Statistics at the tip of a branching random walk, and simple models of evolution with selection

Bernard Derrida

ENS, Paris

E. Brunet 2009-2011

E. Brunet, A. H. Mueller, S. Munier 2006-2007

Saclay June 2011

Outline

Motivations

Bovier, Kurkova 2006
Aizenman, Sims, Staarr 2007
Arguin 2007
Lalley, Sellke 1987

The rightmost particle and the Fisher-KPP equation

Mc Kean 1975, Bramson 1978,1983

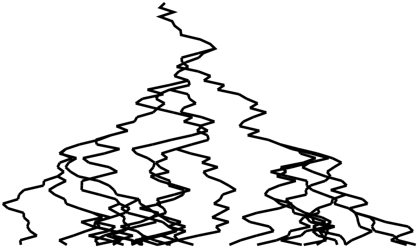
Distances between the rightmost particles

Asymptotic measure

Superposability

Models of evolution with or without selection

Branching Brownian motion



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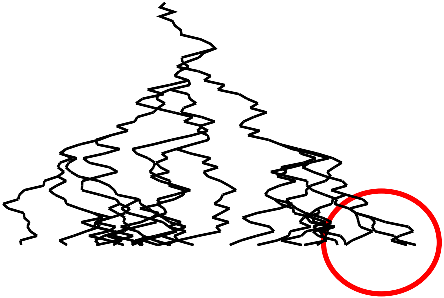

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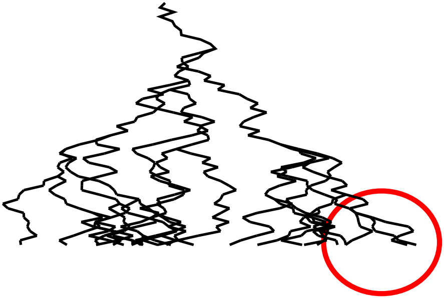

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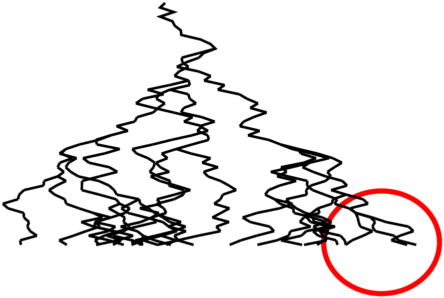

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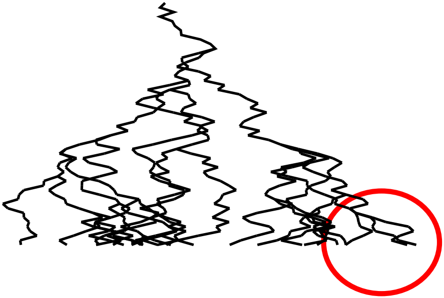
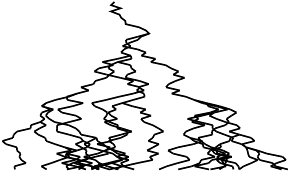


$$\cdots < X_i(t) < \cdots < X_2(t) < X_1(t)$$

$$\lim_{t\to\infty} \mathrm{Prob}(X_1(t) - X_2(t), X_1(t) - X_3(t)\ldots) \quad ?$$

The models



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- Particles diffuse
- They split at rate 1

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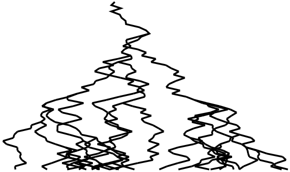

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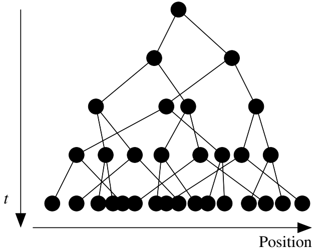

Branching random walk

- At each step, points split into two
- The offspring are shifted by uncorrelated random amounts

