Random Trees and Genealogies

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OUTLINE

Neutral models of evolution

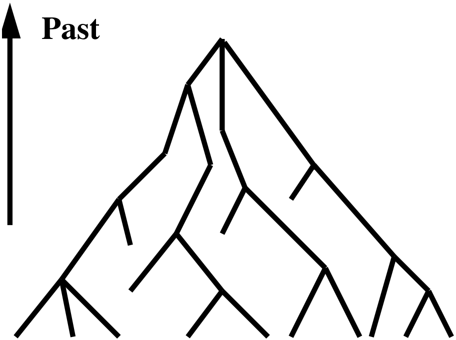
Simple models of evolution with selection

Traveling waves and noise

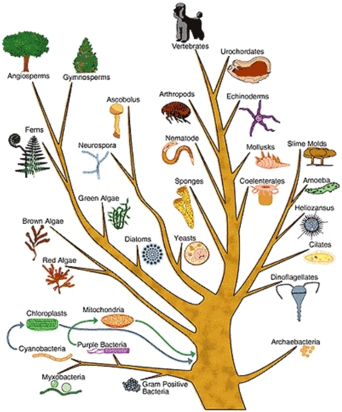
Directed Polymers in a random medium

Branching random walk + a wall

Asexual Reproduction



phylogeny

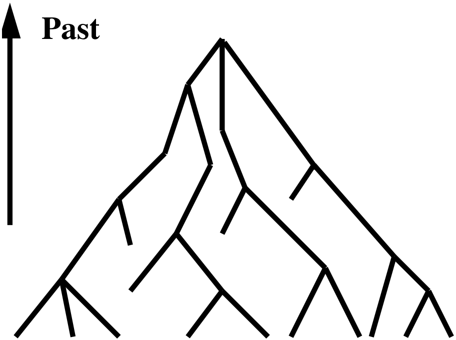


family names

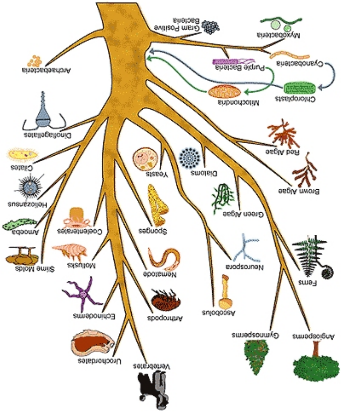
bacteria

languages ...

Asexual Reproduction



phylogeny



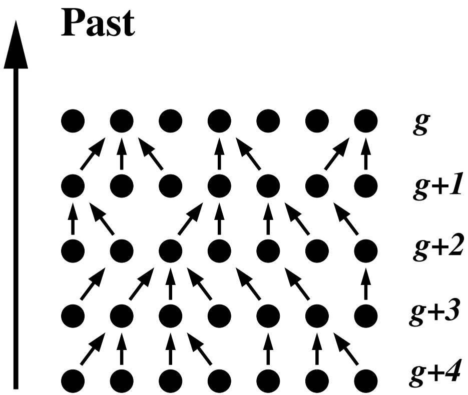
family names

bacteria

languages ...

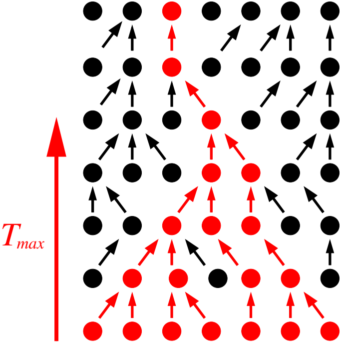
Neutral model of evolution: Wright-Fisher model (1930-1931)

- 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}

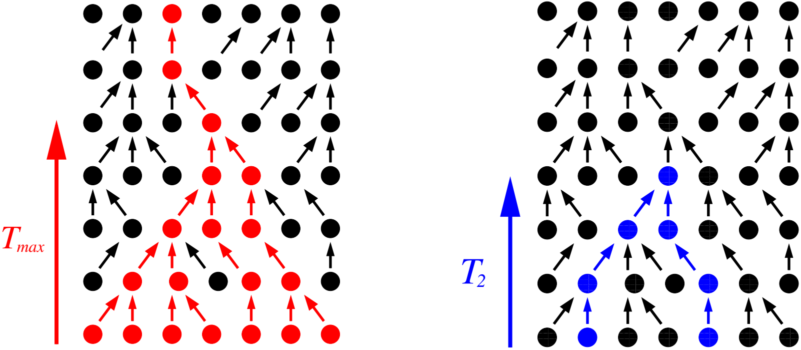


$$T_{max} \sim N$$

T_{max} is a non self-averaging quantity

Coalescence times:

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



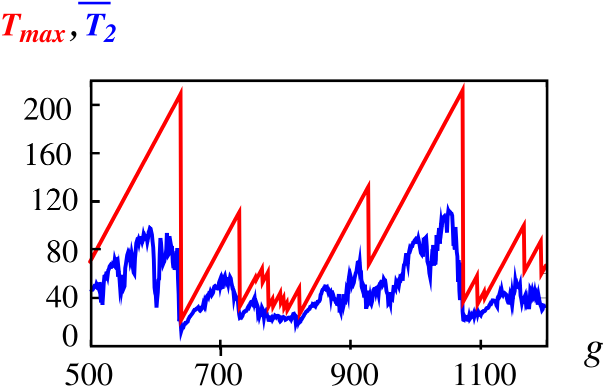
$$T_{max} \sim T_2 \sim N$$

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



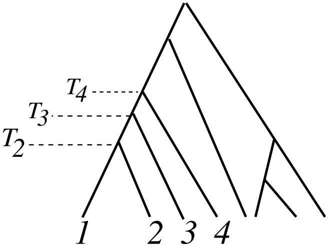
Serva 2005

Simon D. 2006

Coalescence times:

Kingman's coalescent 1982

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



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

$$\langle T_3 \rangle / \langle T_2 \rangle = \frac{4}{3}$$

$$\langle T_4 \rangle / \langle T_2 \rangle = \frac{3}{2}$$

The ratios $\frac{\langle T_p \rangle}{\langle T_2 \rangle}$ are universal

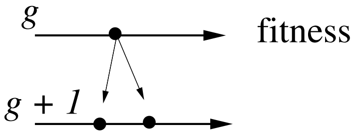
e^{-T_2} plays a role very similar to the overlap in spin-glasses

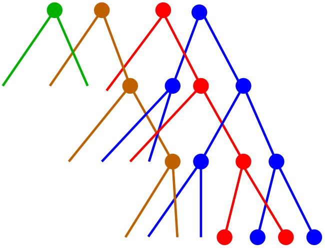
Summary on neutral models of asexual reproduction

- The coalescence times T_p are not selfaveraging
- Kingman's coalescent
- $T_p \sim N$
- Universal ratios $\langle T_p \rangle / \langle T_2 \rangle$
- $d = 1$ is different (non-mean field)

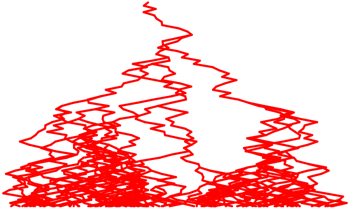
MODELS OF EVOLUTION WITH SELECTION

- 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

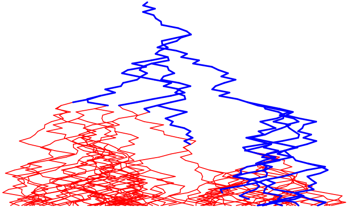




Branching random walk

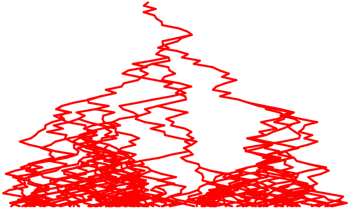


Branching random walk + selection

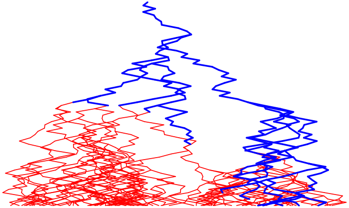


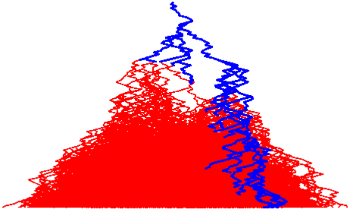
$N \leq 5$

Branching random walk



Branching random walk + selection

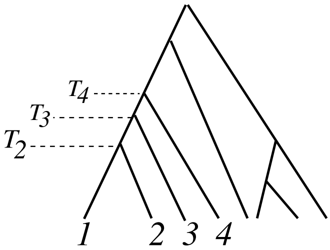




QUESTIONS

For a population of fixed size N

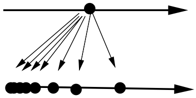
- v_N velocity of the population
- D_N diffusion constant
- Genealogy
  - Ages of the most recent common ancestors



