BIOL 432 - Evolution

Lecture 8

Expected Genotype Frequencies in the Absence of Evolution are Determined by the Hardy-Weinberg Equation.

Assumptions:

1) No mutation

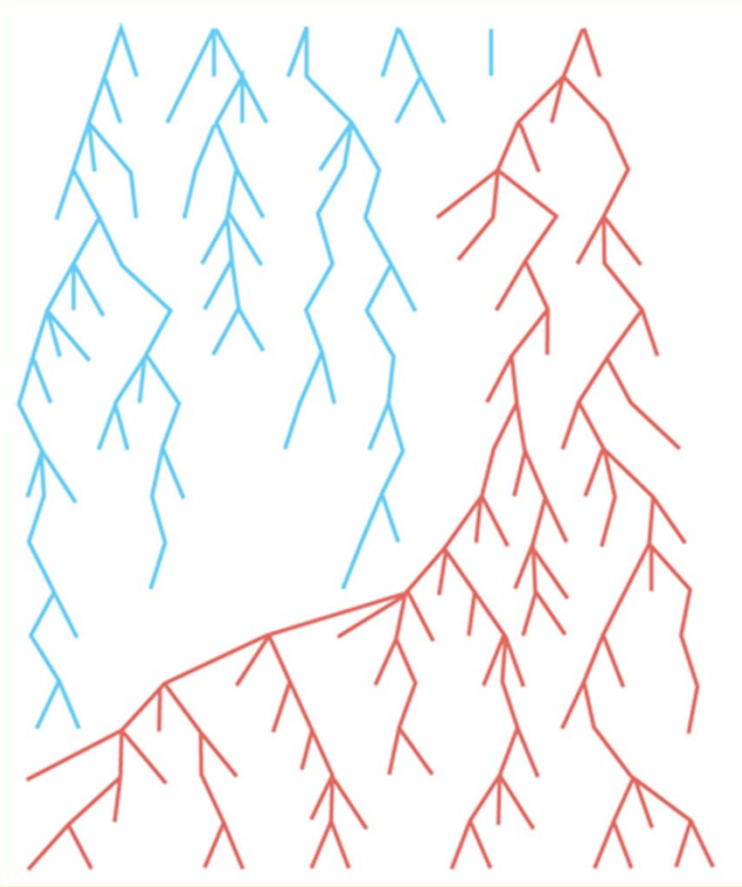
2) Random mating

3) Infinite population size

4) No immigration or emigration

5) No selection

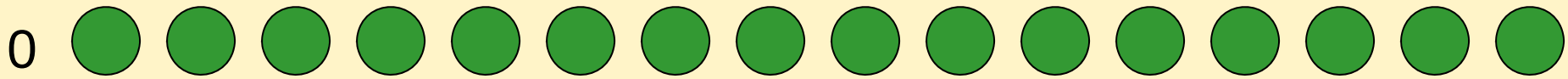
Random genetic drift



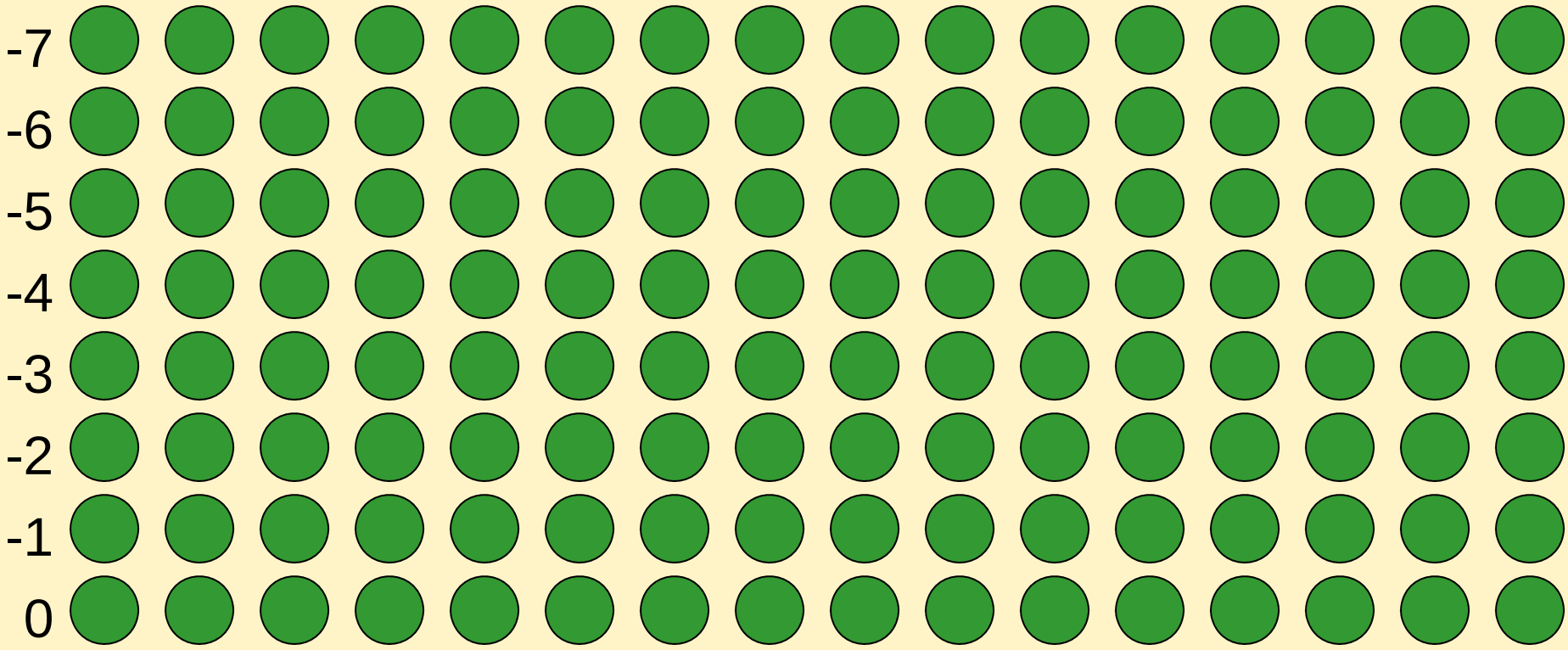
- Evolution = change of allele frequency within a population
- Randomness cannot lead to adaptation
- Can nevertheless be a powerful evolutionary force
- Main mode by which non-coding sequence evolves?

Populations

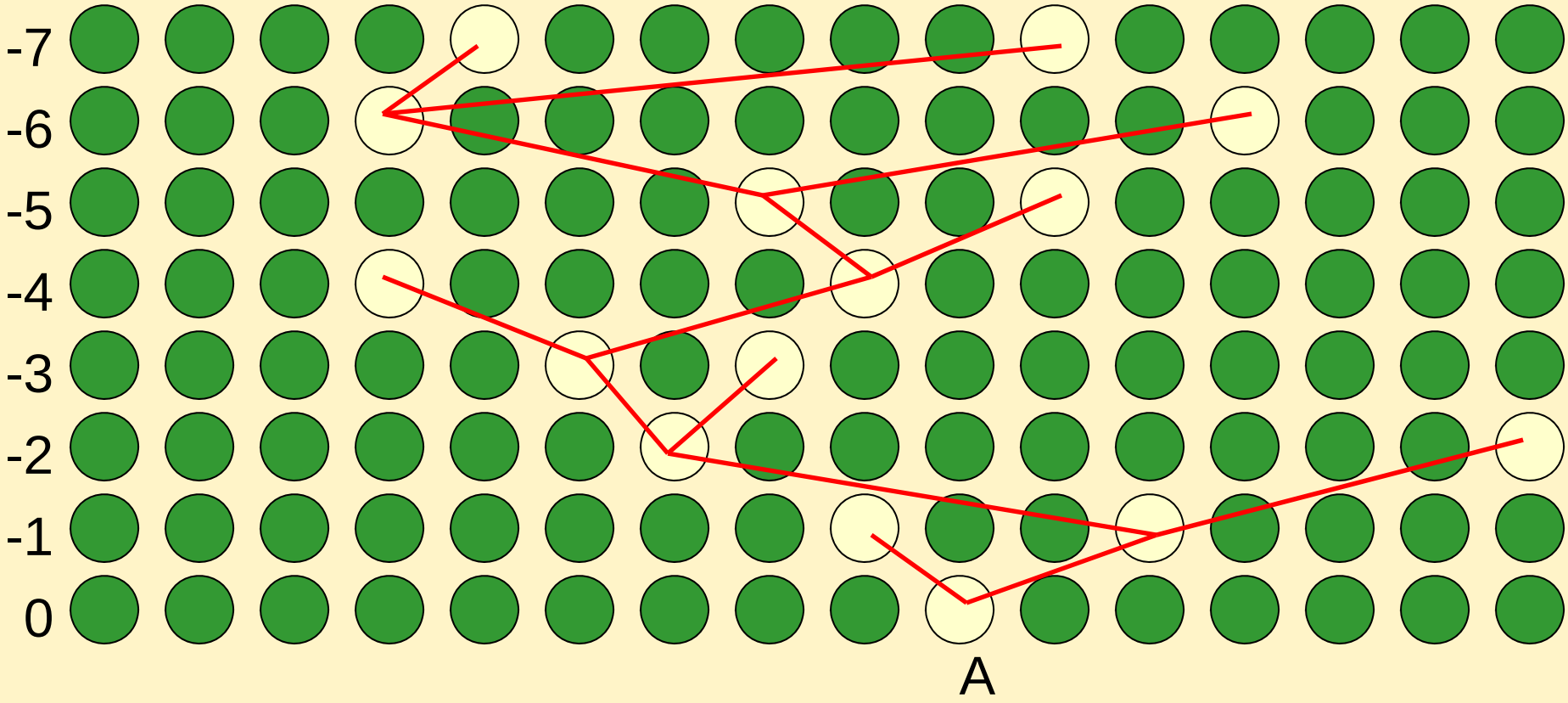
Population: Individuals of the same species in a particular area.
(Geneticists further often assume that mating is random and panmictic)