Motivations

Spin glass

n Ising spins $S_i = \pm 1$

$$E(\mathrm{Conf}) = -\sum_{i,j} J_{i,j} S_i S_j$$

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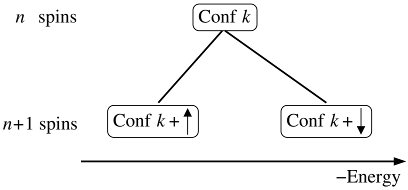

$$E_{n+1} = E_n - S_{n+1} \sum_j J_{j,n+1} S_j$$

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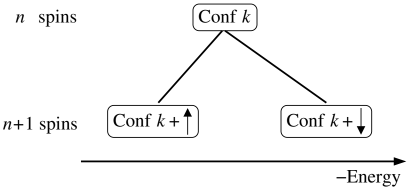

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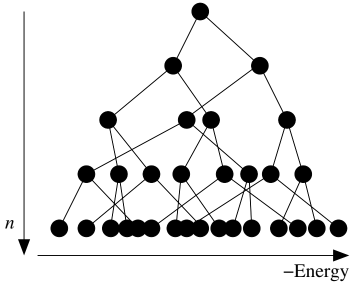

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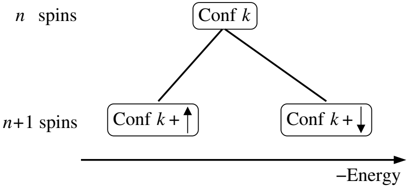

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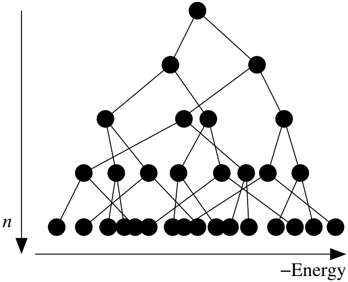
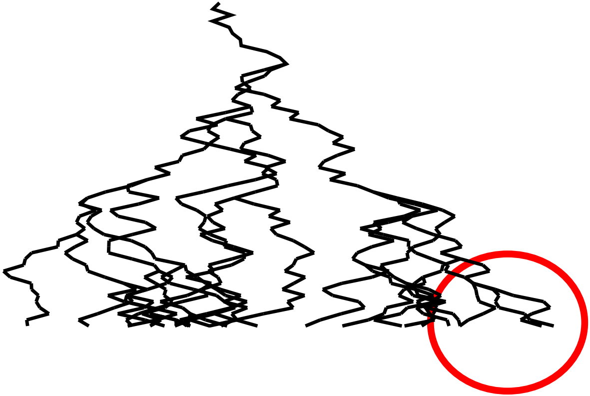


Directed polymers

uncorrelated energy shifts

Branching Brownian motion



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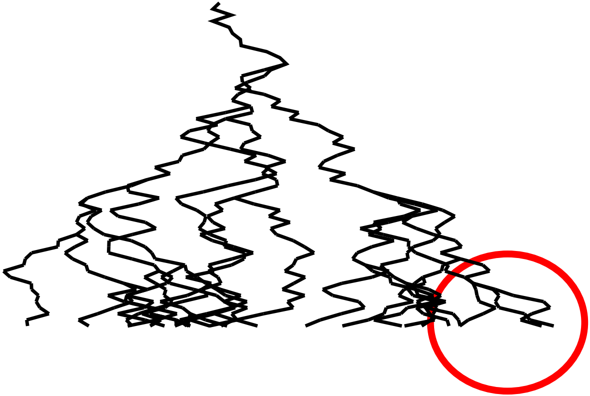

$$\mathrm{Pro}(X_1(t))$$

The rightmost particle

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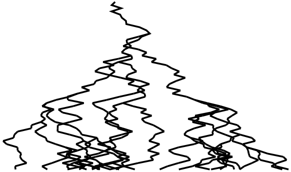

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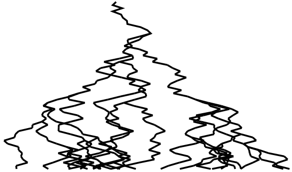

