Statistical Physics of Biological Evolution

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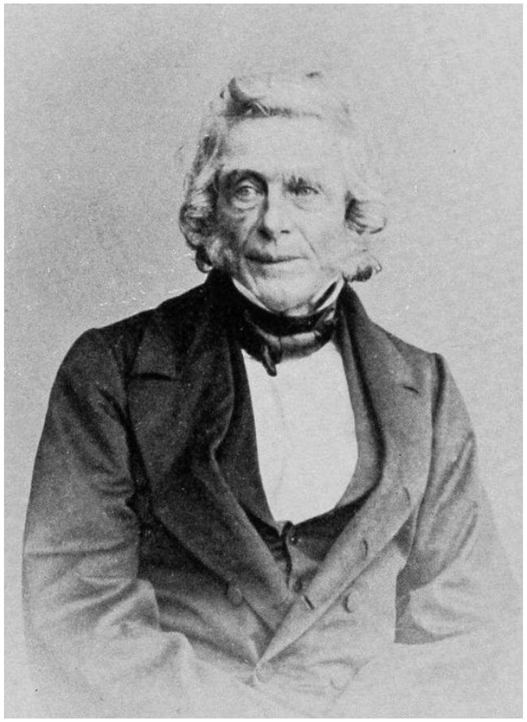
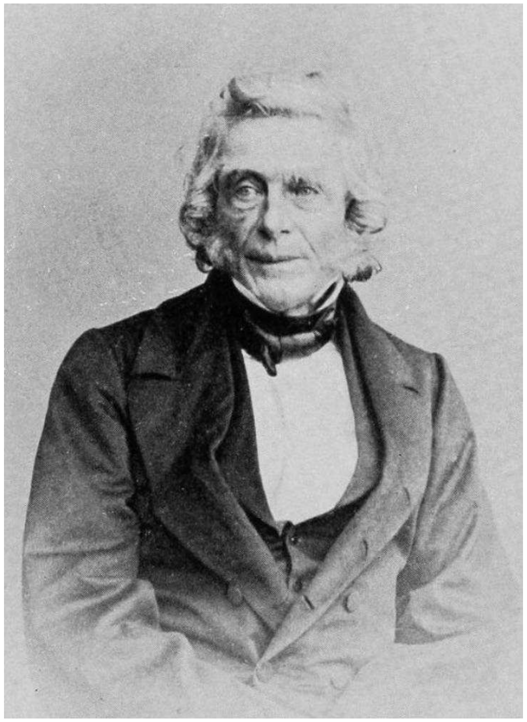
Natural selection



“... those individuals of each species...whose capacities and instincts can best regulate the physical energies to self-advantage according to circumstances - in such immense waste of primary and youthful life, *those* only come forward to maturity from the strict ordeal by which Nature tests their adaptation to her standard of perfection and fitness to continue their kind by reproduction.”

Patrick Matthew, Naval Timber and Arboriculture (1831)

Natural selection



“Patrick Matthew undoubtedly had the right idea, just like Darwin did on September 28, 1838, but he did not devote the next twenty years to converting it into a cogent theory of evolution. As a result it had no impact whatsoever.”

Ernst Mayr, The Growth of Biological Thought (1982)

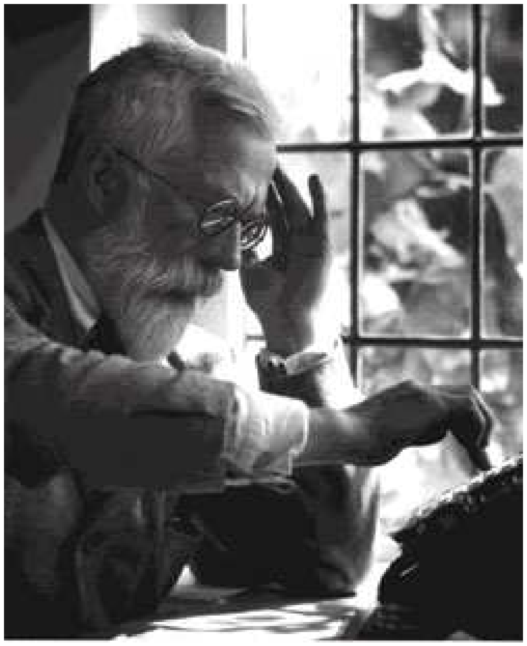
The atoms of heredity

"The gene is to the student of heredity what the atom is to the physicist. No one has ever seen a gene just as no one has ever looked upon an atom."