Populations have a history

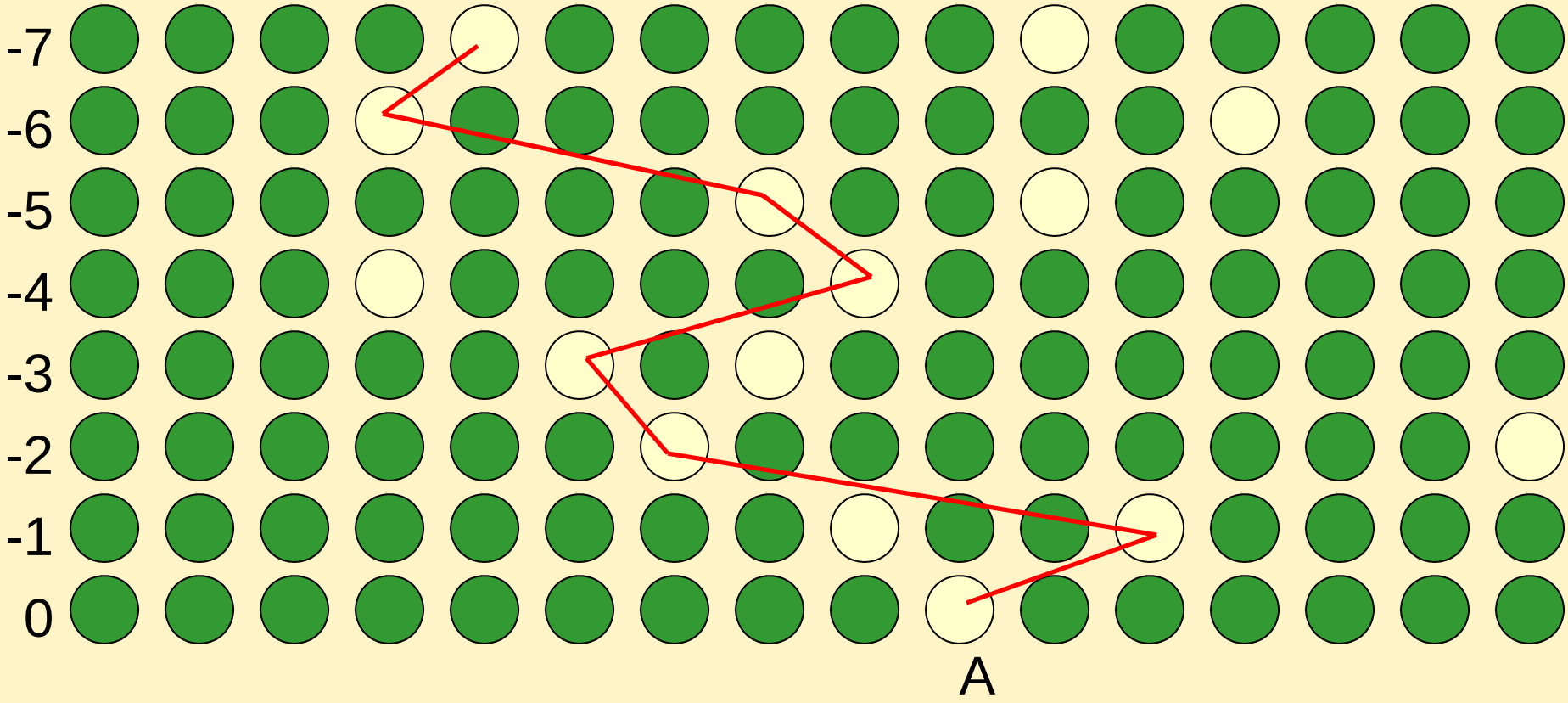


Pedigrees



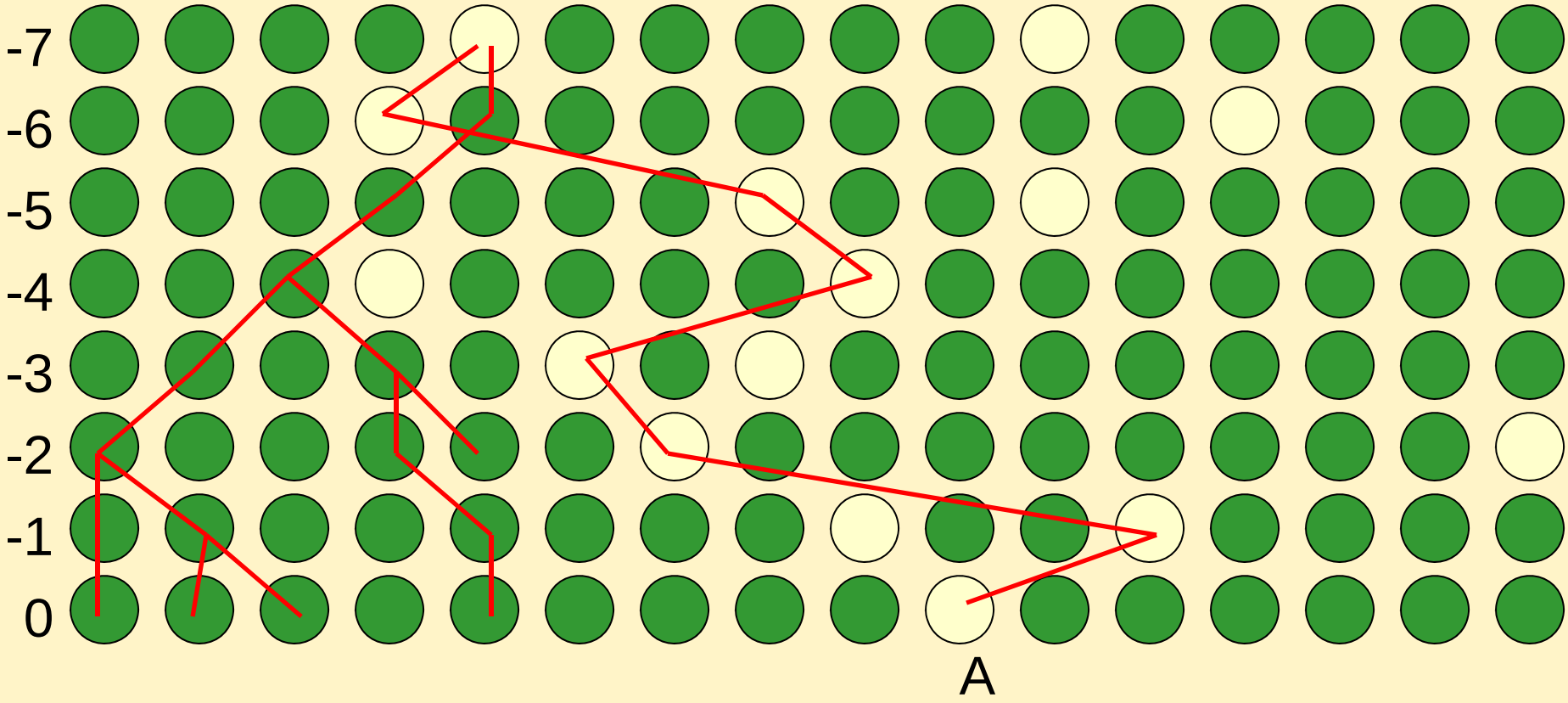
Pedigree showing the ancestors of one individual in generation 1

Genealogy



Ancestry of a an allele carried by individual A

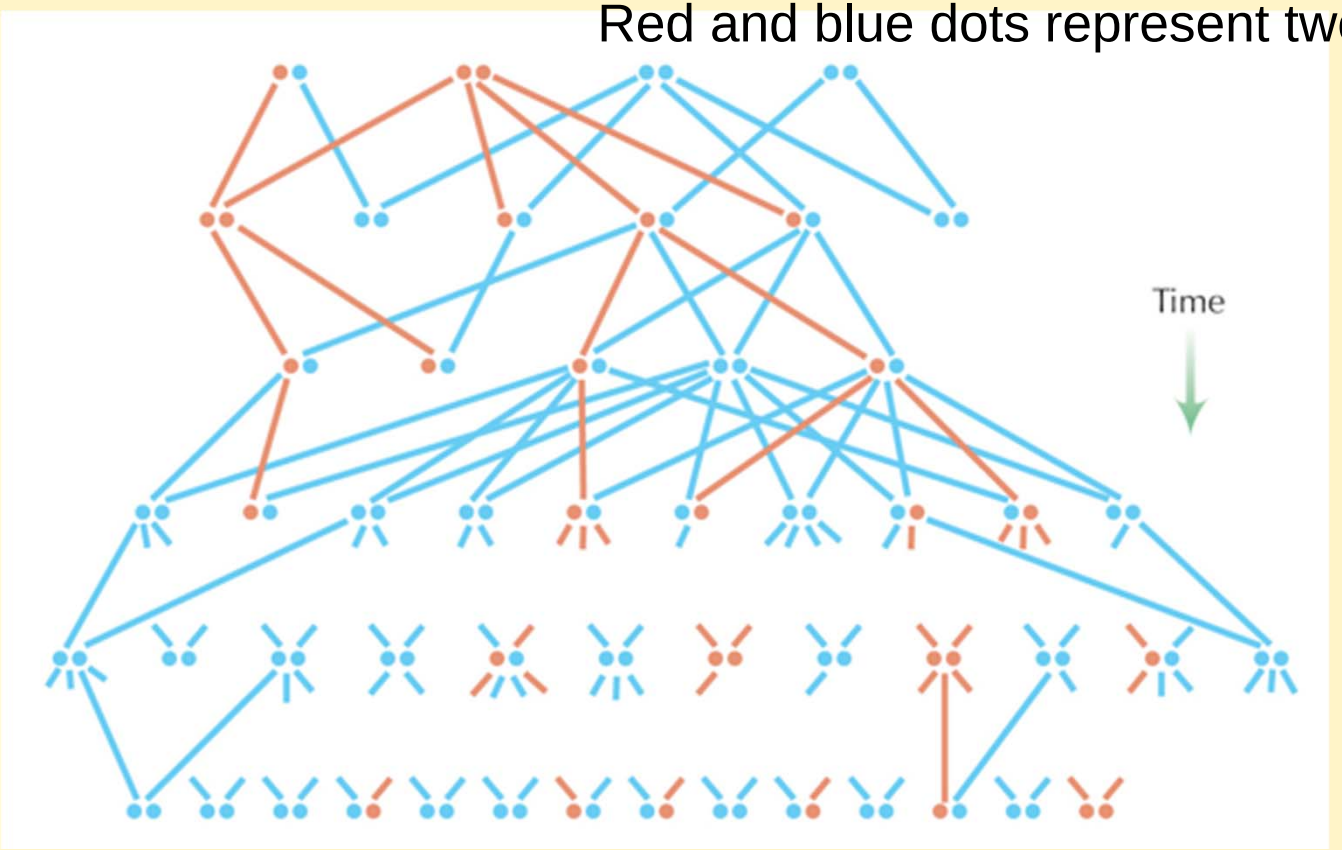
Genealogy



This allele shares its ancestry with other alleles

Demographic and genetic processes are intimately inked on the population level

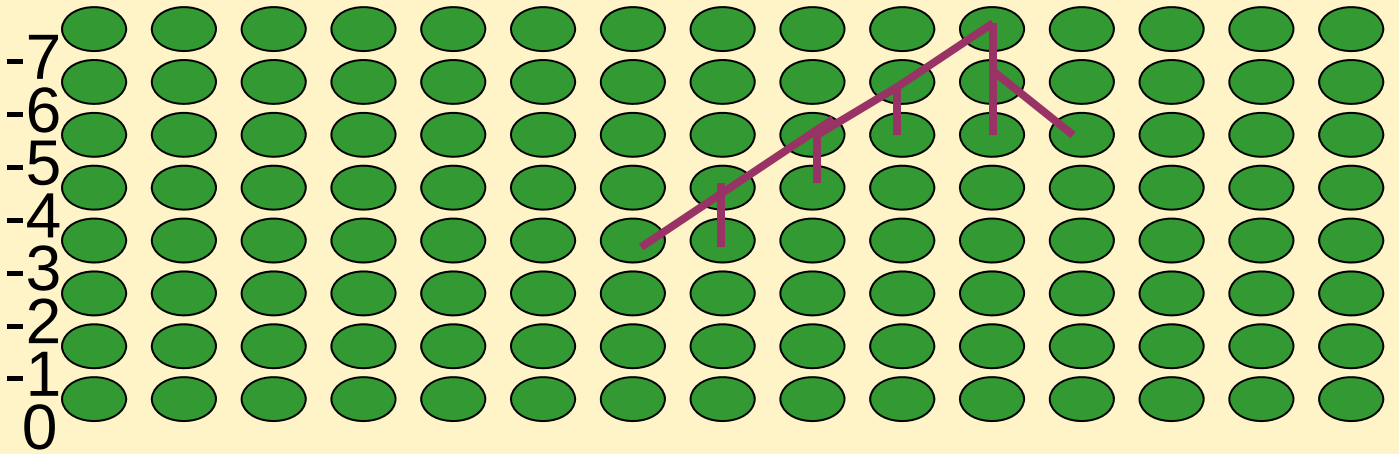
Red and blue dots represent two different alleles



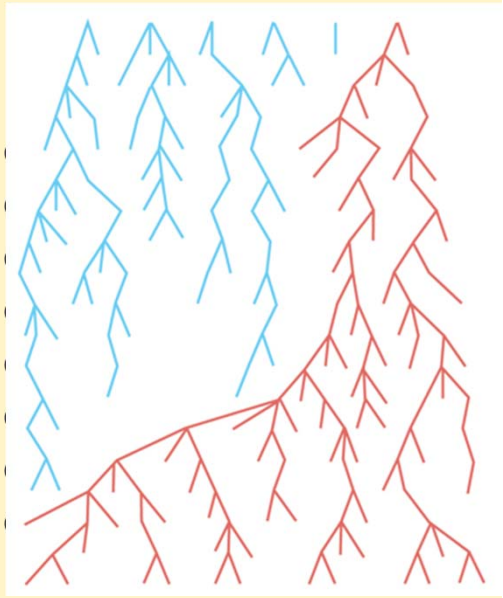
- Average number of offspring is 2.2
  - Overall population growth

The simplest model: A haploid asexual population of constant size

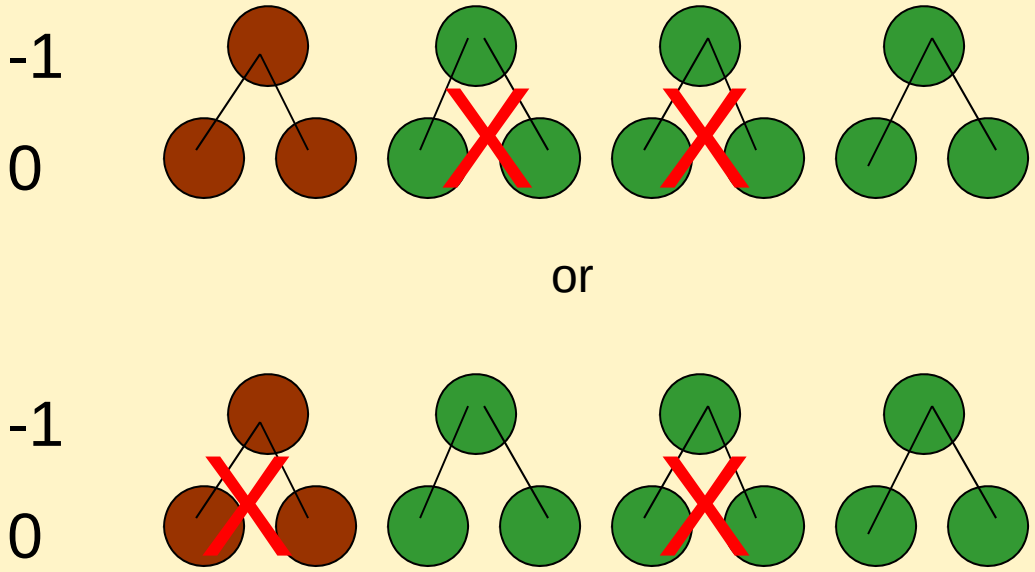
- E.g. an idealized population of bacteria