Distribution of the rightmost particle

$$Q_0(x,t) = \mathrm{Proba}[X_1(t) < x]$$

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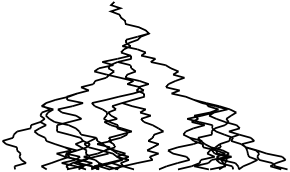

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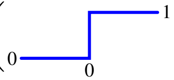

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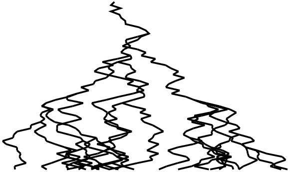

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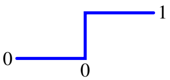

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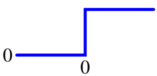

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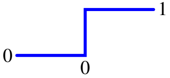
$$Q_0(x,0) = \Bigg($$ 

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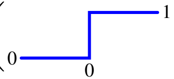
$Q_0(x, 0) = \Big($  $\Big)$

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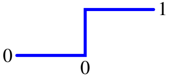
$Q_0(x,0) = \Big($  $\Big)$

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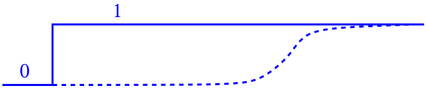

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$$\psi_\lambda(x,t) = \left\langle \lambda^{[\text{number of particles on the right of } x \text{ at time } t]} \right\rangle,$$

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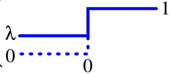

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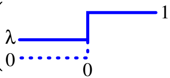
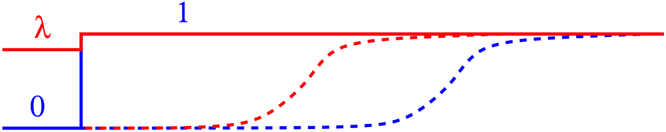
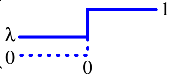
$$\partial_t \psi_\lambda = \partial_x^2 \psi_\lambda - \psi_\lambda + {\psi_\lambda}^2, \quad \text{with} \quad \psi_\lambda(x,0) = \Bigg($$  $$\Bigg),$$



ψ_λ gives the average positions of the rightmost particles

Position of the front   Bramson 1978

$$\partial_t \psi_\lambda = \partial_x^2 \psi_\lambda - \psi_\lambda + {\psi_\lambda}^2, \quad \text{with} \quad \psi_\lambda(x,0) = \Bigg($$ 

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For large t:

$$\psi_\lambda(x,t) \to F\left(x - 2t - \frac{3}{2}\log t - A(\lambda)\right)$$

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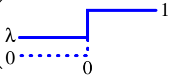

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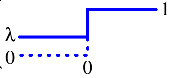

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$d_{n,n+1}$ distance between the n-th and the $n+1$-th point

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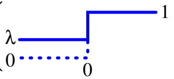

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All the properties of the tip can be obtained as delays

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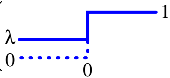

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For $\lambda \to 1$, $\boxed{A(\lambda) \simeq \log(1-\lambda) + \log(-\log(1-\lambda))}$

Asymptotics

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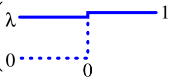
$\partial_t \psi_\lambda = \partial_x^2 \psi_\lambda + {\psi_\lambda}^2 - \psi_\lambda$ $\qquad$ with $\psi_\lambda(x,0) = \Bigg($  $\Bigg)$,

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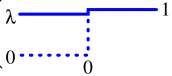

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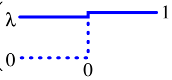
$$\partial_t \psi_\lambda = \partial_x^2 \psi_\lambda + {\psi_\lambda}^2 - \psi_\lambda \qquad \text{with } \psi_\lambda(x,0) = \Bigg($$ 

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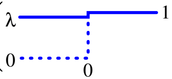