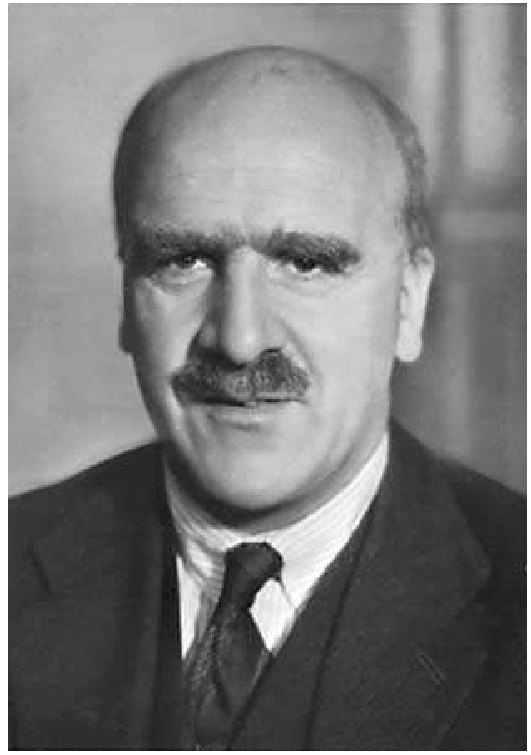
Science News Letter, 1933

- Mendel's laws (1865): Discreteness of the hereditary material
- Rediscovered around 1900 by de Vries, Correns and von Tschermak
- 1933: Nobel prize for the theory of the gene to Thomas Hunt Morgan

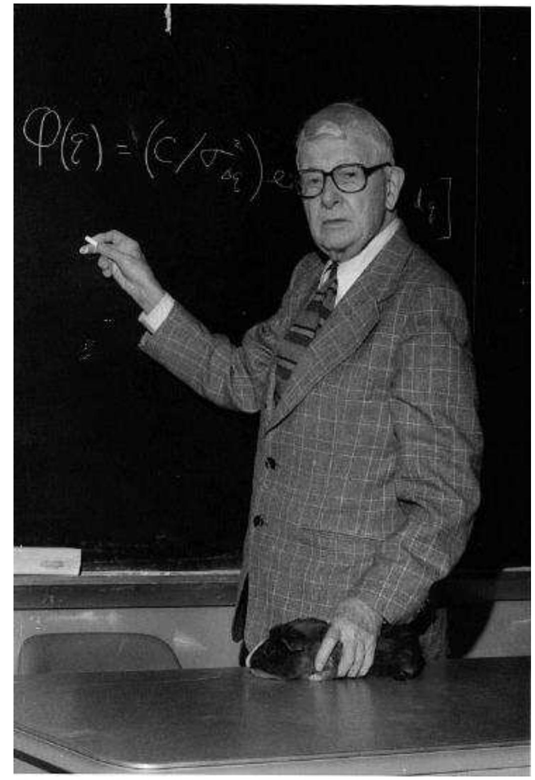
The modern synthesis in evolutionary theory