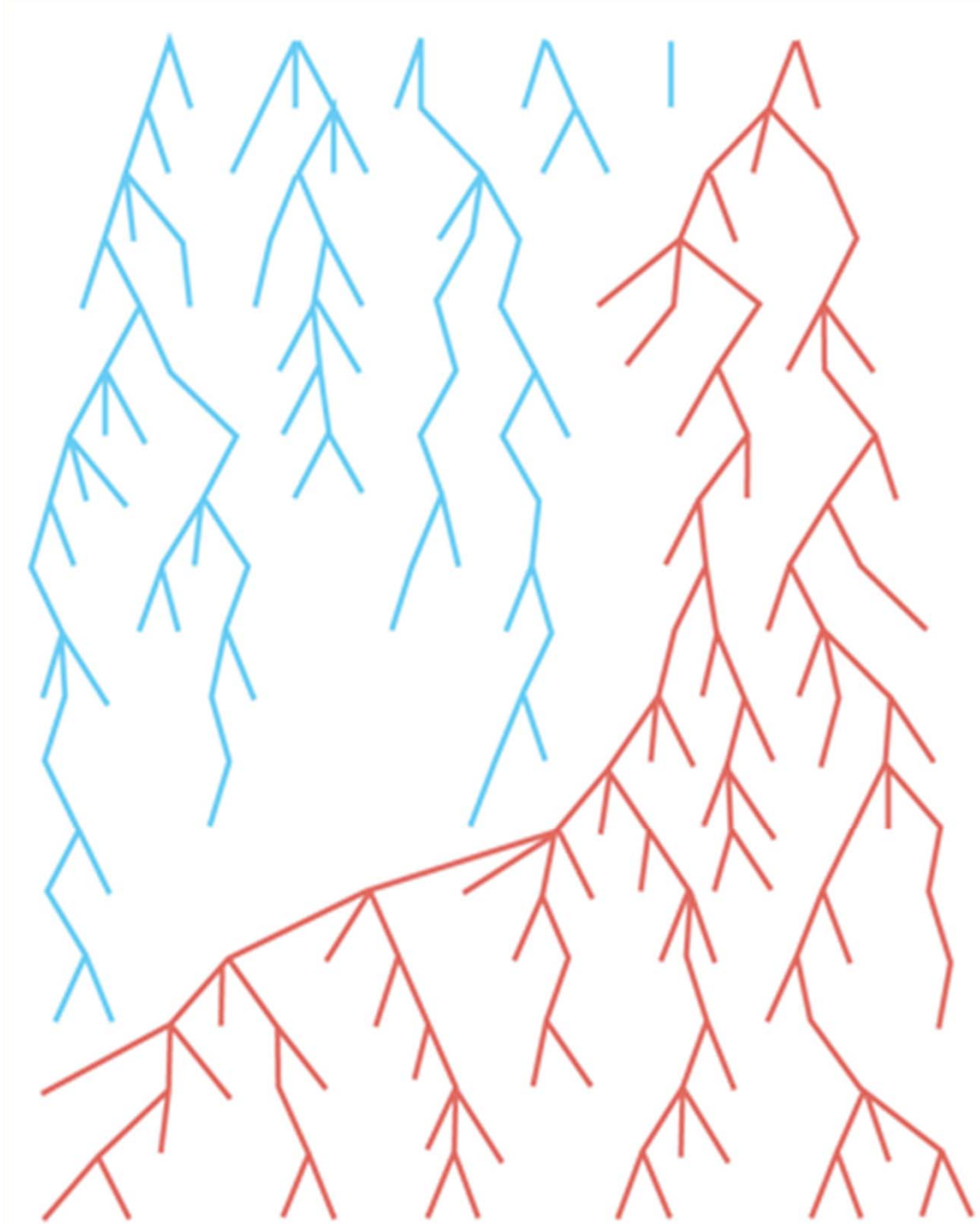
= single neutral mutation



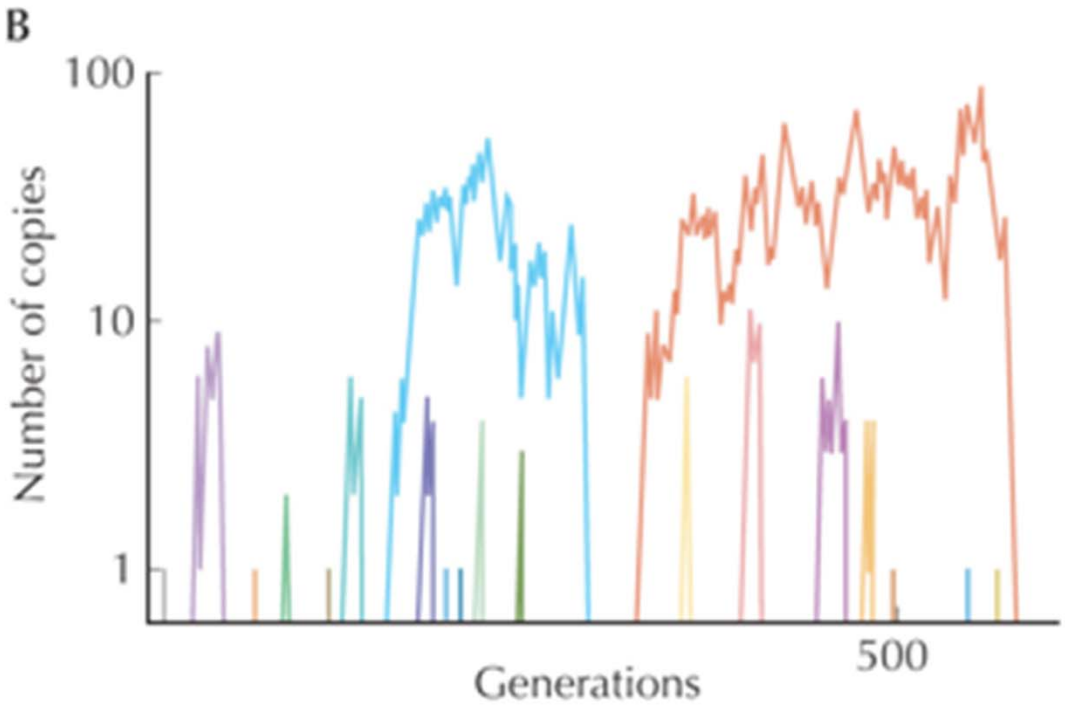
- Assumptions:
  - Mutation is neutral (has no selective advantage or disadvantage)
  - Population size is constant
  - Two possibilities: fission (I.e. reproduction) or death

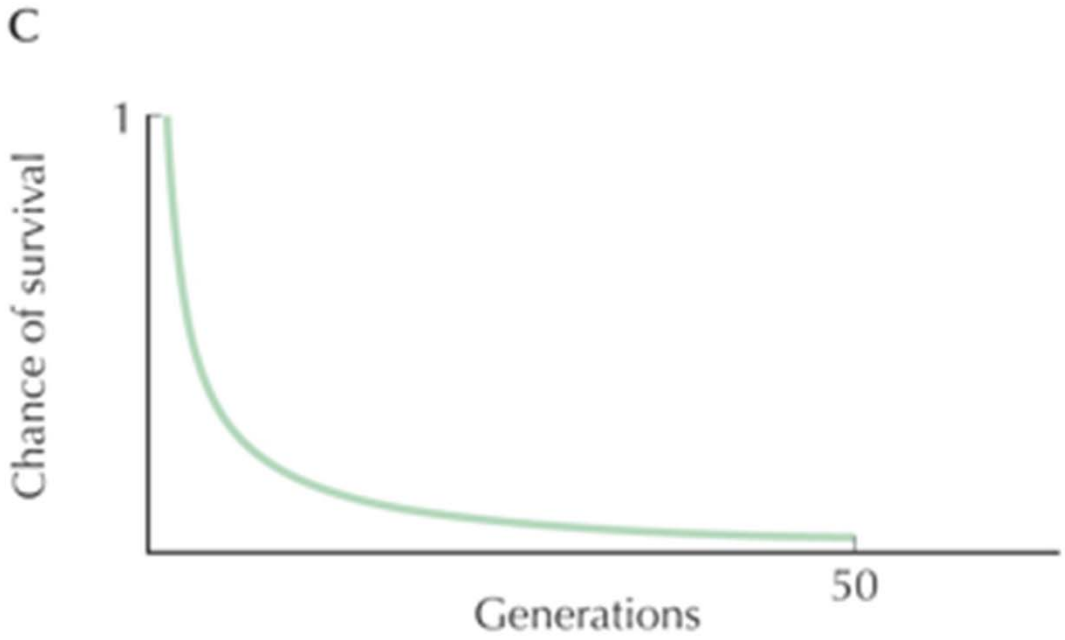


1:1



Eventually every lineage will go extinct



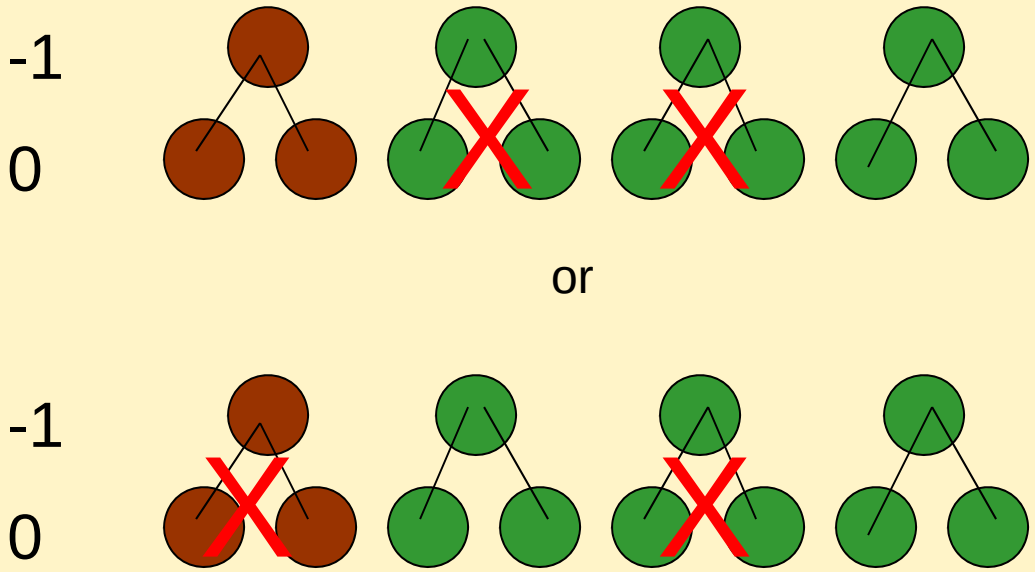


- Population with n=100 genes (copies)

Fate of different alleles

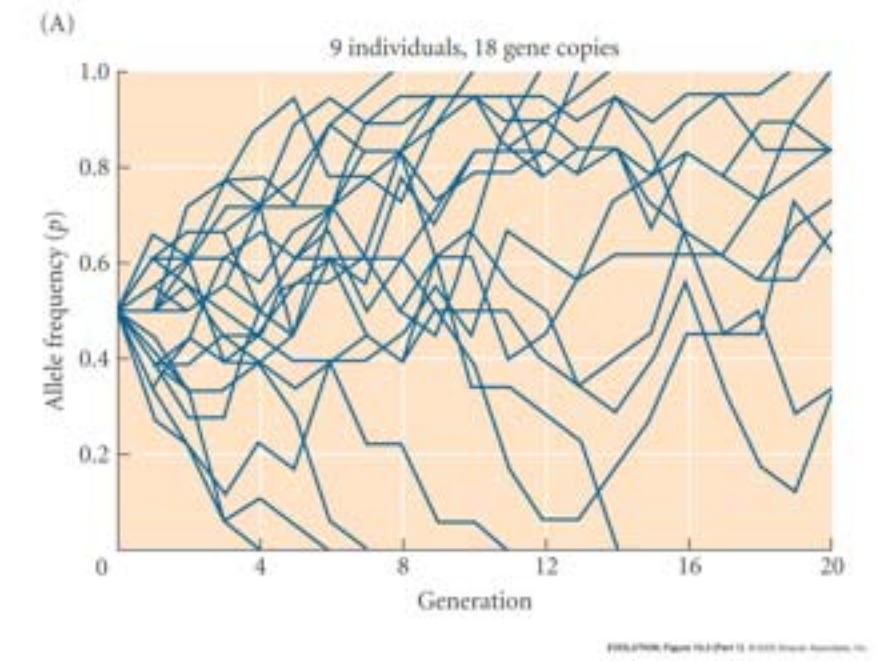
Only very few lineages are long lived

Why is this probability independent of population size?

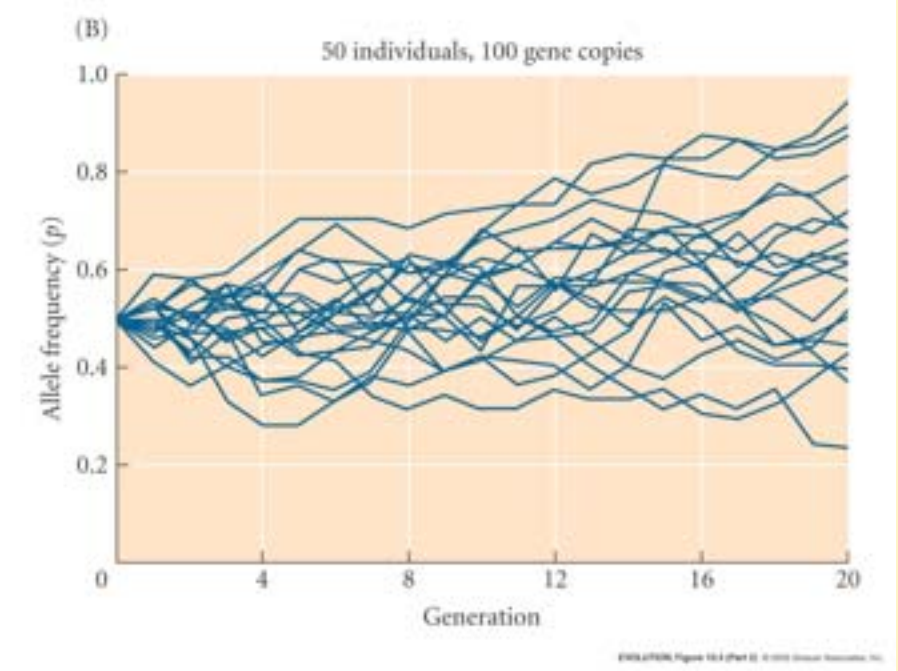


1:1

Then why does drift have a greater effect in small populations?



