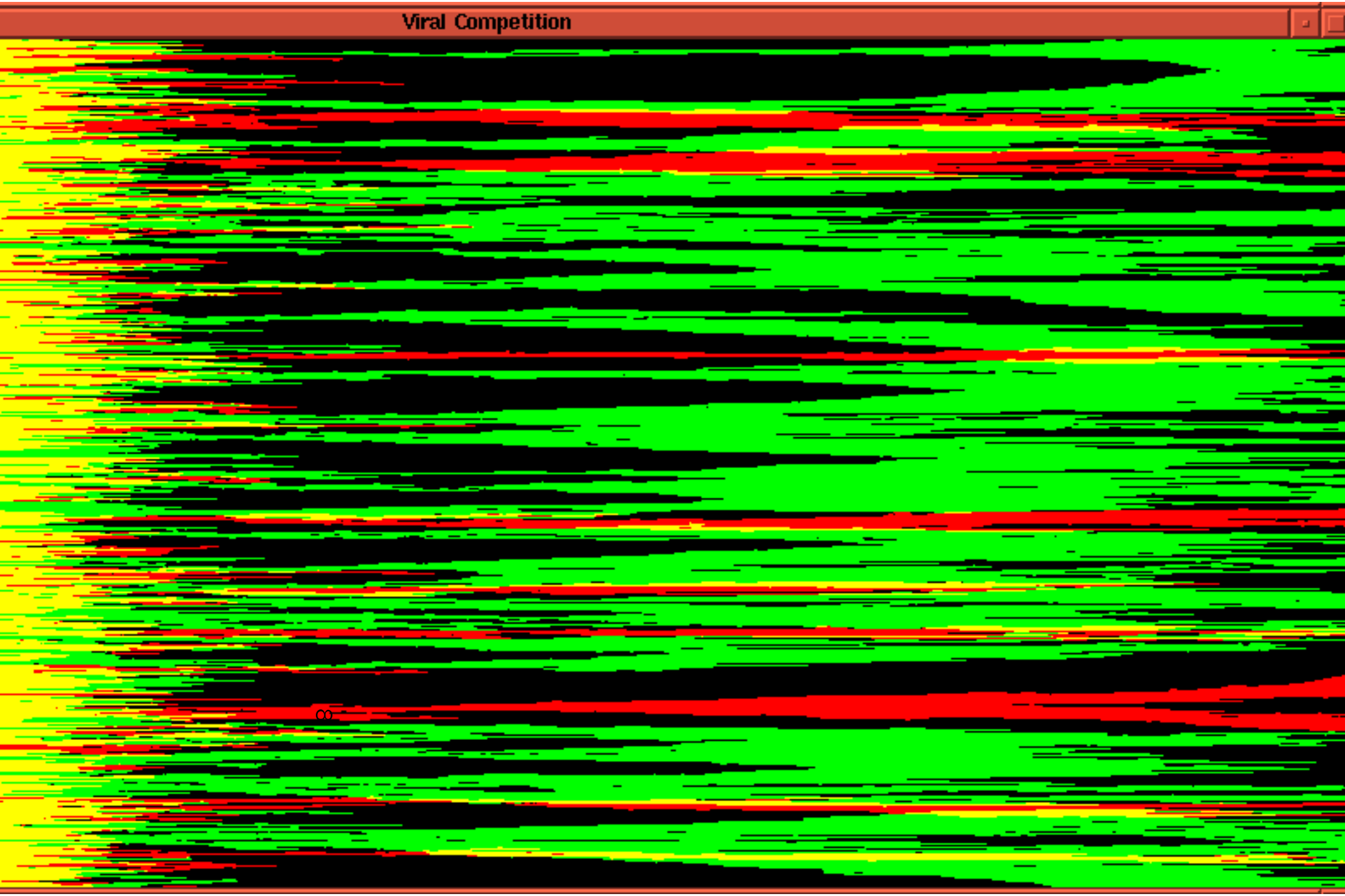
- migration of rabbits (both healthy and infected)

For a sufficiently large number of colonies, the illness becomes globally endemic but a given warren alternates times having ill-rabbits and times were rabbits are healthy.