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Results : average distances

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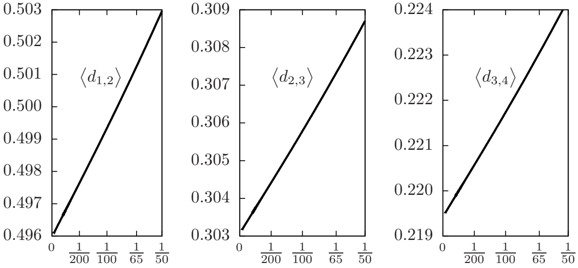

Average distances as a function of $1/t$. In the long time limit:

$$\langle d_{1,2}\rangle \simeq 0.496 \quad \langle d_{2,3}\rangle \simeq 0.303 \quad \langle d_{3,4}\rangle \simeq 0.219$$

$$\langle d_{4,5}\rangle \simeq 0.172 \quad \langle d_{5,6}\rangle \simeq 0.142 \quad \langle d_{6,7}\rangle \simeq 0.121$$

The rightmost particles of a Poisson process

Definition

- $(x, x + dx)$ is occupied by a particle with probability $\rho(x)dx$
- no correlation between the occupations of disjoint intervals

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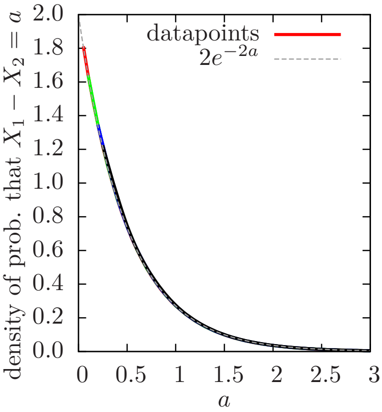
Distance between the n and $n+1$ particle

$$\langle d_{n,n+1} \rangle = \frac{1}{\alpha n}$$

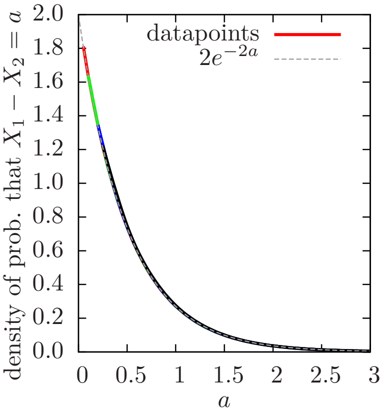
Results : distance d_{12} in the BBM

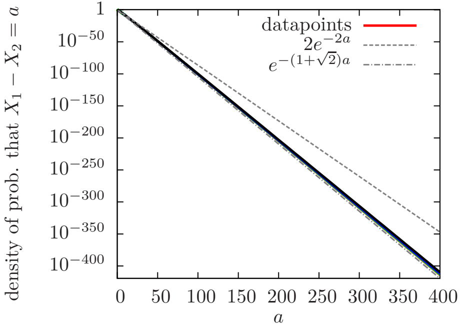


$$P(d_{12} = a) \simeq 2e^{-2a}$$

Numerics

Results : distance d_{12} in the BBM





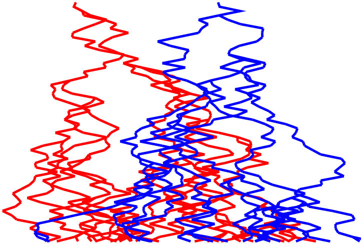
$$P(d_{12} = a) \simeq 2e^{-2a}$$

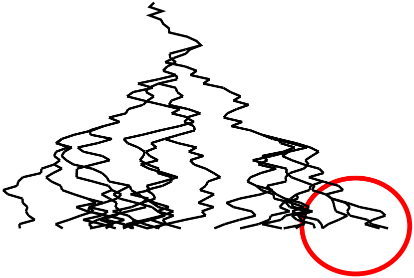
$$P(d_{12} = a) \sim e^{-(1+\sqrt{2})a}$$