18 gene copies

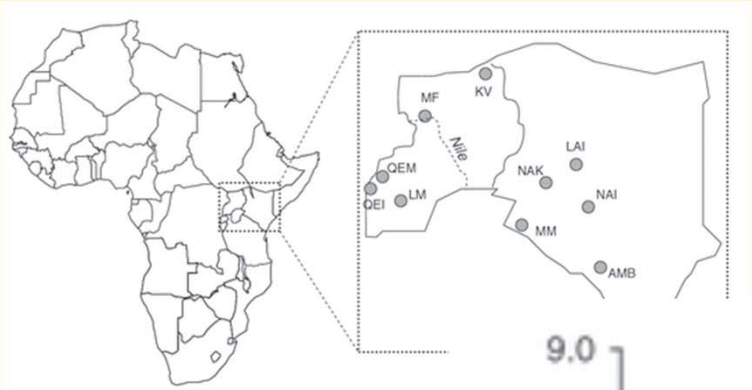


100 gene copies

Example: cape buffalo in game reserves of different size

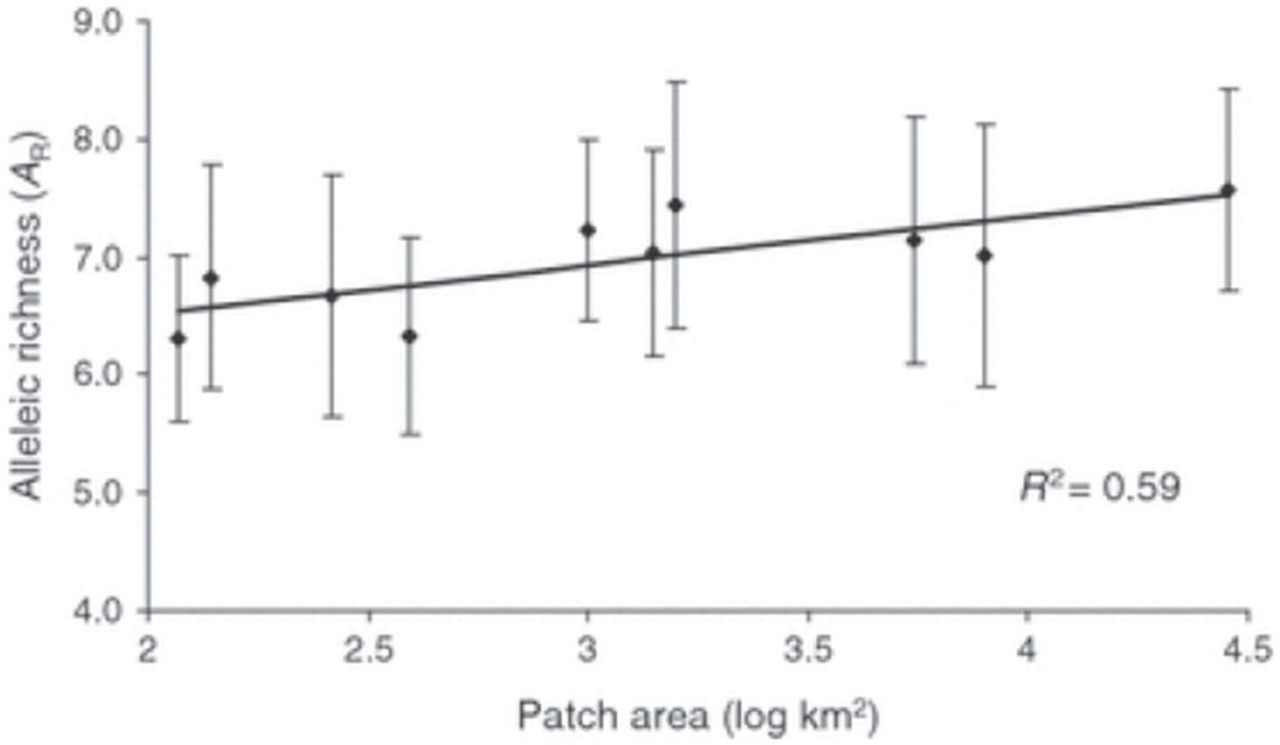
- Microsatellite study by Heller et al. 2010

Example: cape buffalo in game reserves of different size

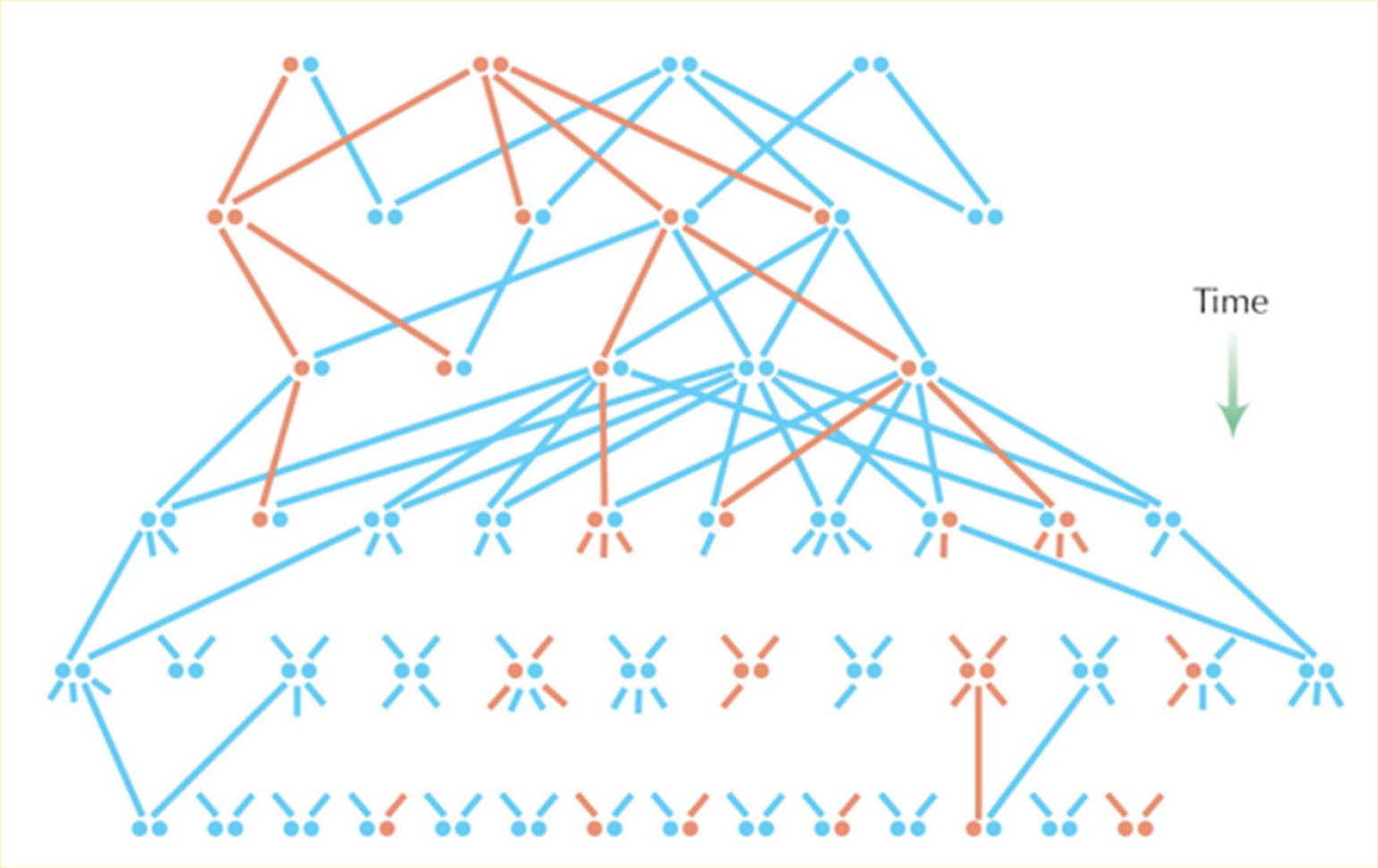


- Reserves ranged in size from 100 to 28,000 km^2

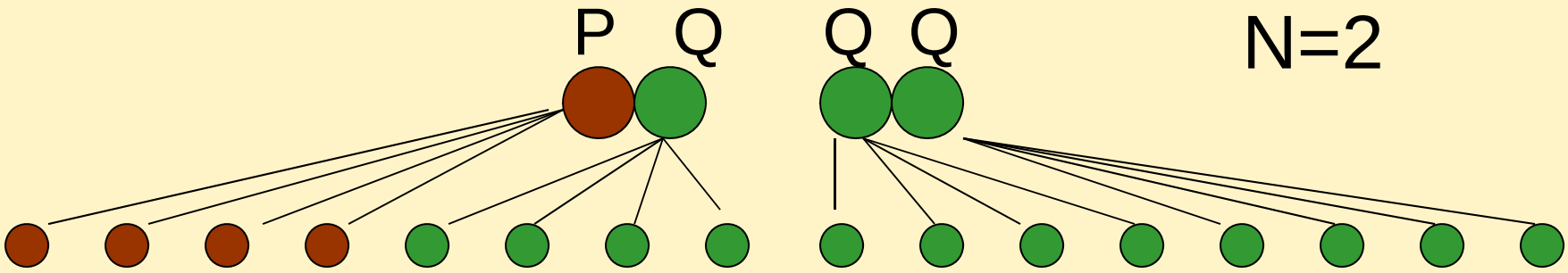
Allelic richness = mean number of alleles across multiple microsatellite loci



In diploid organisms meiosis adds randomness



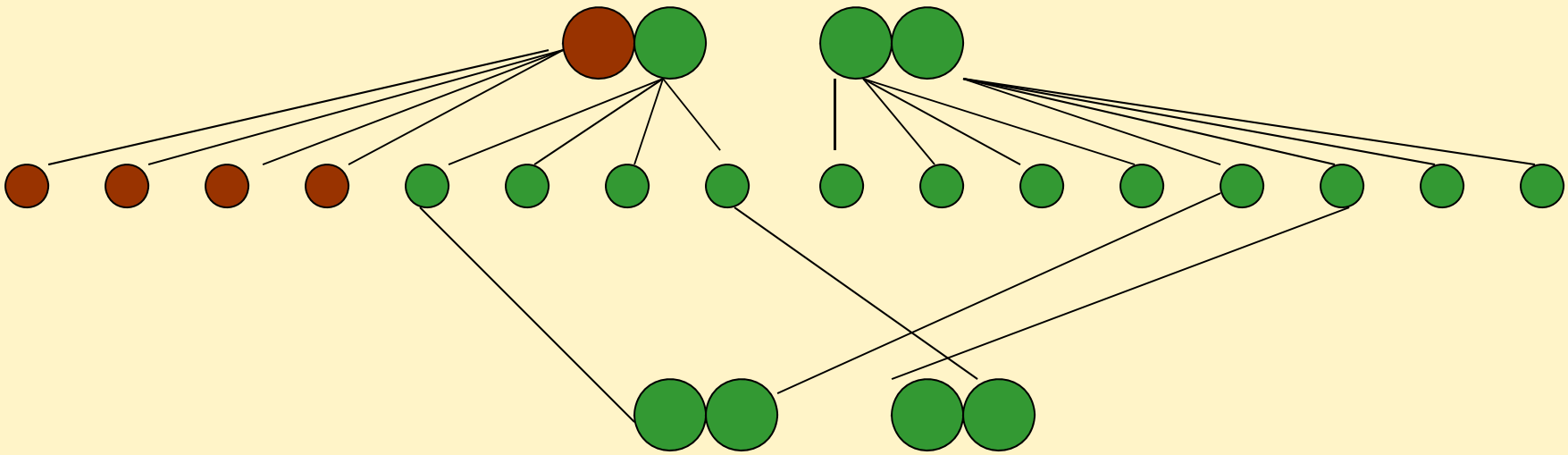
The Wright-Fisher Model



Frequency P = p = #P/2N =0.25 **Frequency Q = q = #Q/2N = 0.75**

- Assumption: Population size is constant
- Assumption: Each individual produces a large number of gametes
- Assumption: Gametes are produced in proportion to parental allele frequencies
- Assumption: Mating of alleles is random
- Assumption: Generation are discrete