  - 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

$$v_N \simeq \log \log N$$

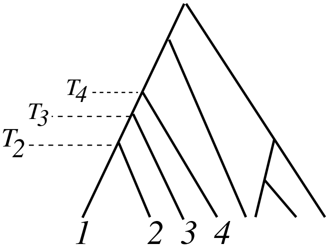
$$D_N \sim \frac{1}{\log N}$$

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

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

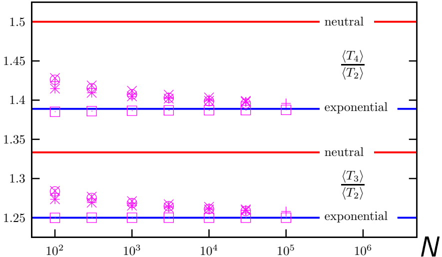
$$\frac{\langle T_4 \rangle}{\langle T_2 \rangle} \to \frac{25}{18}$$

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



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

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

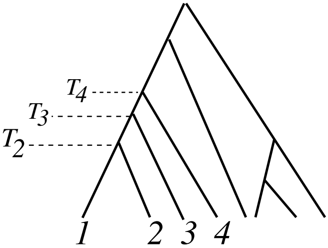


$$\frac{\langle T_3 \rangle}{\langle T_2 \rangle} \to \frac{5}{4} \neq \frac{4}{3}$$

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

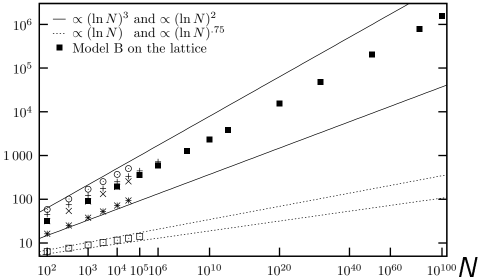
selection $\neq$ neutral

Coalescence times: simulations $N \to 10^{100}$



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

Time $\langle T_2 \rangle$



$$\langle T_2 \rangle \sim \log^3 N$$

exponential model:
$\langle T_2 \rangle \sim \log N$

neutral model:
$\langle T_2 \rangle \sim N$

Today's lecture: Evolution with **selection**

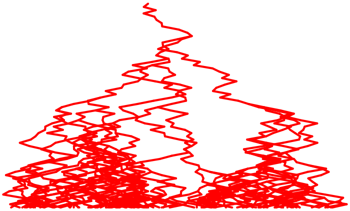
	neutral	selection
T_3/T_2	$4/3$	$5/4$
T_4/T_2	$3/2$	$25/18$
T_p/T_2	$2(p-1)/p$	long expression
Trees	Kingman 82	Parisi (79-80) Bolthausen-Sznitman (98)
$T_p \sim$	N	$(\log N)^3$

Fisher equation and branching random walk

The Fisher-KPP equation

Fisher 1937
Kolmogorov Petrovsky Piscounov 1937

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



McKean 1975

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

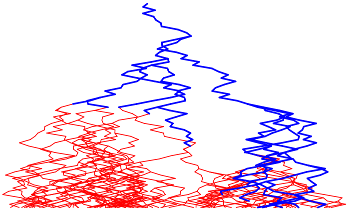
$$\frac{dQ}{dt} = \frac{d^2Q}{dx^2} + Q - Q^2$$

Fisher equation and branching random walk

The Fisher-KPP equation

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

Fisher 1937
Kolmogorov Petrovsky Piscounov 1937



selection

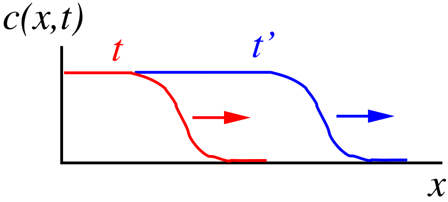
$Q(x,t)$ probability that the right-most walker is at the right of x