R.A. Fisher



J.B.S. Haldane

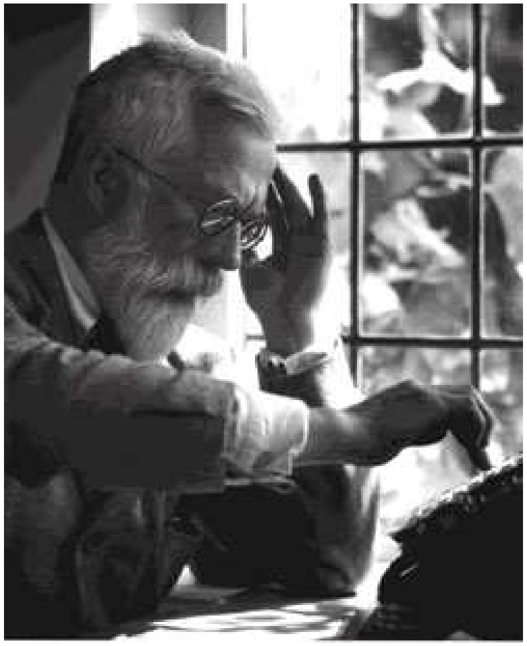


S. Wright

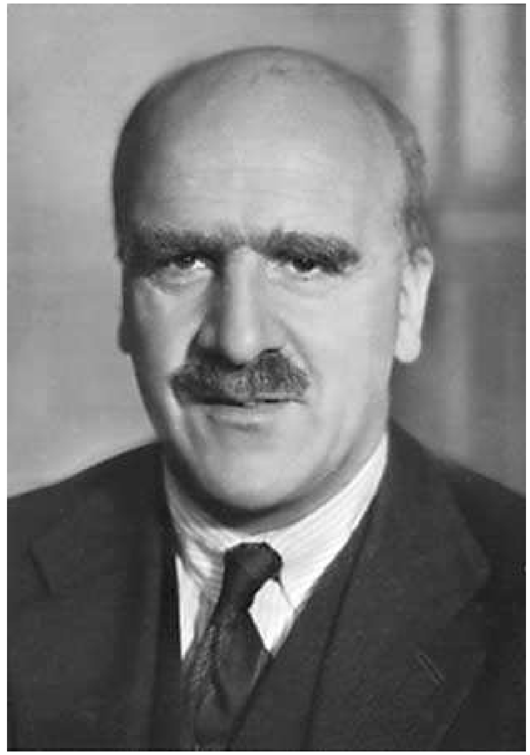
"The evolutionary process is concerned, not with individuals, but with the species, an intricate network of living matter, physically continuous in space-time, and with modes of response to external conditions which it appears can be related to the genetics of individuals only as a statistical consequence of the latter."

Sewall Wright (1931)

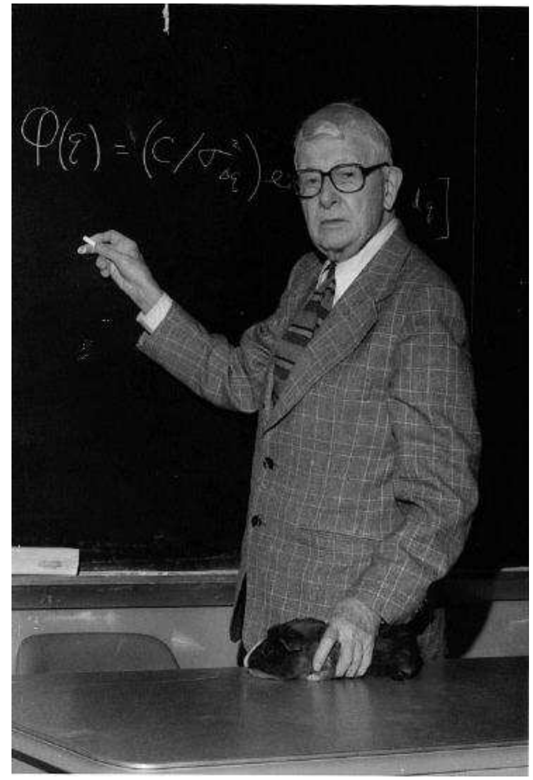
The modern synthesis in evolutionary theory



R.A. Fisher



J.B.S. Haldane



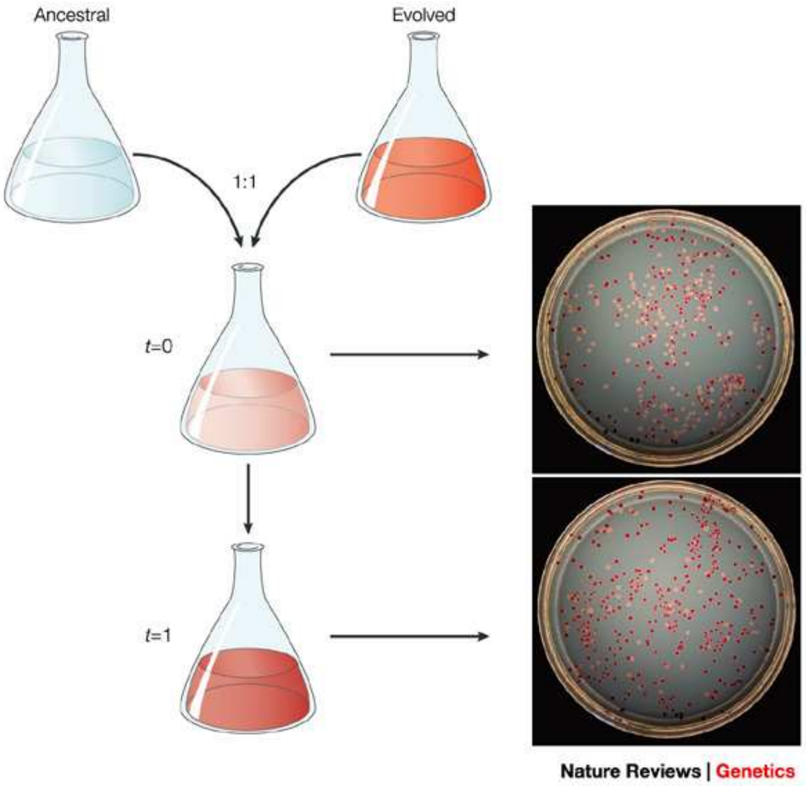
S. Wright

- Discrete mutations in the genes of individuals lead to continuous adaptation on the level of populations
- Theory of evolution as a statistical mechanics of genes