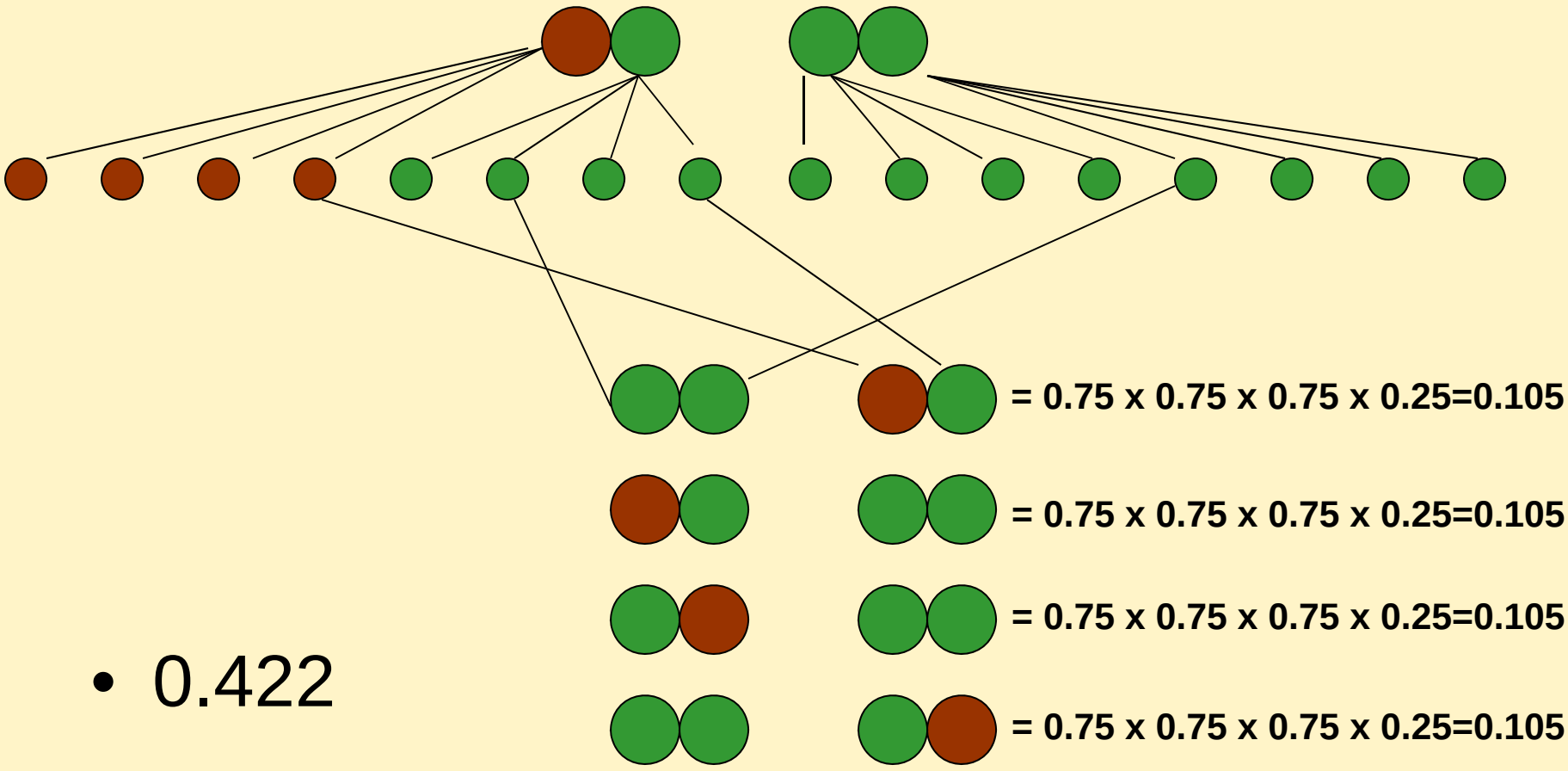
The Wright-Fisher Model



= 0.75 x 0.75 x 0.75 x 0.75=0.32

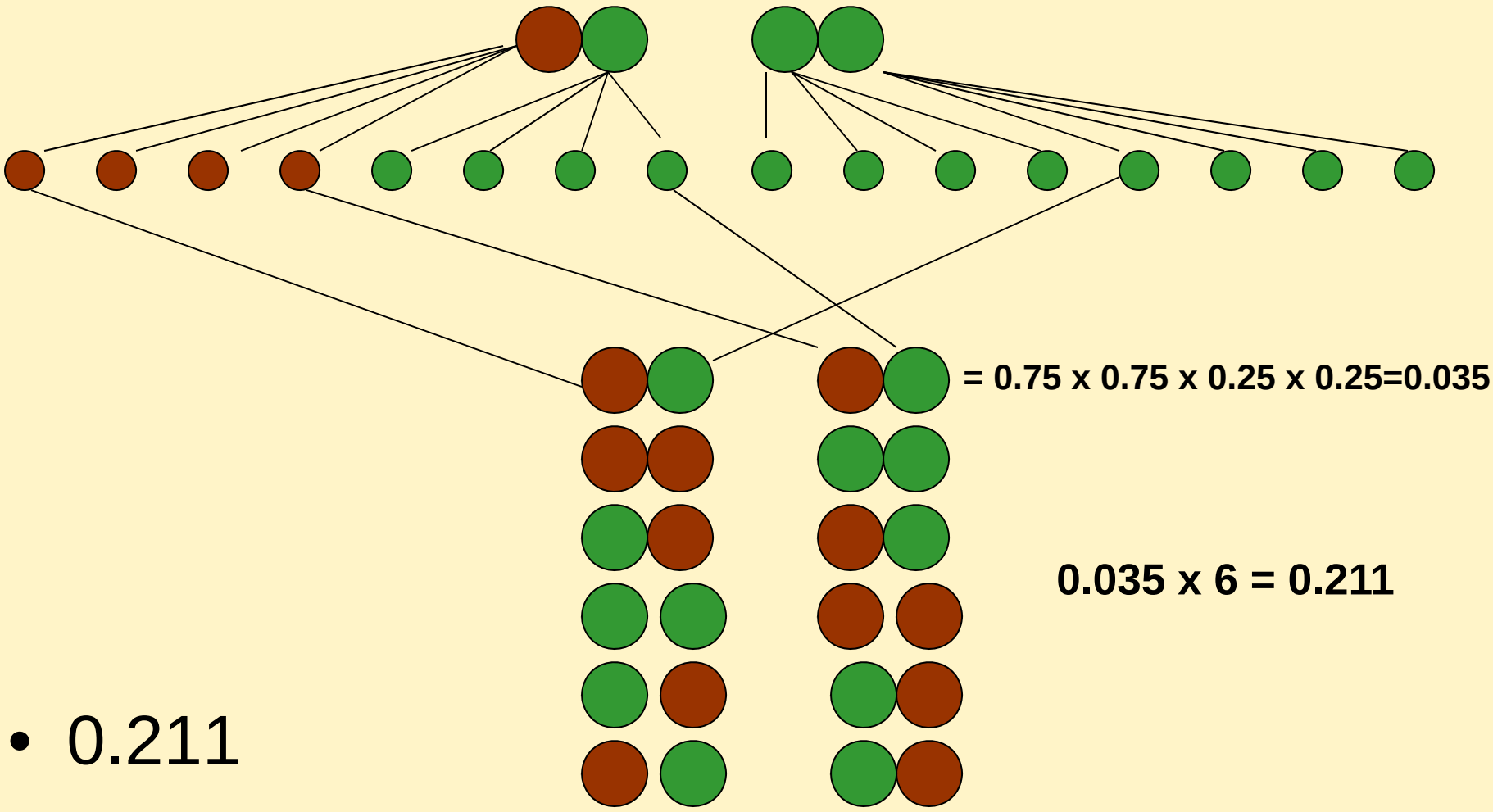
- 0.32
- Which of the following outcomes is more likely?

The Wright-Fisher Model



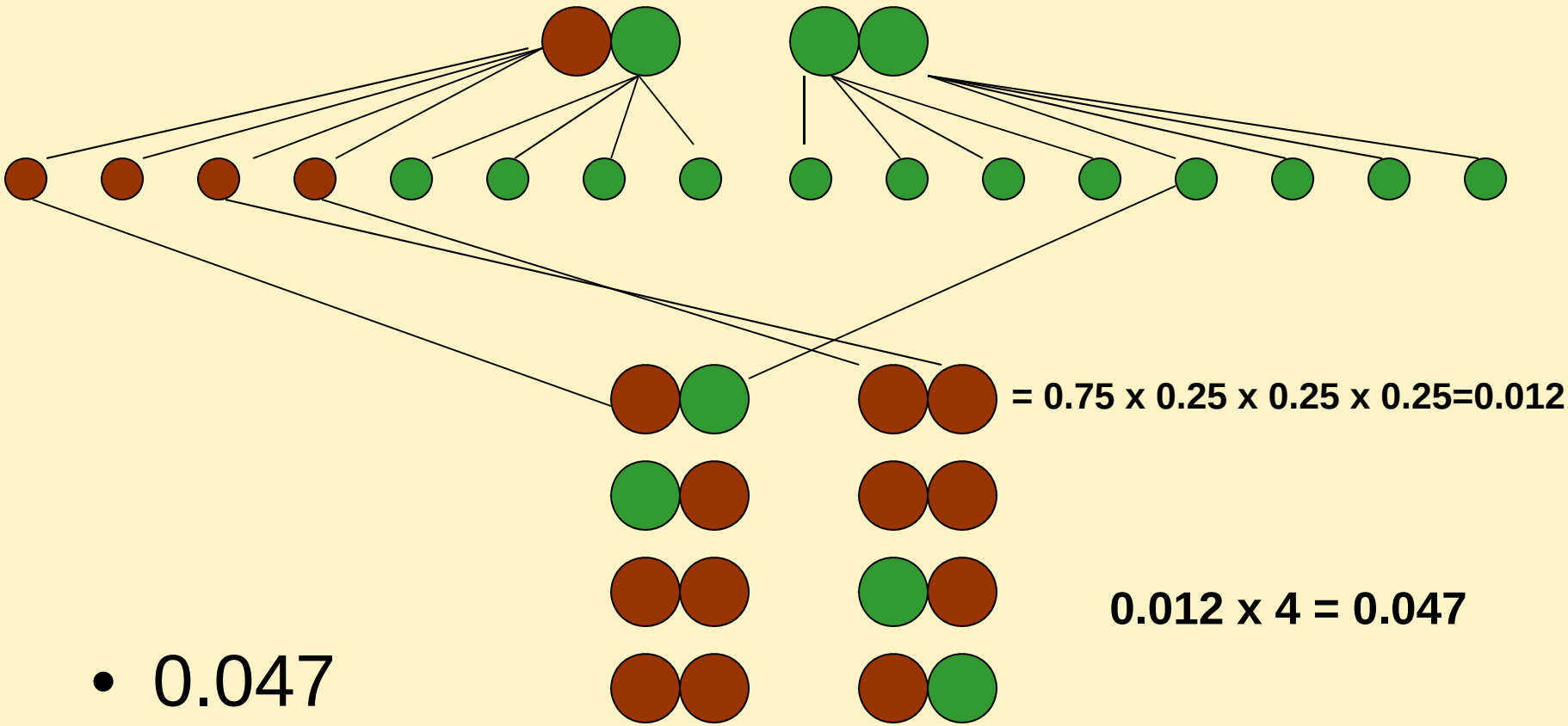
- 0.422

The Wright-Fisher Model



- 0.211

The Wright-Fisher Model

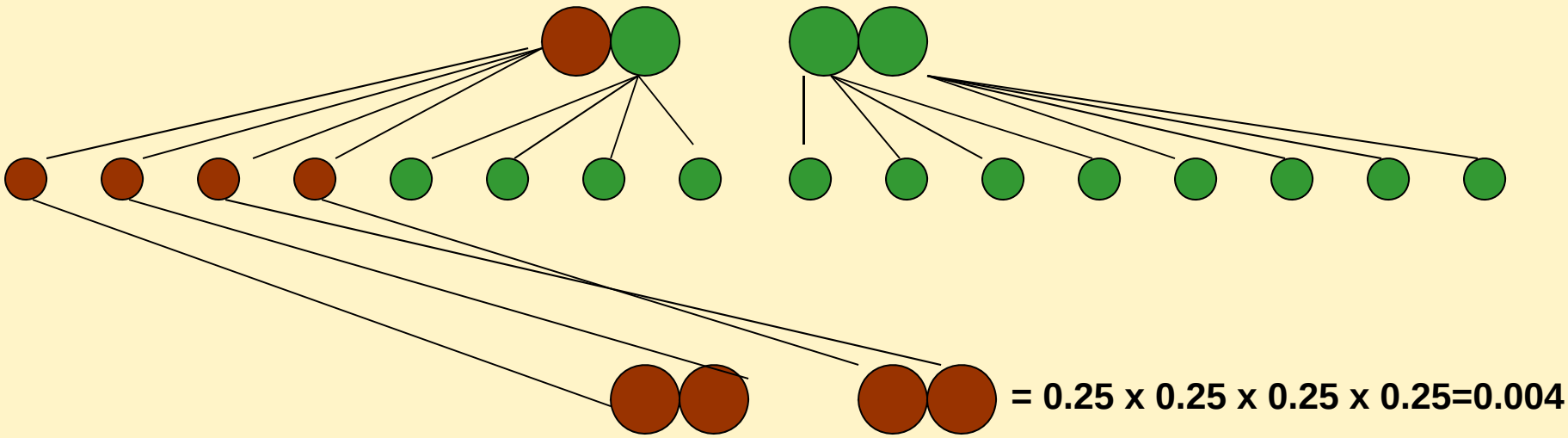


= 0.75 x 0.25 x 0.25 x 0.25=0.012

0.012 x 4 = 0.047

- 0.047

The Wright-Fisher Model



- 0.004

The outcome of the Wright-Fisher model is described by the binomial distribution

Binomial $\frac{n!}{i!(n-i)!} q^{n-i} p^{i}$

2N = n

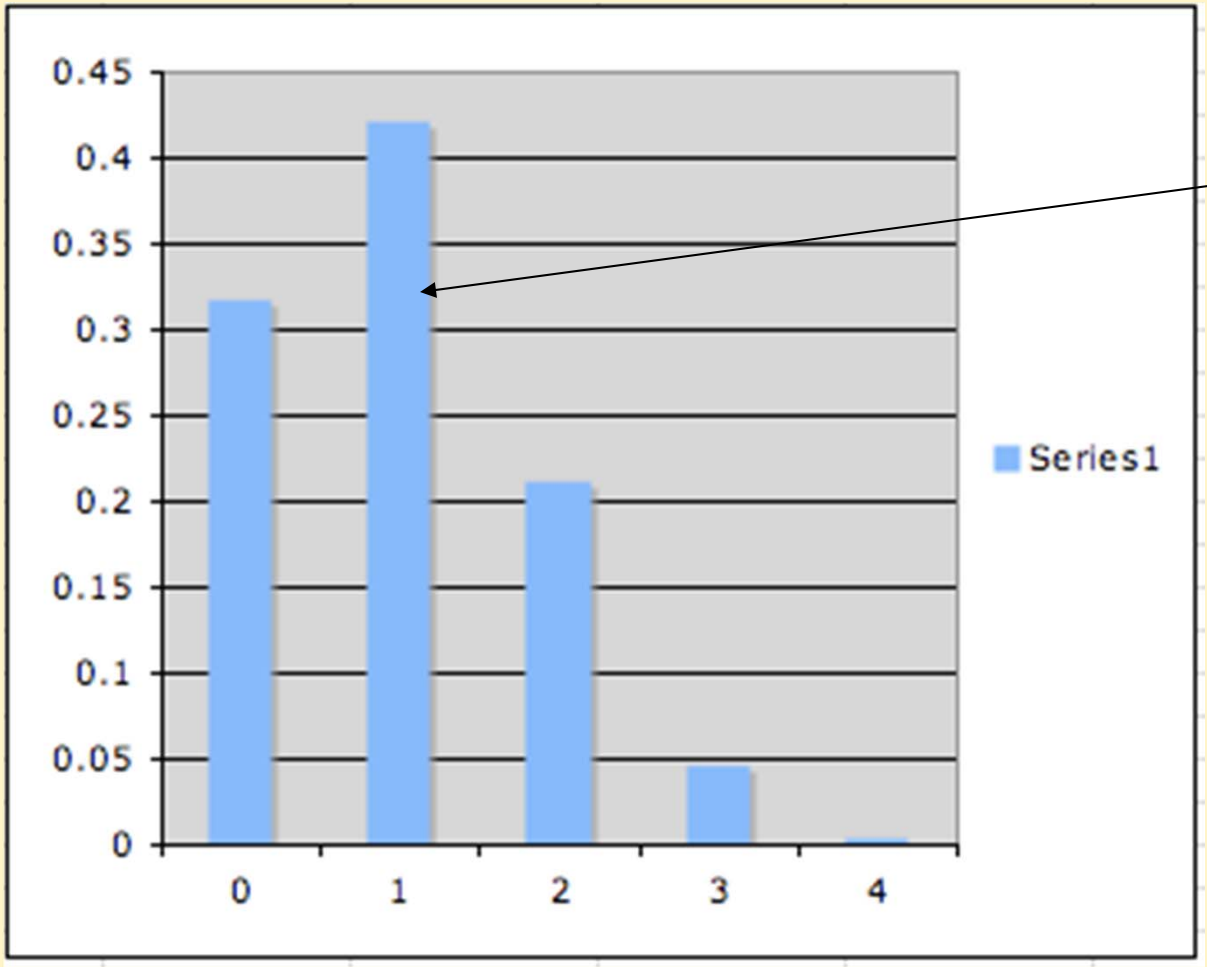
Mean: 2Np

Variance: 2Npq

i = outcome with probability p (e.g. drawing a P allele for the next generation)