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

Traveling wave equation + noise

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

Brunet D. 1997



Brunet D. Mueller Munier 2006

Mueller Mytnik Quastel 2008

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

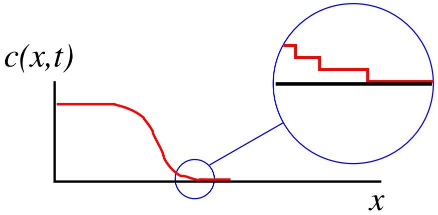
$$D_N \simeq \frac{2\pi^4}{3\log^3 N}$$

Cut-off approximation

Brunet Derrida 1997, 2001

Branching random walk + selection

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



Replace the noise by a cut-off

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

Motivations

- Evolution with seclection

  Snydner 2003, Kloster 2005
  Brunet D. Mueller Munier 2006-2007

- Reaction diffusion

  Pechenik Levine 1999
  Conlon Doering 2005
  Mueller Mytnik Quastel 2006

- Theory of disordered systems: directed polymers

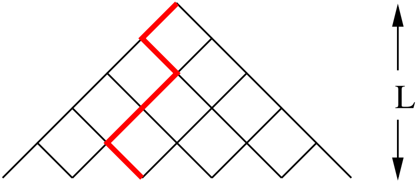
  D. Spohn 1988
  Brunet D. 1987-2004

- QCD

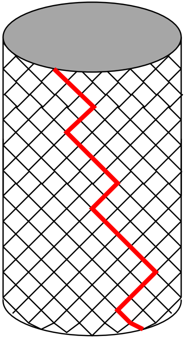
  Munier Peschanski 2003
  Marquet Peschanski Soyez 2005

Directed Polymers in a random medium

1+1 dimension



Torus



Random energy ϵ_b

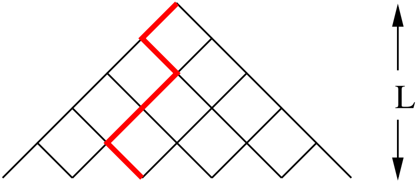
on each bond b

$$E_W = \sum_{b \in W} \epsilon_b$$

Energy of a path = position of a random walker in the branching radom walk problem

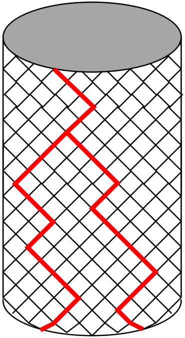
Directed Polymers in a random medium

1+1 dimension



Random energy ϵ_b on each bond b

Torus



$$E_W = \sum_{b \in W} \epsilon_b$$

Energy of a path = position of a random walker in the branching radom walk problem

Universal ratios

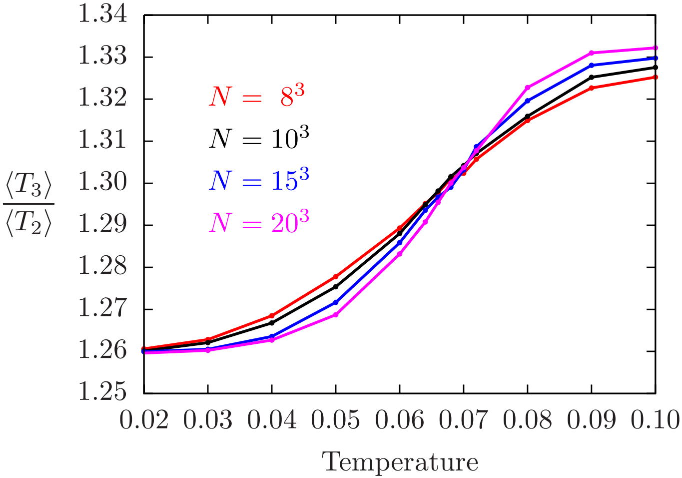
	T_3/T_2	T_4/T_2
Neutral $d \geq 2$= Kingman	$4/3$	$3/2$
Neutral $d = 1$	$7/5$	$8/5$
Directed Polymers $1 + \infty$	$5/4 = 1.25$	$25/18 \simeq 1.39$
Directed Polymers $1 + 2$	1.29	1.42
Directed Polymers $1 + 1$	1.36	1.55