Coexistence of strains is observed in large (and realistic) regions of parameter space, but very few warrens are infected with two strains simultaneously.

The dynamics is dominated by an extinction-reinfection process.

Next slide:
Evolution in time after a transient (time in the x-axis). The initial condition has all warrens shared by both virus strains.
Warrens ocupied by strain-A (red), strain-B (green), shared by both strains (yellow) and not-infected (black).

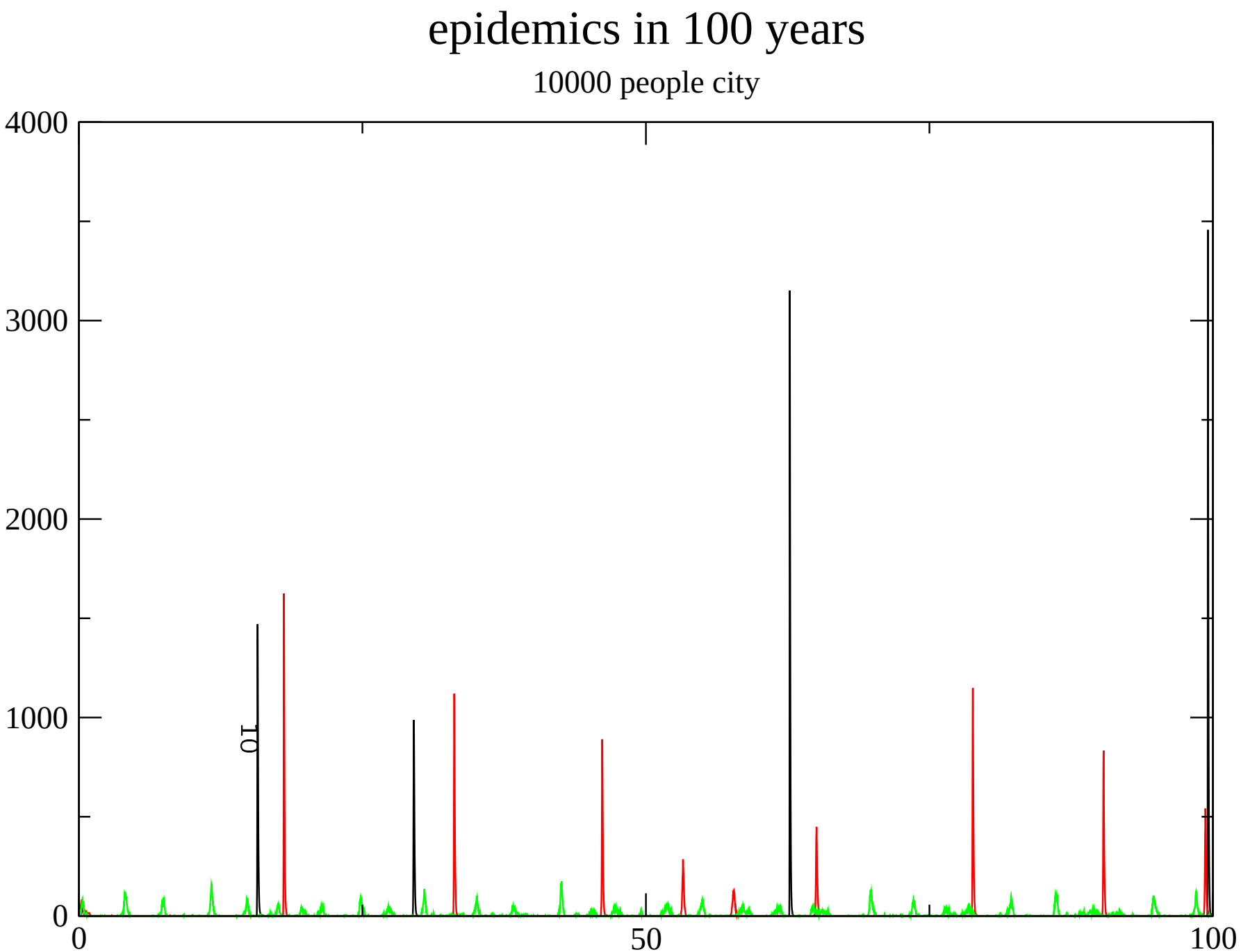

Viral Competition

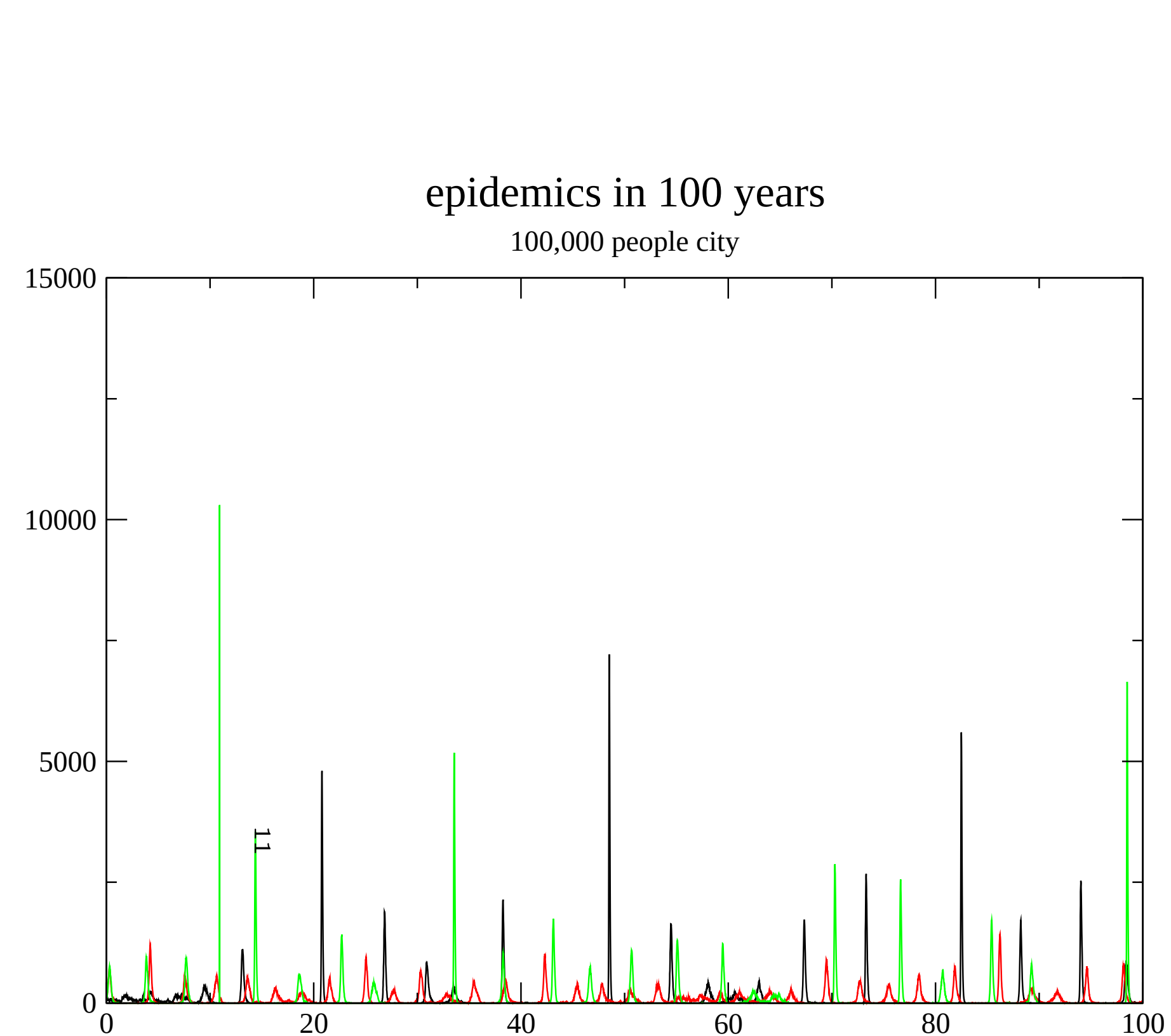
Comparison in a simple epidemic model of measles with external reinfection for 'Montecarlo" (fully stochastic) process, a Poisson approximation recently propossed (Phys. Rev. Lett. **86**, 4183-4186 (2001)) and a Langevin approximation (determinism plus noise) for different sizes of cities.