- See table 28.1 (online on textbook site)

The Wright-Fisher model



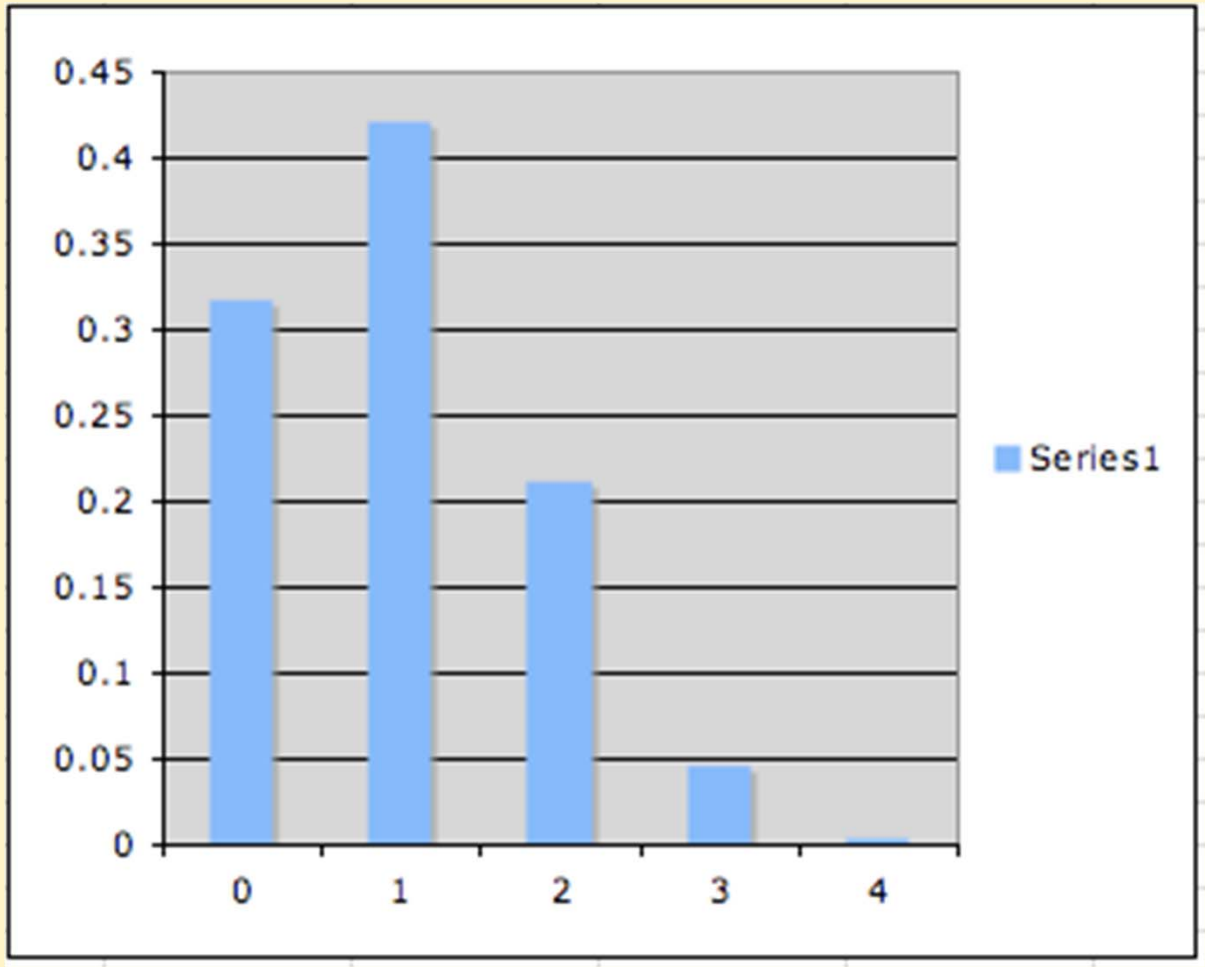
Mean=2Np
=2*2*0.25
=1

1/4=0.25

Mean allele frequency is expected to stay the same

- The probability for each of the 5 outcomes follows the binomial distribution

The Wright-Fisher model



Variance=2Npq
=2*2*0.25*0.75
=0.75

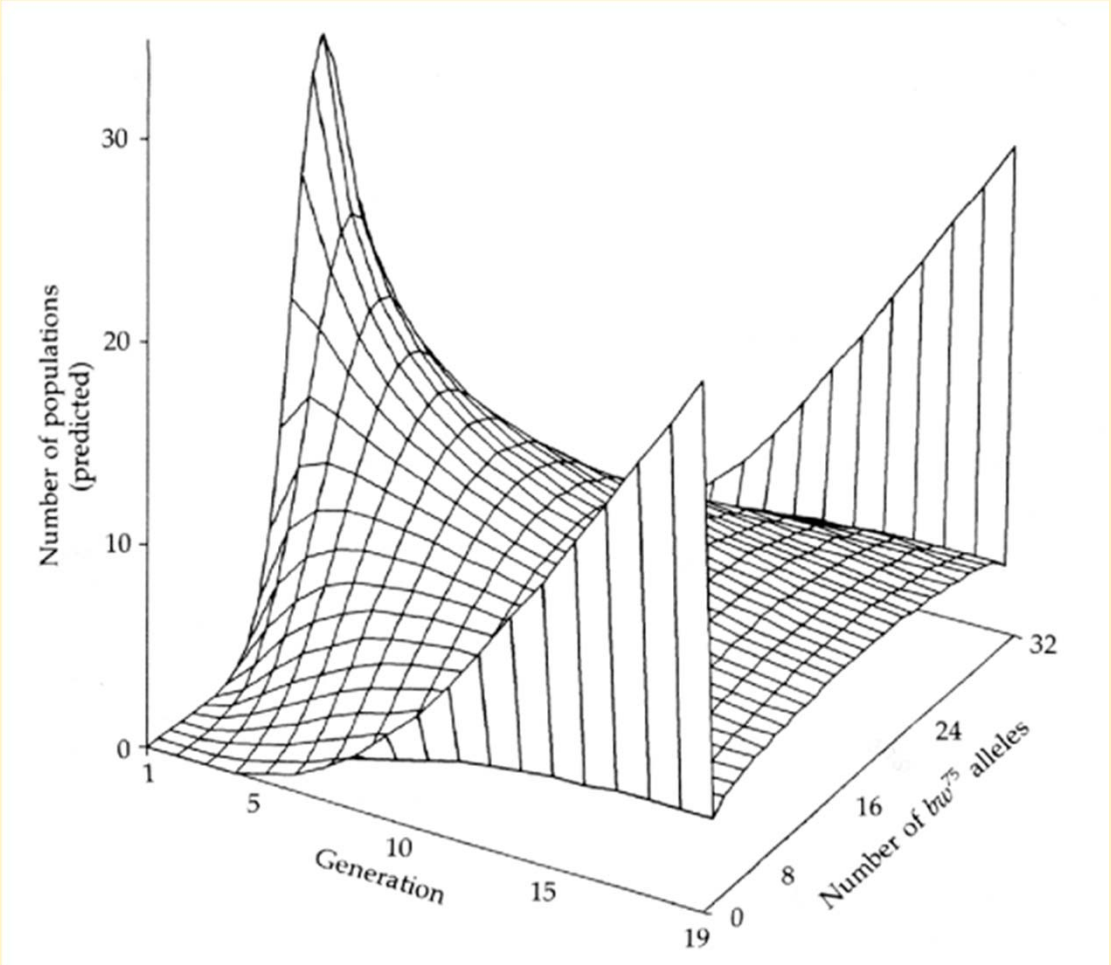
Variance for allele frequency:
(p*q)/2N
=(0.25*0.75)/(2*2)
=0.047

- The probability for each of the 5 outcomes follows the binomial distribution

Under the Wright-Fisher model the two alleles behave like competing clones

- http://www.coalescent.dk/

The Wright-Fisher Model

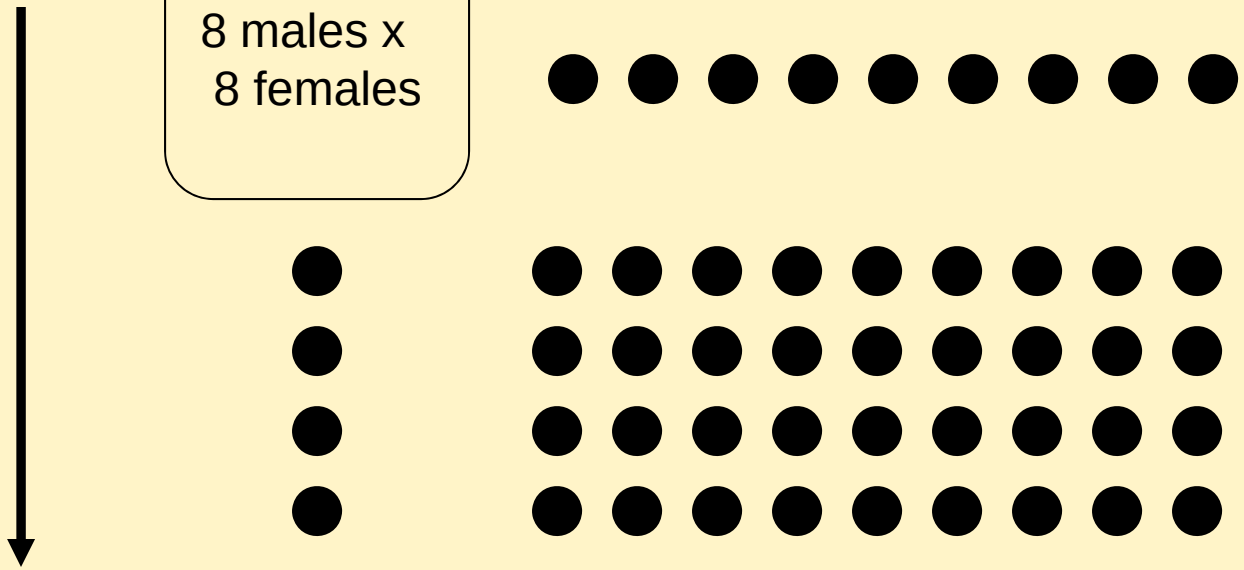


- Theoretical expectation for allele frequency if drift continues for several generations

An experimental study of genetic drift in *Drosophila*

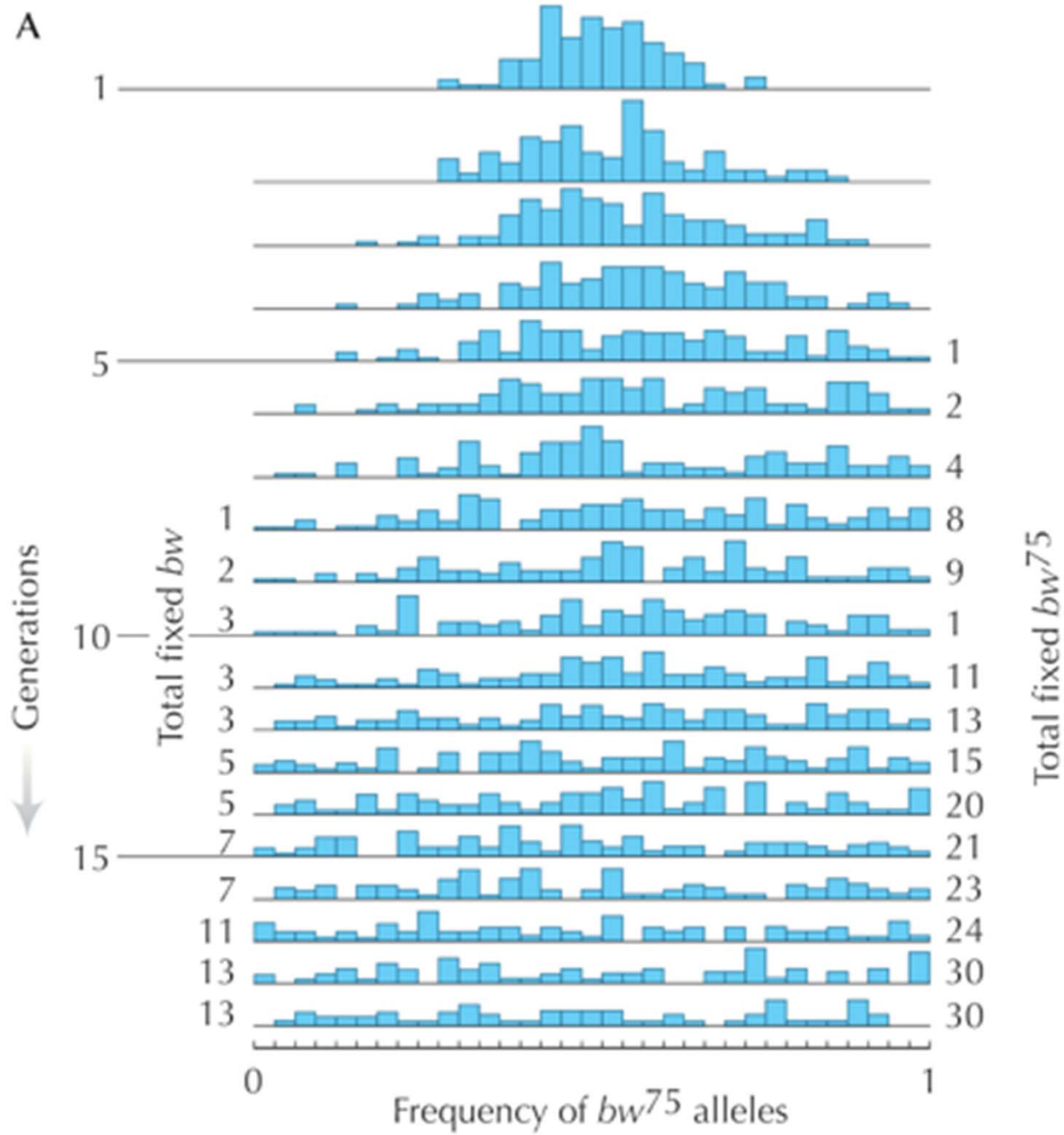
Generation 0:
Frequency brown mutation = p = 0.5