Numerics

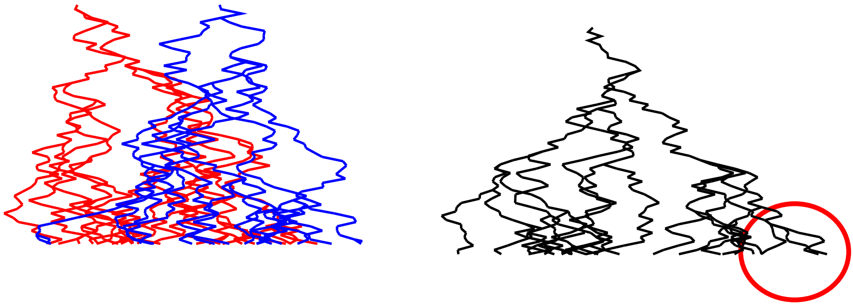
Analytic

Superposability





Superposability

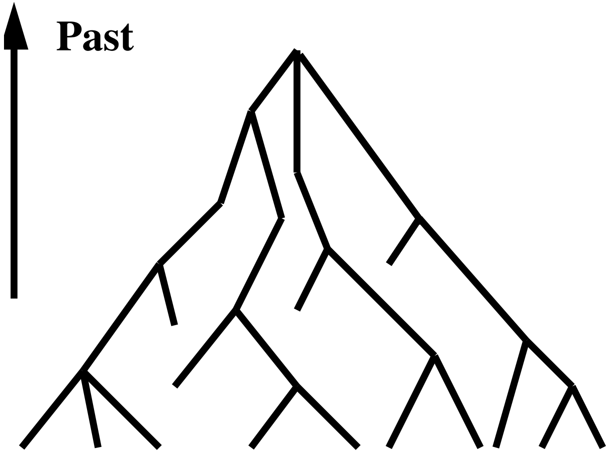


For large t, for the limiting measure of the distances

$$\text{BBM} + \text{BBM} = \text{BBM}$$

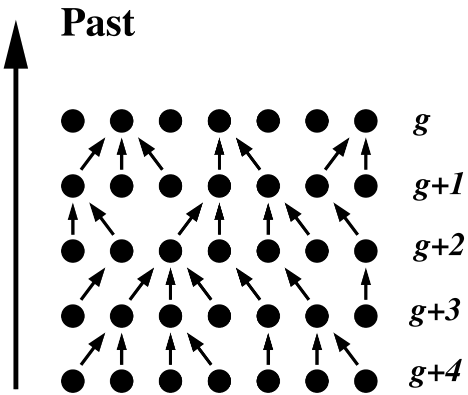
Genealogies with and without selection

Asexual Reproduction



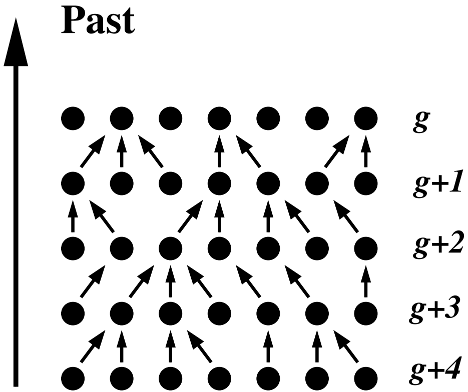
Wright-Fisher model (1930-1931)

- One parent model (asexual reproduction)
- Population of fixed size N
- Each individual i has n_i offspring (n_i random) (neutrality)
- One chooses N survivors among these $n_1 + n_2 + \ldots$ offspring (neutrality)



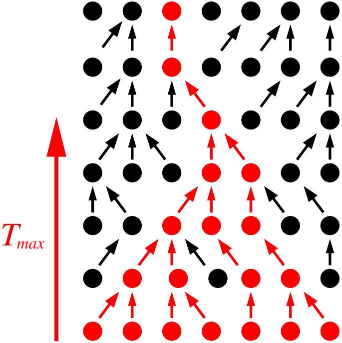
Wright-Fisher model (1930-1931)

- One parent model (asexual reproduction)
- Population of fixed size N
- Each individual has its parent chosen at random in the previous generation (neutrality)



Coalescence times:

Age of the most recent common ancestor T_{max}

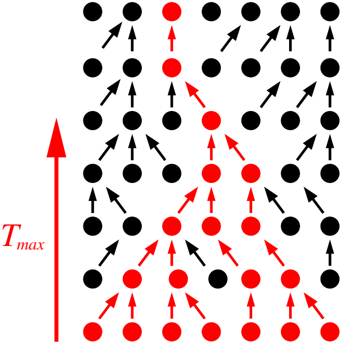


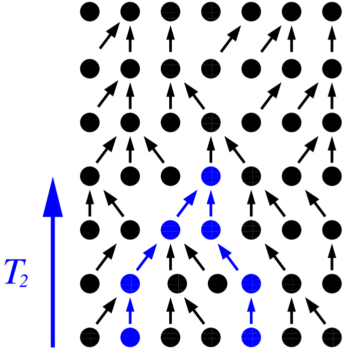
$$T_{max} \sim N$$

T_{max} is a non self-averaging quantity

Coalescence times:

Ages of the most recent common ancestors T_{max} and T_2





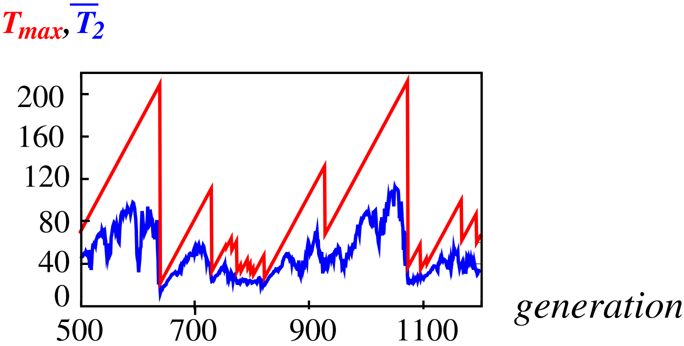
$$T_{max} \sim T_2 \sim N$$

T_{max} and T_2 are non self-averaging quantities

Evolution of T_{max} and $\overline{T}_2$

T_{max} = age of the most recent common ancestor

$\overline{T}_2$ = average over the population of T_2

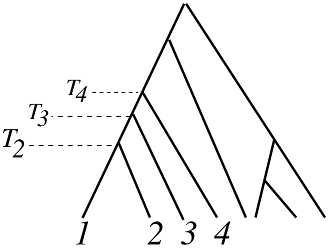


Serva 2005
Simon D. 2006

Coalescence times:

Age T_p Kingman theory

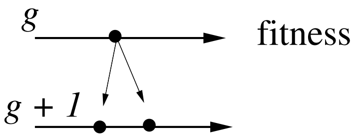
T_p = age of the most recent common ancestor of p individuals chosen at random

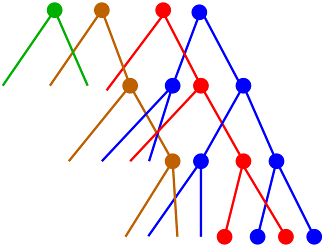


$$\langle T_p \rangle \simeq \frac{2(p-1)}{p} N$$

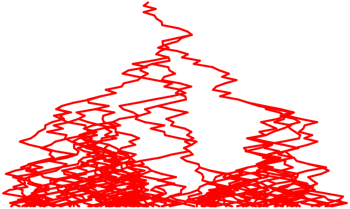
MODELS OF EVOLUTION WITH SELECTION

- Population of size N
- Each individual has 2 offspring at the next generation
- The fitness is transmitted up to some small change due to mutations
- The N right-most individuals are selected



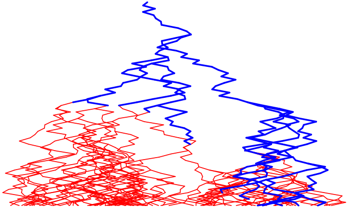


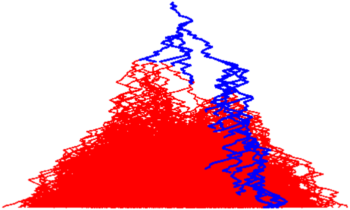
Branching random walk



$N \leq 5$

Branching random walk + selection

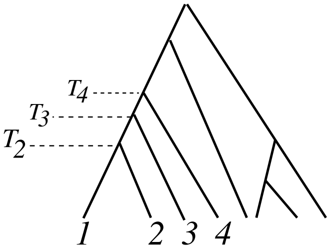




QUESTIONS

For a population of fixed size N

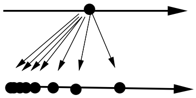
- Ages of the most recent common ancestors