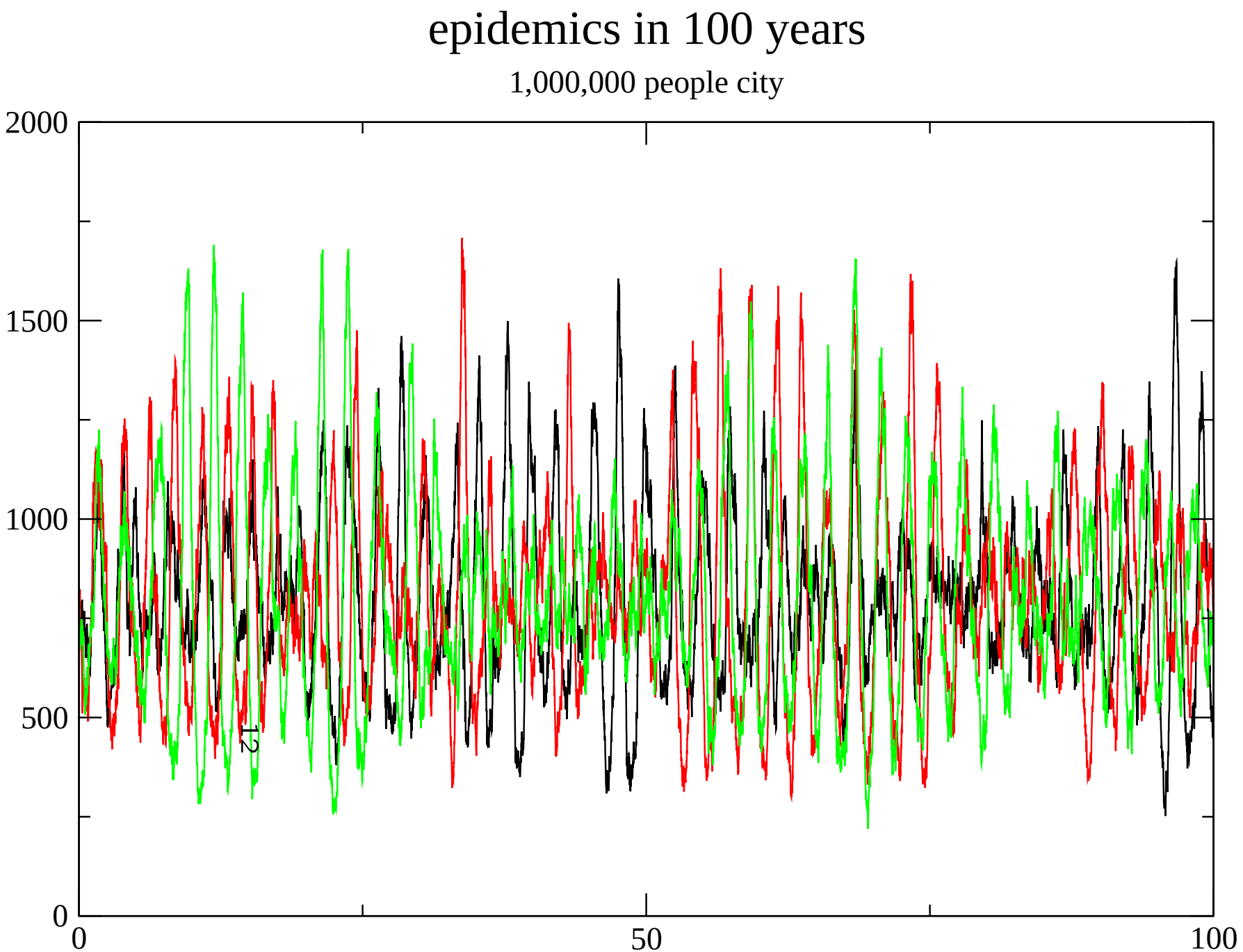
10,000 people city: black = Montecarlo, Red = Poisson, Green = Langevin