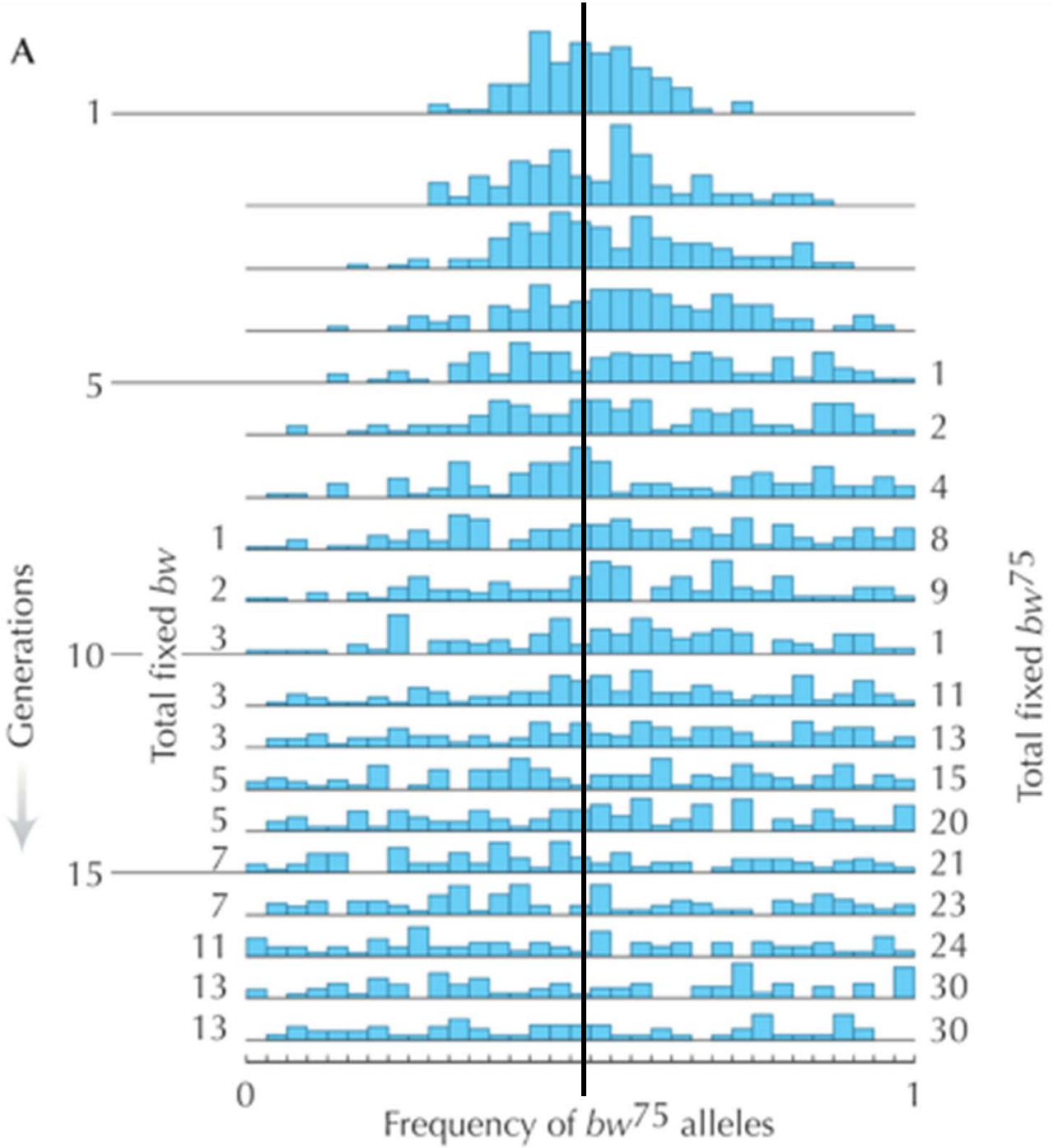
8 males x
8 females



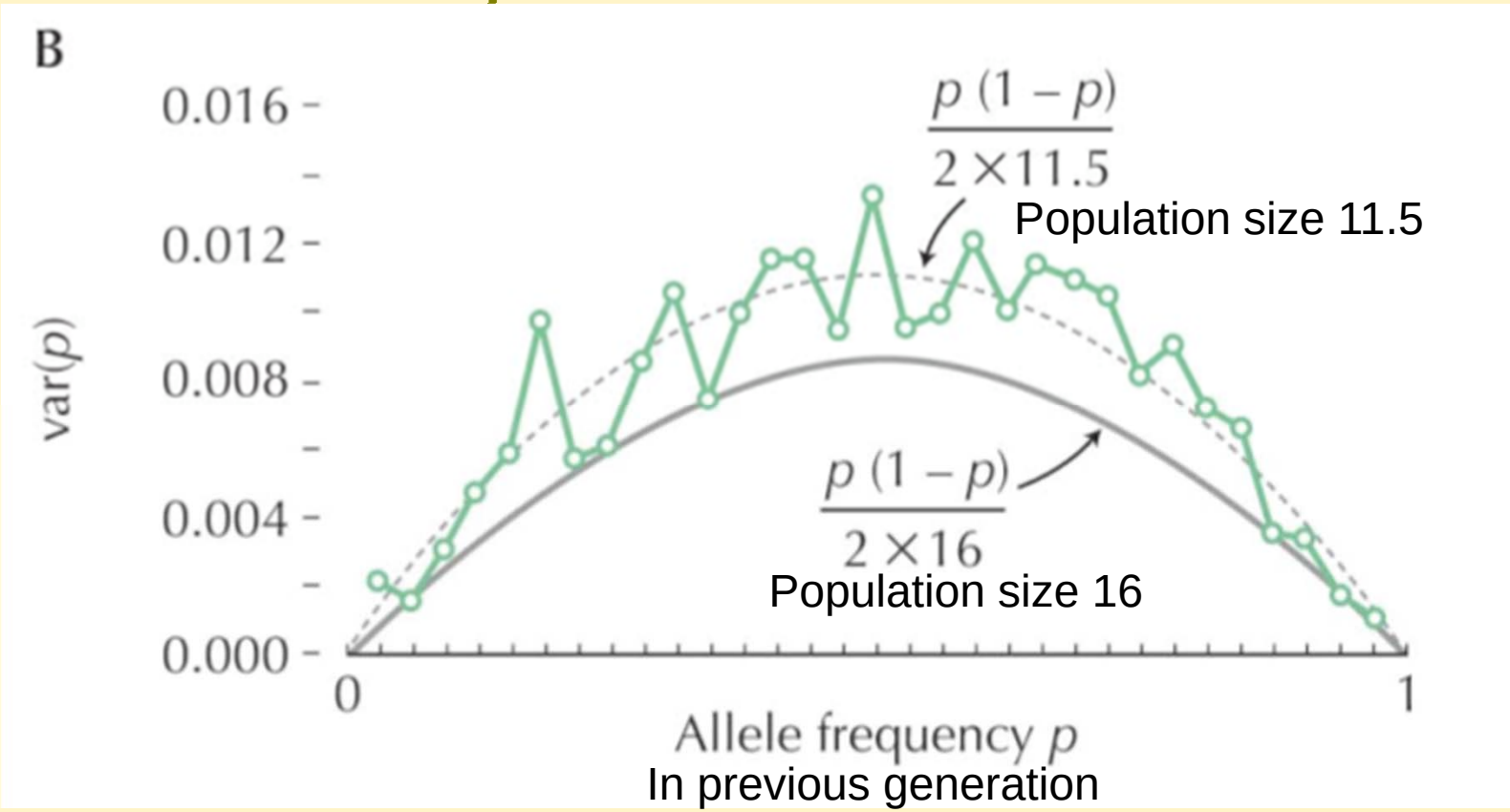
N = 100 populations

t = 19 generations


A
Generations
1
5
10
15
Total fixed bw
1
1
2
3
3
3
5
5
7
7
11
13
13
Total fixed bw75
1
2
4
8
9
1
11
13
15
20
21
23
24
30
30
0
1
Frequency of bw75 alleles


A
Generations
1
5
10
15
Total fixed bw
1
2
3
3
3
5
5
7
7
11
13
13
Total fixed bw75
1
2
4
8
9
1
11
13
15
20
21
23
24
30
30
0
1
Frequency of bw75 alleles

Observed variance of allele frequency in *Drosophila* experiment does not fit the expected variance



- But it fits for a smaller than the census population size, the **effective population size**

Effective Population size

The size of the ideal Fisher-Wright population that would give the same rate of random drift as the actual population

(I.e. if the census population size and the effective population size do not match the population deviates from the Wright-Fisher model)

Population Size (N) vs. Effective Population Size (N_e)

N_e is what determines the strength of genetic drift

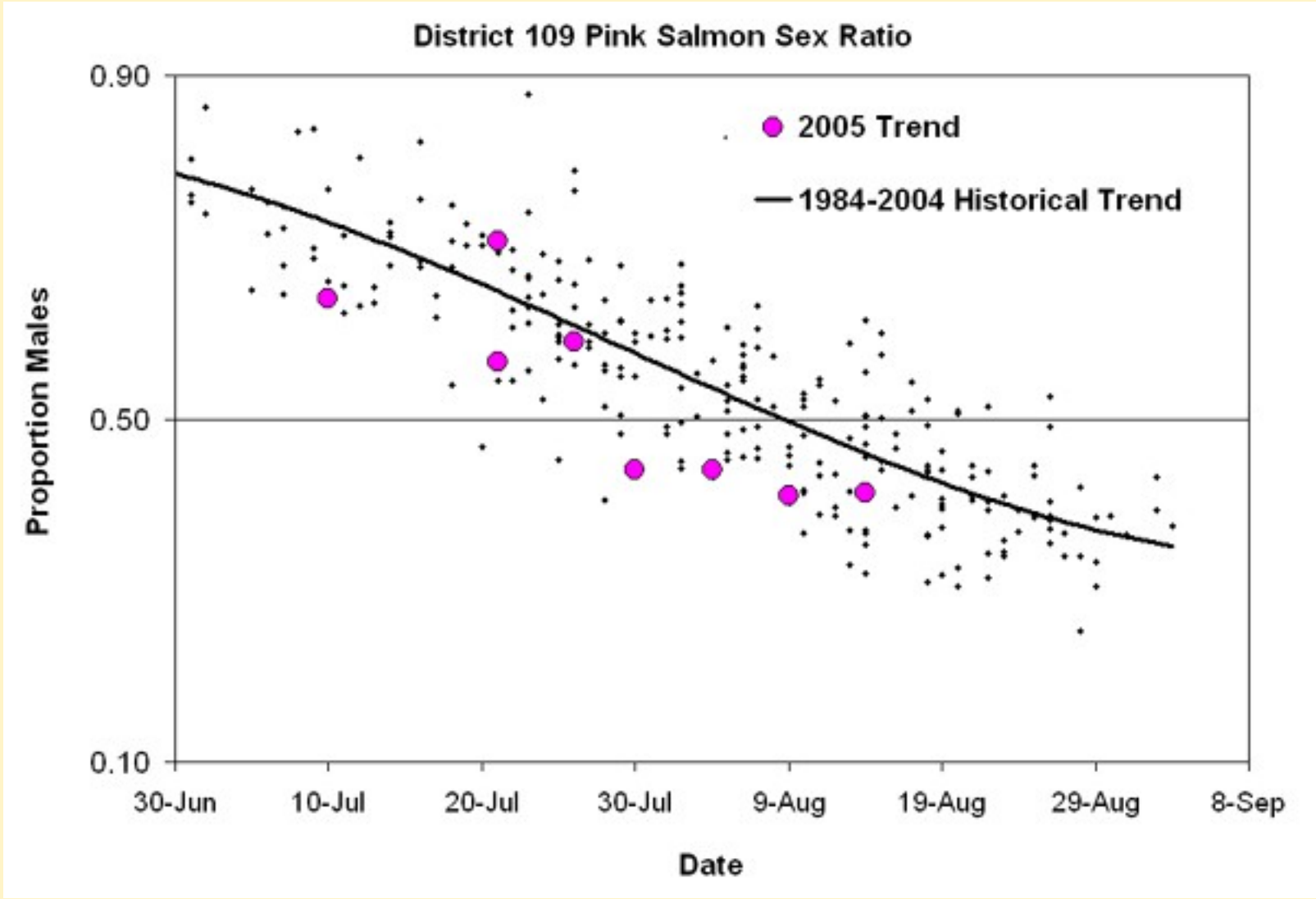
Factors that cause N_e to be less than N

- **overlap of generations**
- **variation among indivs in reproductive success**

Population Size (N) vs. Effective Population Size (N_e)