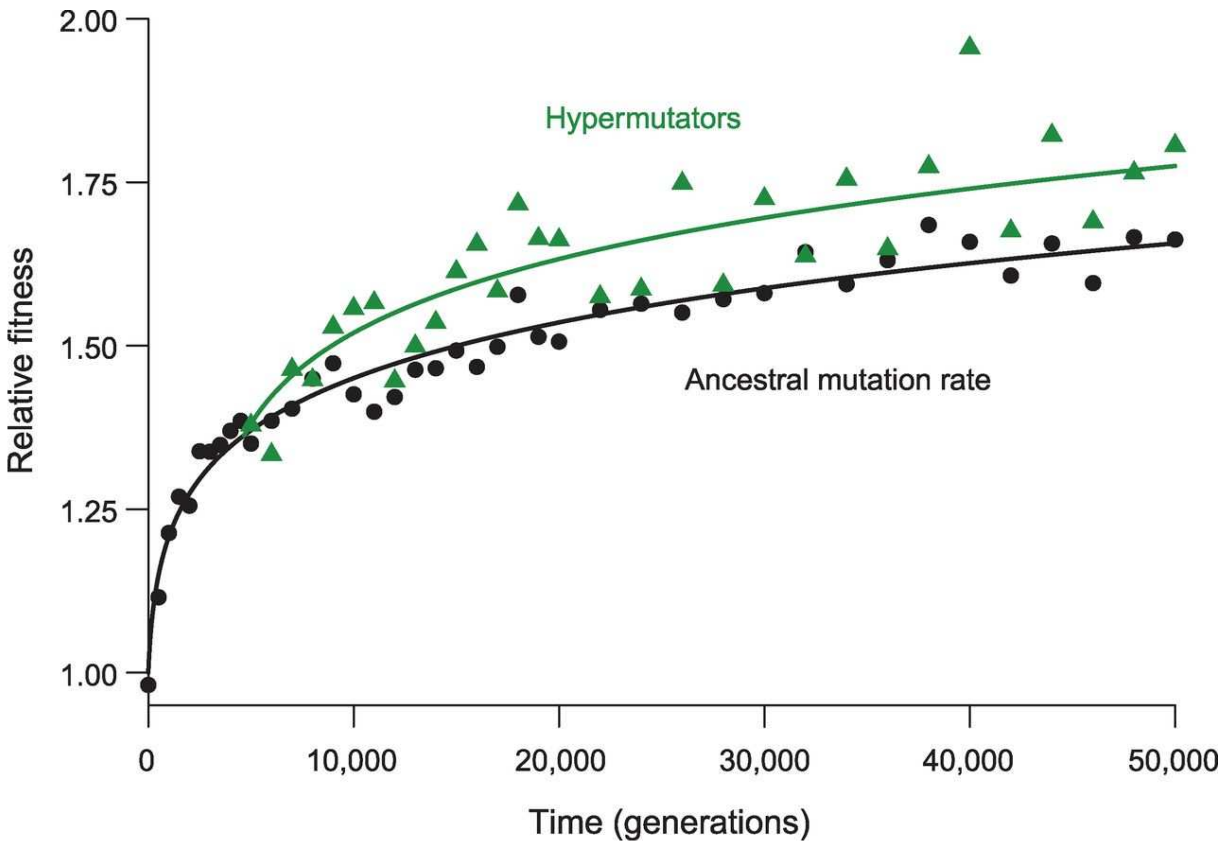
Experimental evolution

S.F. Elena, R.E. Lenski, Nature Reviews Genetics **4**, 457 (2003)

- Populations of bacteria or viruses propagated in the lab over hundreds to tens of thousands of generations
- Controlled environment, mutation rate & population size
- Fitness monitored by competition against ancestral population
- Phenotypic characterization & sequencing of mutants
- Allows to study repeatability & predictability of evolution