Brunet D. Simon 2008

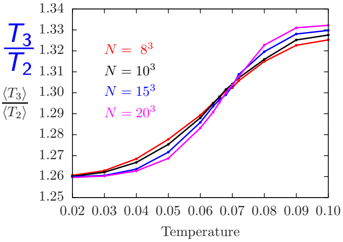
Phase transitions in dimension $3+1$

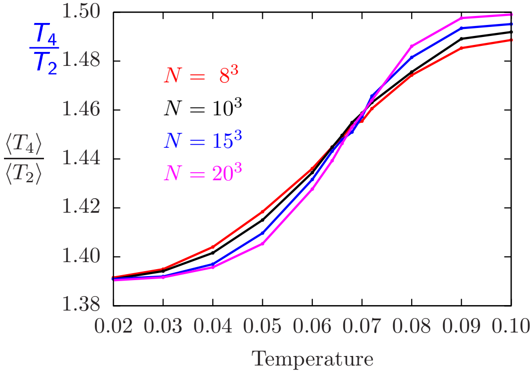
Brunet D. 2009?

Lattice infinite in the special direction and finite of N sites in the transverse direction

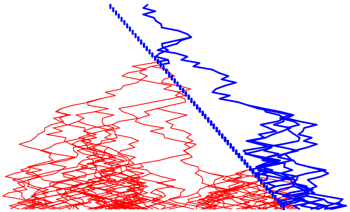


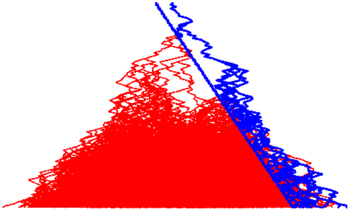
Phase transitions in dimension $3 + 1$





Branching random walk + wall





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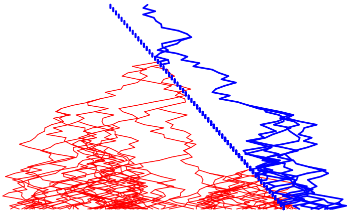
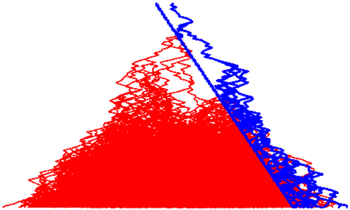
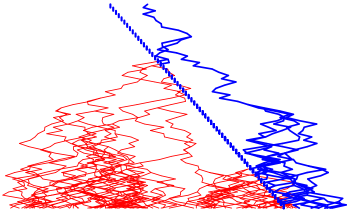




The red population by itself spreads with a known velocity v_0

The wall moves at velocity v

Branching random walk + wall



The red population spreads with a known velocity v_0

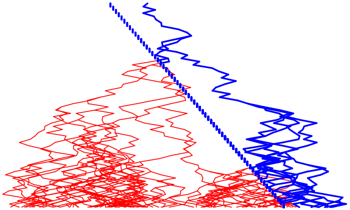
The wall moves at velocity v

$Q(x,t)$= survival probability of an individual initially at distance x from the wall

$$\boxed{\frac{dQ}{dt} = \frac{d^2Q}{dx^2} - v\frac{dQ}{dx} + Q - Q^2} \text{ with } \boxed{Q(0,t)=0}\ ,\ Q(x,0)=1$$

Fisher 1937 - Kolmogorov Petrovsky Piscounov 1937

Survival probability



The red population spreads with a known velocity v_0

The wall moves at velocity v

$v > v_0$ $\qquad Q(x,t) \to 0$

D. Simon 2007

$v < v_0$ $\qquad Q(x,\infty) \sim \exp[-\pi(v_0 - v)^{-1/2} + x]$

Kesten 1978

$v = v_0$ $\qquad Q(x,t) \sim \exp[-(3\pi^2 t)^{1/3}]$

CONCLUSION

- Coalescence times $\longrightarrow$ Universality Classes
- Neutral $\neq$ Selection
- Link to disordered systems
- Noisy traveling wave equations
- Abraham never met Lucy
- All human beings have **all** their ancestors in common

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