- Shape of the genealogical trees

Exponential model

- Population of size N
- Each individual has infinitely many offspring at the next generation
- An individual at position x has an offspring in $(x+y, x+y+dy)$ with probability $e^{-y}dy$ (Poisson process).



- The N right-most individuals are selected

Brunet D. Mueller Munier 2006-2007

$$\frac{\langle T_3 \rangle}{\langle T_2 \rangle} \to \frac{5}{4}$$

$$\frac{\langle T_4 \rangle}{\langle T_2 \rangle} \to \frac{25}{18}$$

$$\langle T_2 \rangle \simeq \log N$$

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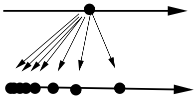

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$$\langle T_2 \rangle \simeq \log N$$

spin glass trees

Statistics of the trees

	spin–glass	neutral
	$\frac{3}{4}$	1
	$\frac{1}{4}$	0

spin-glass $\equiv$ mean-field spin glasses

Parisi 79-80

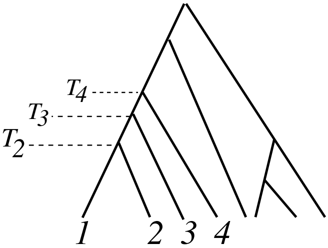
Mézard-Parisi-Sourlas-Toulouse-Virasoro 84

... Bolthausen-Sznitman 98

neutral $\equiv$ Wright-Fisher model

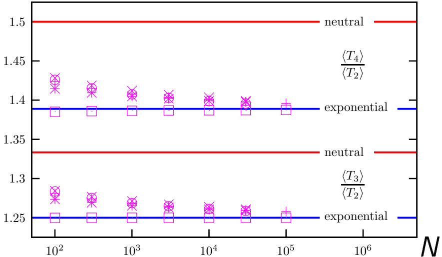
	spin–glass	neutral
	$\frac{1}{3}$	$\frac{2}{3}$
	$\frac{1}{6}$	$\frac{1}{3}$
	$\frac{1}{6}$	0
	$\frac{2}{9}$	0
	$\frac{1}{9}$	0

Coalescence times: simulations $N \to 10^5$



T_p = age of the most common ancestor of p individuals chosen at random

Ratios $\frac{\langle T_p \rangle}{\langle T_2 \rangle}$



$$\frac{\langle T_3 \rangle}{\langle T_2 \rangle} \to \frac{5}{4} \neq \frac{4}{3}$$

$$\frac{\langle T_4 \rangle}{\langle T_2 \rangle} \to \frac{25}{18} \neq \frac{3}{2}$$

selection $\neq$ neutral

Conditionning on the speed

Brunet D. 2011

X_t position of the population at time t

Weight the events by

$$e^{-\beta X_t}$$

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Then

$$\left.\frac{\langle T_3\rangle}{\langle T_2\rangle}\right|_\beta = \frac{5+4\beta}{4+3\beta}$$

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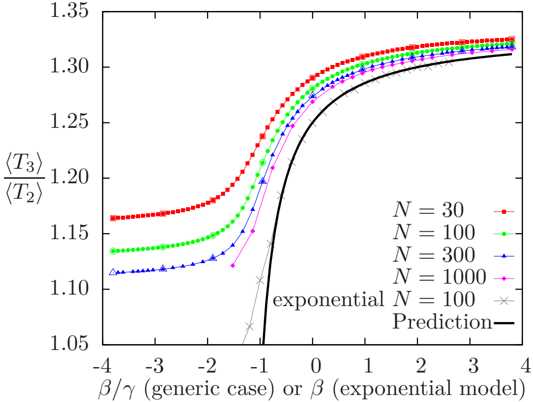
Brunet D. 2011



Coalescence rates

q_p rate at which p branches coalesce into 1.