100,000 people city: black = Montecarlo, Green = Poisson, Red = Langevin

1,000,000 people city: black = Montecarlo, Red = Poisson, Green = Langevin


epidemics in 100 years
10000 people city
4000
3000
2000
1000
0
0
50
100
10


epidemics in 100 years
100,000 people city
15000
10000
5000
0
0
20
40
60
80
100
11


epidemics in 100 years
1,000,000 people city
2000
1500
1000
500
0
0
50
100
I2

Proposed model for the sedimentation of SiO_2 nano-spheres (Edward -Wilkinson Model)

$$\frac{\partial h(x,t)}{\partial t} = V + \nu \nabla^2 h(x,t) + \eta(x,t)$$

Noise term

$$\langle \eta(x_1,t_1)\eta(x_2,t_2)\rangle = C\delta(x_1 - x_2)\delta(t_1 - t_2)$$

Usual test plot $\psi(t)$ (roughening) versus time

$$\psi(t) \equiv \left\langle (h(x,t) - \int_0^L h(x,t)dx/L)^2 \right\rangle$$

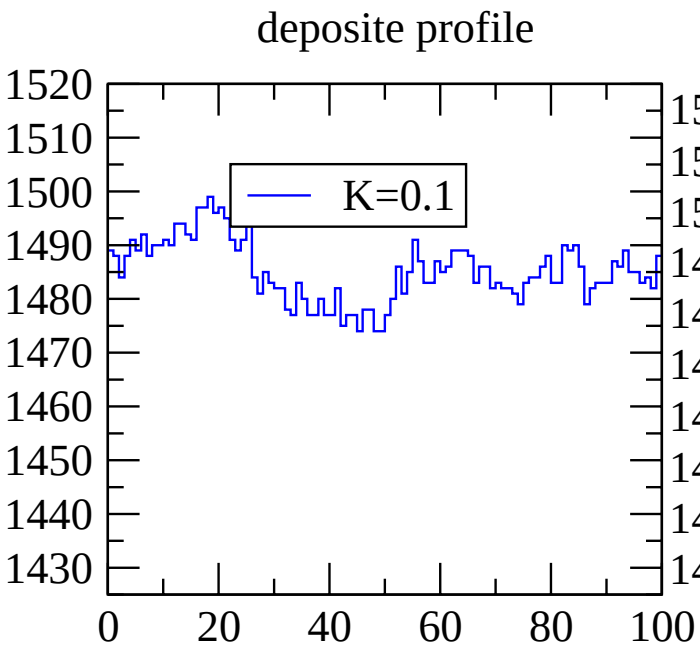
A simple stochastic model for deposition

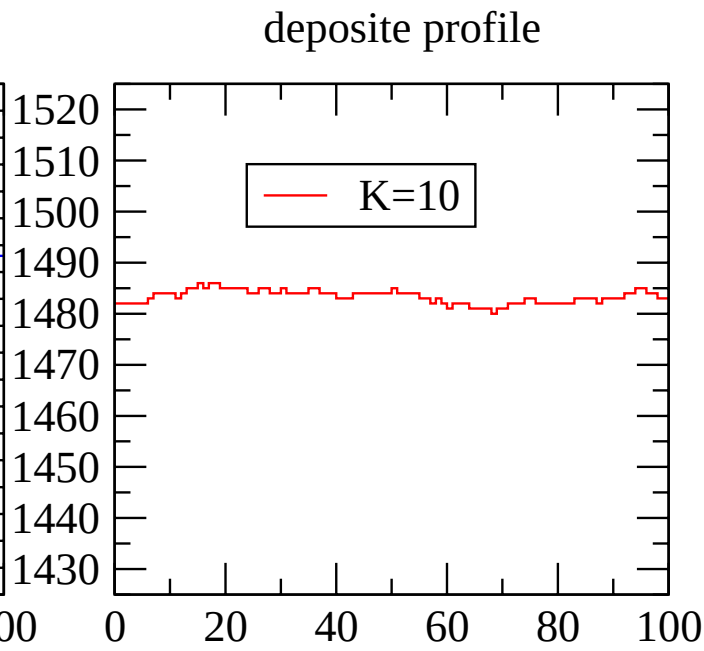
h_i height of deposit at site i
S_i number of particles trying to deposit at the site i