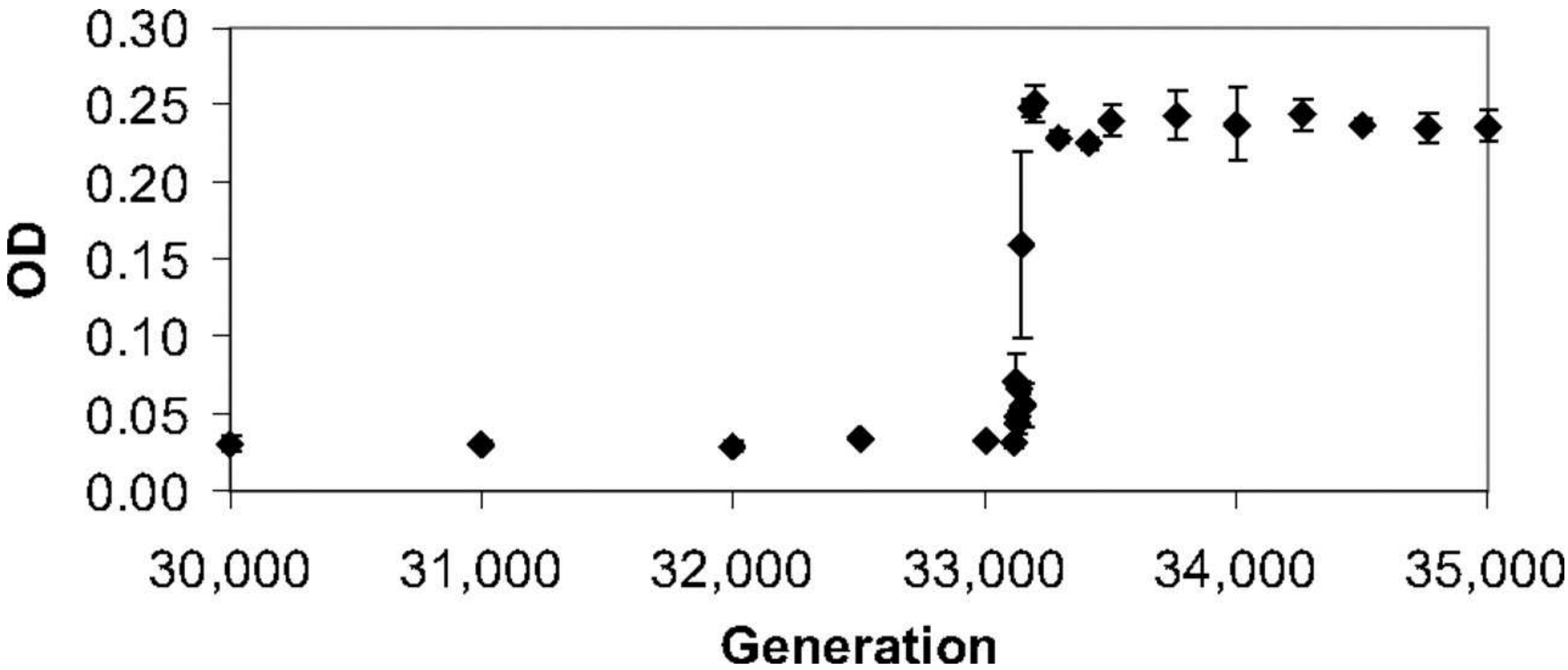
Richard Lenski's long-term evolution experiment



Wiser et al., Science 2013

- 12 populations of *Escherichia coli* evolved under constant nutrient-poor conditions since 1988

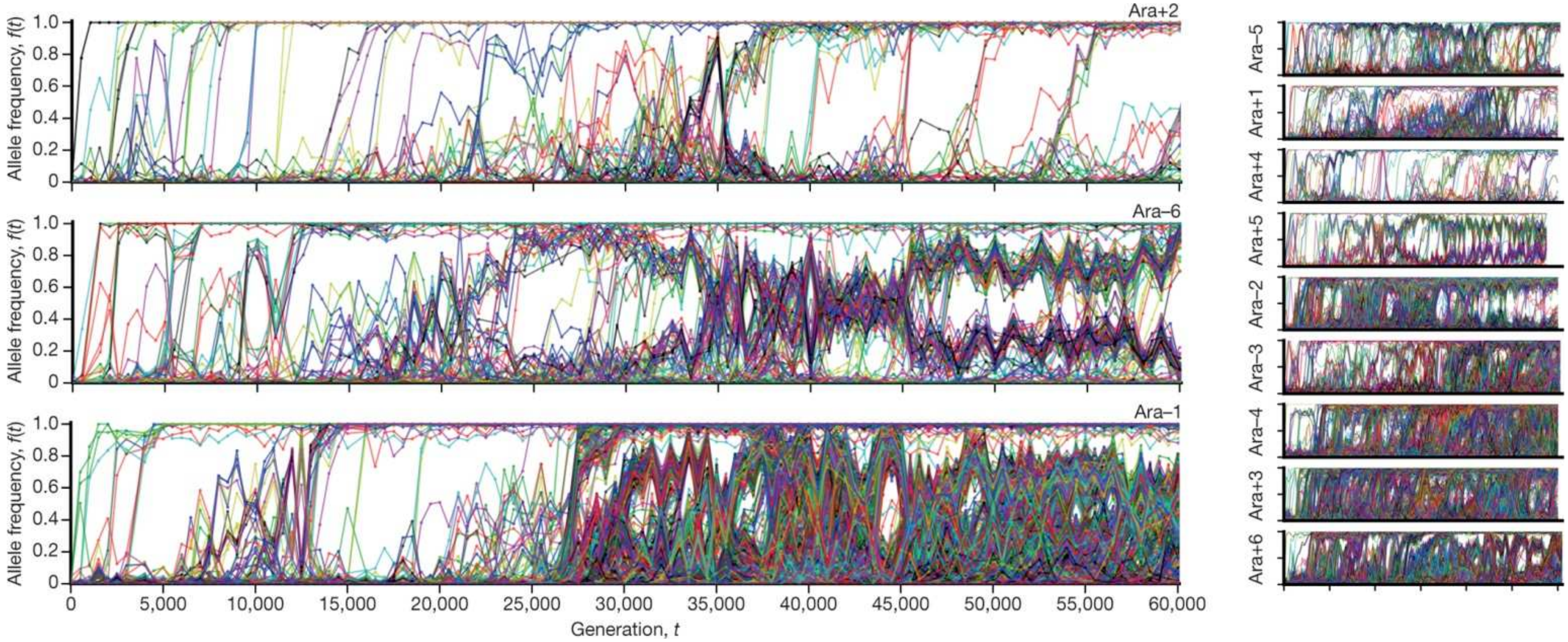
Ability to exploit citrate evolved after 31,500 generations