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	$q_p/q_2 \quad \text{for} \quad p > 2$
neutral	0
selection	$\frac{1}{p-1}$
$e^{-\beta X_t}$	$\frac{(p-2)!\ \Gamma(\beta+2)}{\Gamma(\beta+p)}$

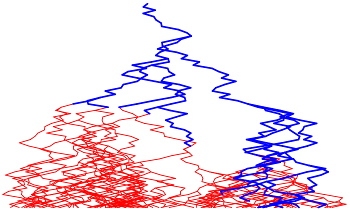
Fisher equation and branching random walk

The Fisher-KPP equation

Fisher 1937

Kolmogorov Petrovsky Piscounov 1937

$$\frac{dc}{dt} = \frac{d^2c}{dx^2} + c - c^2$$



selection

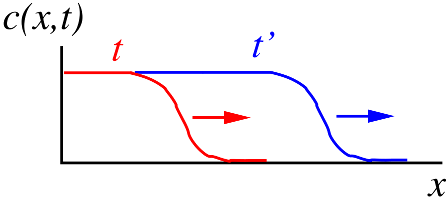
$Q(x, t)$ probability that the right-most walker is at the right of x

$$\frac{dQ}{dt} = \frac{d^2Q}{dx^2} + Q - Q^2 + \text{Noise}$$

Traveling wave equation + noise

$$\frac{dc}{dt} = \frac{d^2c}{dx^2} + c - c^2 + \frac{1}{\sqrt{N}} \;\; \eta(x,t)\sqrt{c(1-c)}$$

Brunet D. 1997



Brunet D. Mueller Munier 2006

Mueller Mytnik Quastel 2008

$$v_N \simeq 2 - \frac{\pi^2}{\log^2 N} + \frac{6\pi^2 \log\log N}{\log^3 N}$$

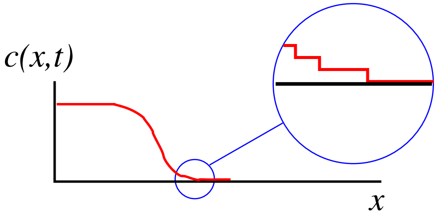
$$D_N \simeq \frac{2\pi^4}{3\log^3 N}$$

Cut-off approximation

Brunet Derrida 1997, 2001

Branching random walk + selection

$$\frac{dc}{dt} = \frac{d^2c}{dx^2} + c - c^2 + \frac{1}{\sqrt{N}}\,\eta(x,t)\sqrt{c(1-c)}$$



Replace the noise by a cut-off

$$\frac{dc}{dt} = \frac{d^2c}{dx^2} + a(c)(c - c^2)$$ where $$a(c) = \begin{cases} 1 & \text{if } Nc \geq 1 \\ 0 & \text{if } Nc \ll 1 \end{cases}$$

Conclusion

Tip of a branching random walk $\neq$ Poisson process

Selection $\Rightarrow$ Bolthausen-Sznitman coalescent

Conditionning on the speed interpolates between Kingman and Bolthausen-Sznitman

Steady state measure for large N

Soluble case for the measure of the tip

Shape of the noisy KPP equation conditionned on the speed

E. Brunet, B. Derrida
Statistics at the tip of a branching random walk and the delay of traveling waves
Europhysics Letters 87, 60010, 2009

A branching random walk seen from the tip
J. Stat. Phys. 143, 420-446 2010

*How genealogies are affected by the speed of evolution*k
preprint 2011

E. Brunet, B. Derrida, A. H. Mueller, S. Munier
Noisy traveling waves: Effect of selection on genealogies
Europhysics Letters, 76, 1-7 (2006)

Effect of selection on ancestry: an exactly soluble case and its phenomenological generalization
Physical Review E 76, 041104 (2007)