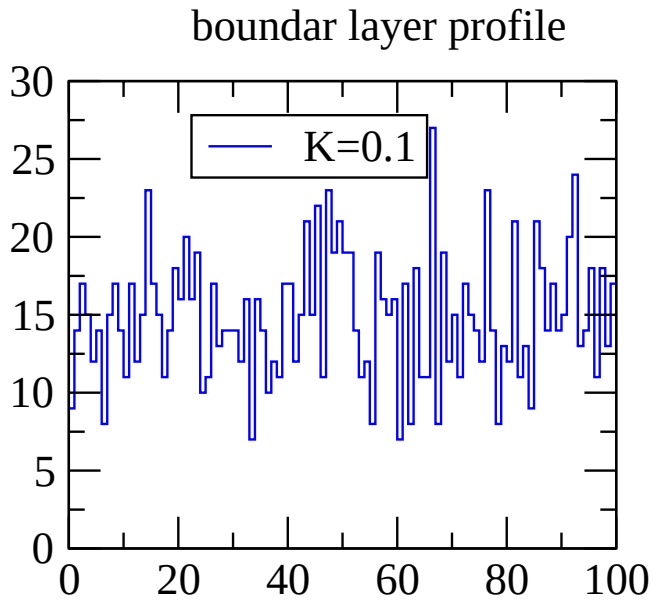
Event	Effect	Transition rate
Particle rain	$S_i \rightarrow 1 + S_i$	R
Deposition	$(H_i, S_i) \rightarrow (1 + H_i, -1 + S_i)$	$ps * S_i/N_i$
Right migration	$(S_i, S_{i+1}) \rightarrow (-1+S_i, 1+S_{i+1})$	$(1-ps)S_i/N_i * F(h_i - h_{i+1})$
Left migration	$(S_i, S_{i-1}) \rightarrow (-1+S_i, 1+S_{i-1})$	$(1-ps)S_i/N_i * F(h_i - h_{i-1})$

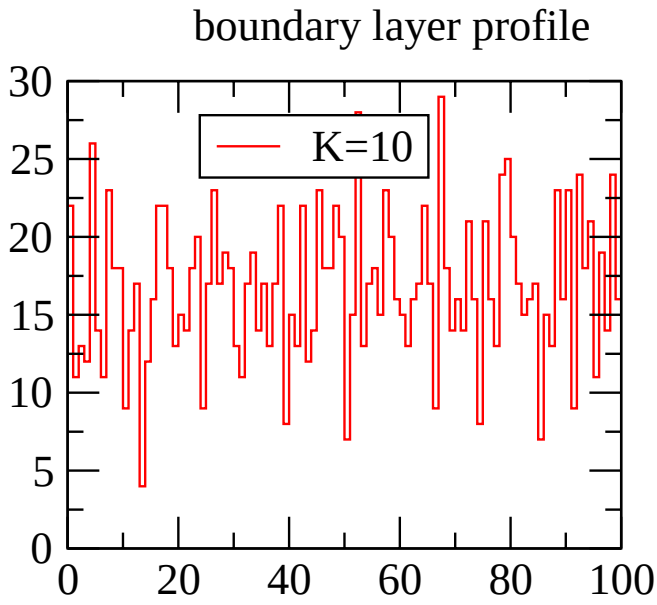
$$N_i = (e^{K*(h_i - h_{i+1})} + e^{(K*(h_{i-1} - h_i)} + 1)^{-1}$$
$$F(x) = \exp(K * x)$$