Blount et al., PNAS **105**, 7899 (2008)

Clonal interference

Good et al., Nature **551**, 44 (2017)



- Sequencing at 500 generation intervals allows to track all *de novo* mutations that reach at least 10 % frequency

Outline of lectures

- <u>Lecture 1: Stochastic models of population genetics</u>
  Wright-Fisher and Moran dynamics; fixation; diffusion theory

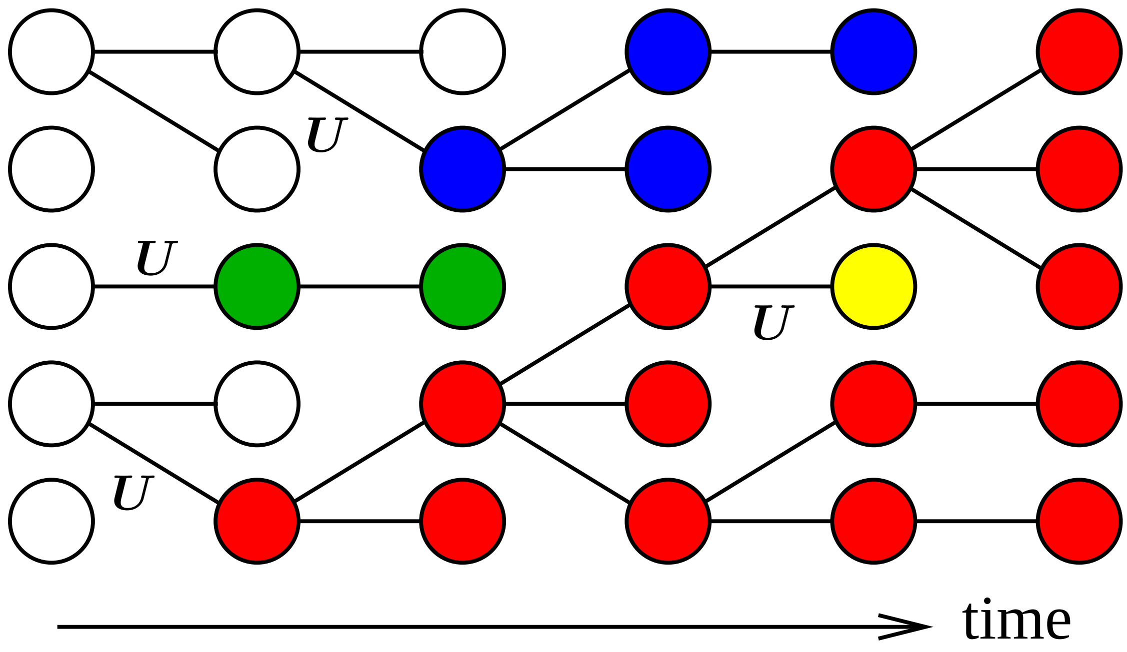
- <u>Lecture 2: Fitness landscapes I</u>
  Epistasis and sign epistasis; sequence spaces; quantifying fitness landscape topography

- <u>Lecture 3: Fitness landscapes II</u>
  Random field models; accessibility percolation

- <u>Lecture 4: Dynamics on fitness landscapes I</u>
  Origin-fixation models; mutational landscape model and adaptive walks