Deposite and boundary layer profiles R=5 Ps=0.5

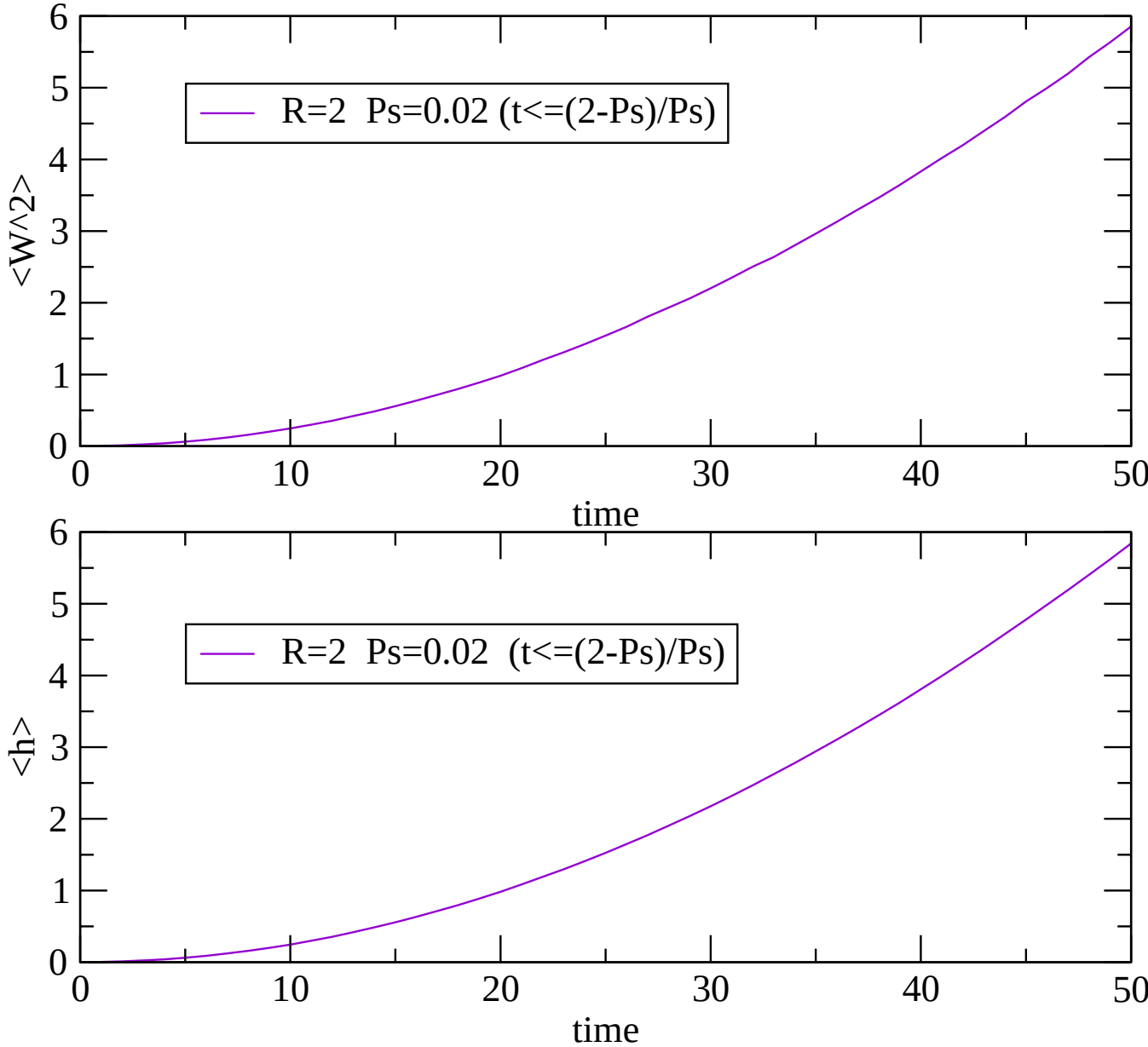








L=300 Est=100 K=0



Conclusions:

- In small populations, to preserve the integrity of individuals is essential to the description, the stochastic nature of the phenomena is usually as relevant (or more) than the mean field (deterministic) part.

- Present models for technologically relevant process (the coming nano-structure technology) also require stochastic models on discrete variables. Sound models and the methods of analysis of them are yet to be produced.

- Some models are able to describe some part of the phenomena but fail in other regions or times, they **lack predictive character**. This usually arise as:

  > One faces very early the need for a different representation, such that the evolution can be represented by partial differential equations in a continuous space.

  Il Nouvo Chimento **100** 733-742 (1987) (first paragraph of the work)

- Large populations can be successfully described by Langevin type equations.

- Many observed features of the population dynamics of the rabbits+mixoma virus system can only be accounted for by stochastic models with spatial extension.