- <u>Lecture 5: Dynamics on fitness landscapes II</u>
  Rank order processes; extreme value theory in evolutionary biology

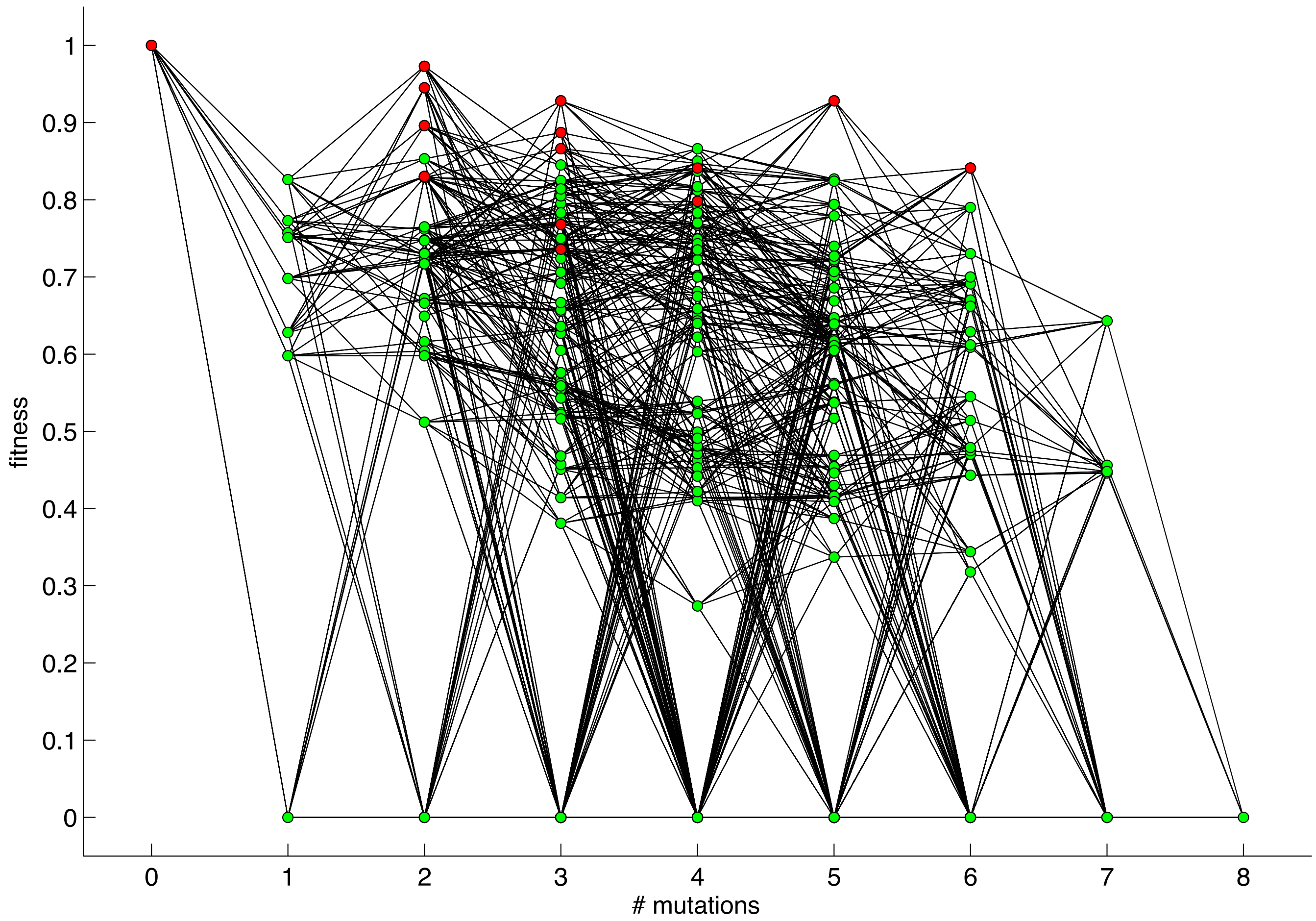
Wright-Fisher model



- N individuals, discrete generations
- Individuals have types which can change through mutations (rate U)
- Fitness: Expected number of offspring in the next generation
- Fixation occurs when one type takes over the population

An empirical fitness landscape

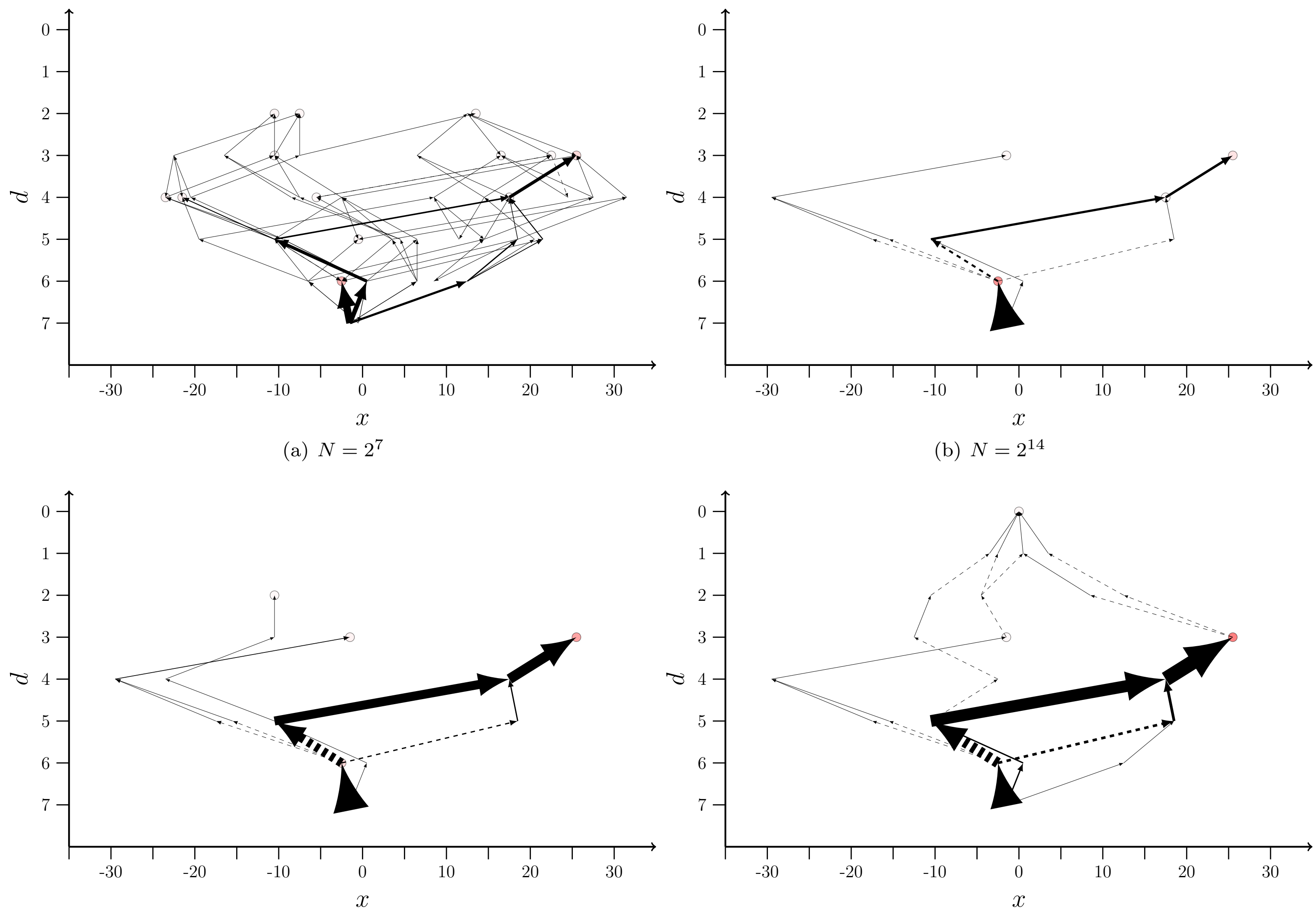
J. Franke et al., PLoS Comp. Biol. **7** (2011) e1002134



- All $2^8 = 256$ combinations of 8 deleterious marker mutations residing on different chromosomes of *Aspergillus niger*

Evolutionary trajectories on the *A. niger* landscape

I.G. Szendro et al., PNAS 110:571 (2013)



(a) $N = 2^7$

(b) $N = 2^{14}$

(c) $N = 2^{17}$

(d) $N = 2^{23}$

Suggested reading (available on BSSP web page)

- JK: *Population genetics and evolution*, arXiv:1803.08474
- I.G. Szendro et al., *Quantitative analyses of empirical fitness landscapes*, J. Stat. Mech. P01005 (2013)
- JK, *Accessibility percolation in random fitness landscapes*, arXiv:1903:11913
- D.M McCandlish and A. Stoltzfus: *Modeling evolution using the probability of fixation: History and implications*, Quart. Rev. Biol. 89:225 (2014)
- J. Neidhart and JK, *Adaptive walks and extreme value theory*, Phys. Rev. Lett. 107:178102 (2011)