Factors that cause N_e to be less than N

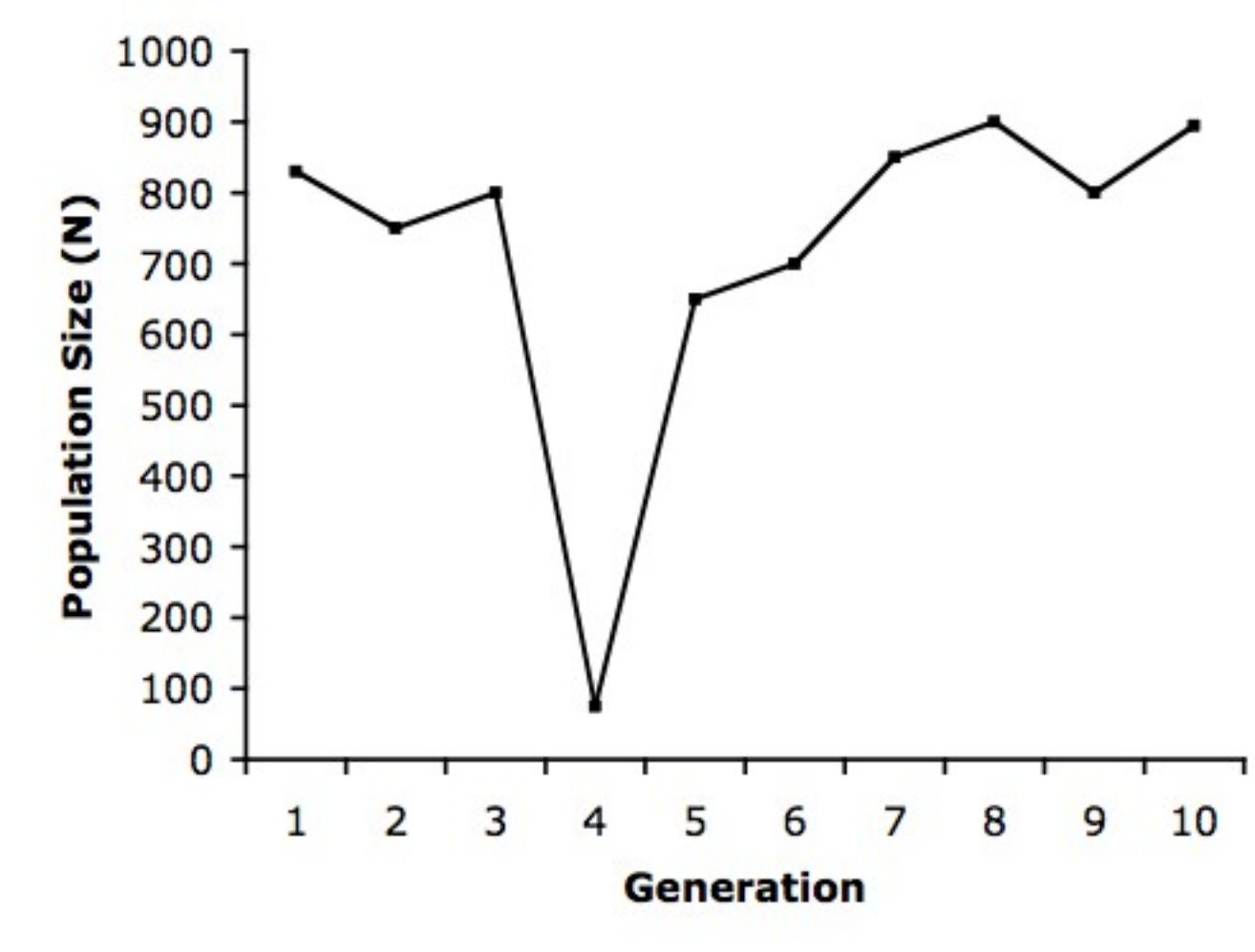
- **overlap of generations**
- **variation among indivs in reproductive success**
- **unequal sex ratio**


District 109 Pink Salmon Sex Ratio
0.90
0.50
0.10
Proportion Males
2005 Trend
1984-2004 Historical Trend
30-Jun
10-Jul
20-Jul
30-Jul
9-Aug
19-Aug
29-Aug
8-Sep
Date

Population Size (N) vs. Effective Population Size (N_e)

Factors that cause N_e to be less than N

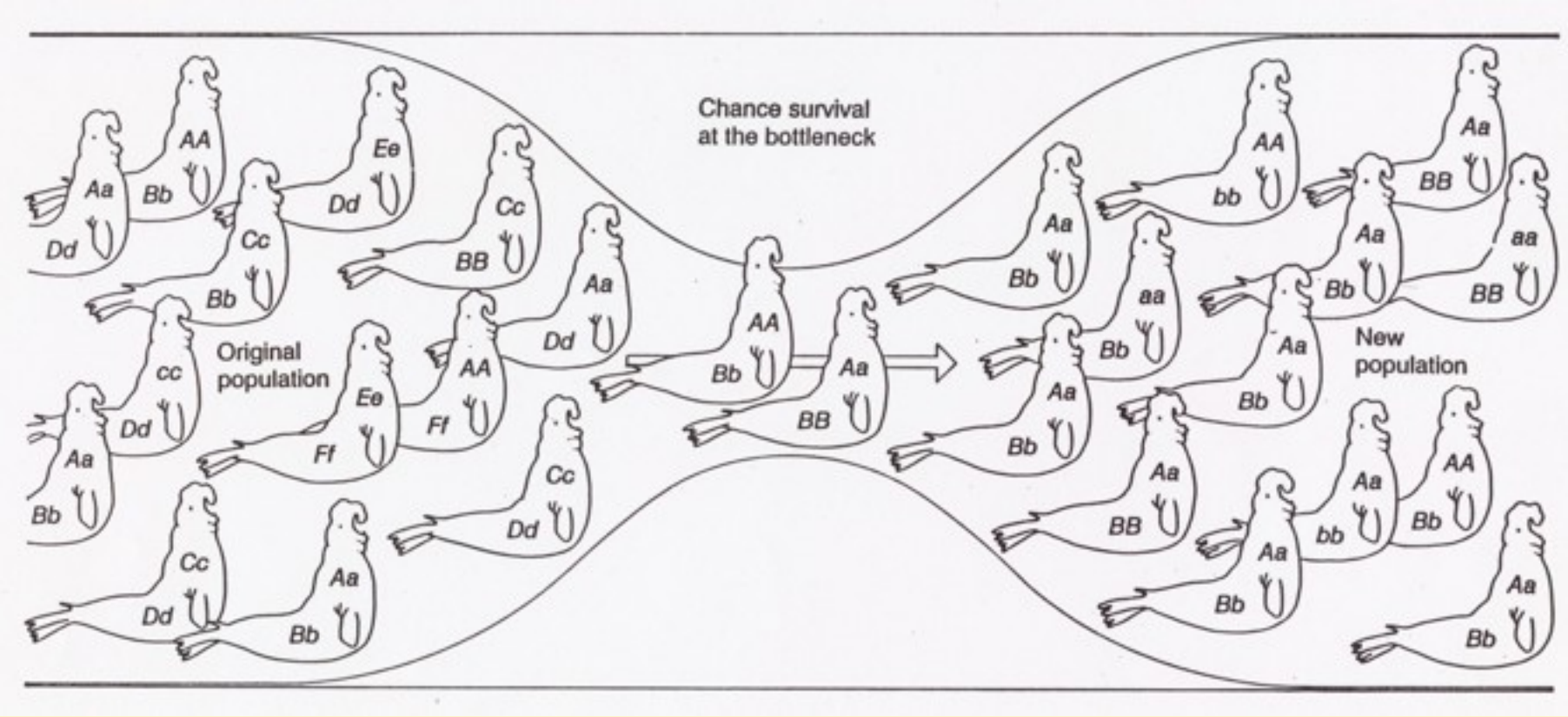
- **overlap of generations**
- **variation among indivs in reproductive success**
- **unequal sex ratio**
- **fluctuations in population size**

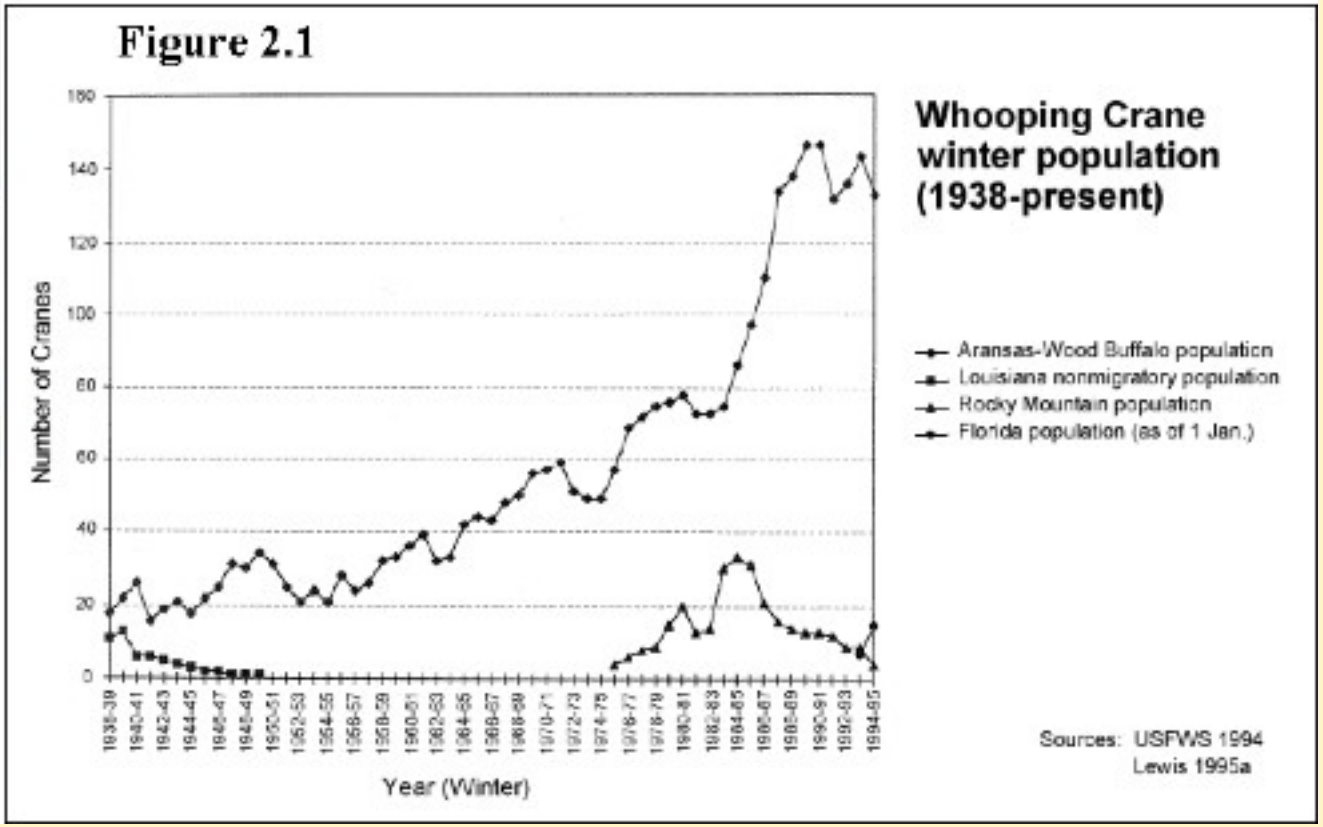


Average N: 725

N_e: 404

Population bottlenecks reduce variation and enhance genetic drift





(approx. 1000 indivs in 1850s)

mtDNA variation in Whooping Cranes

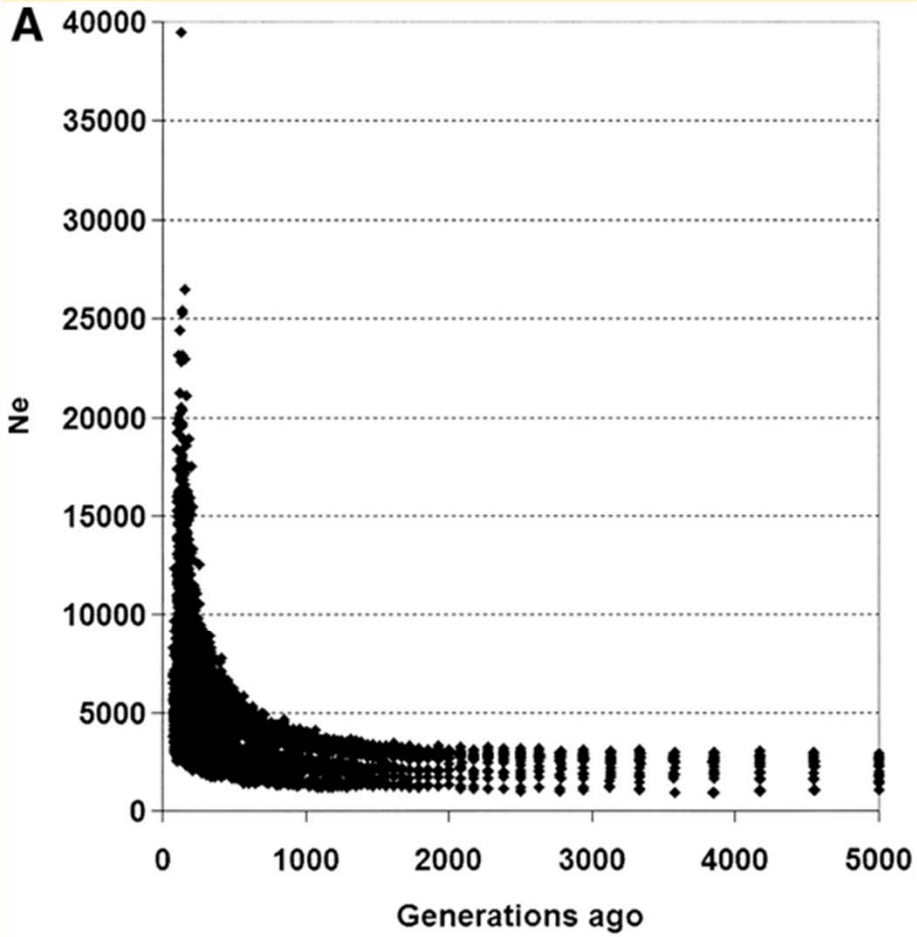
Haplotype	Pre-bottleneck	Post-bottleneck
1	0	12
2	0	2
3	5	3
4	0	1*
5	1	0
6	1	0
7	2	0
8	1	0
9	1	0

***Present immediately after the bottleneck (1951), but not today.**

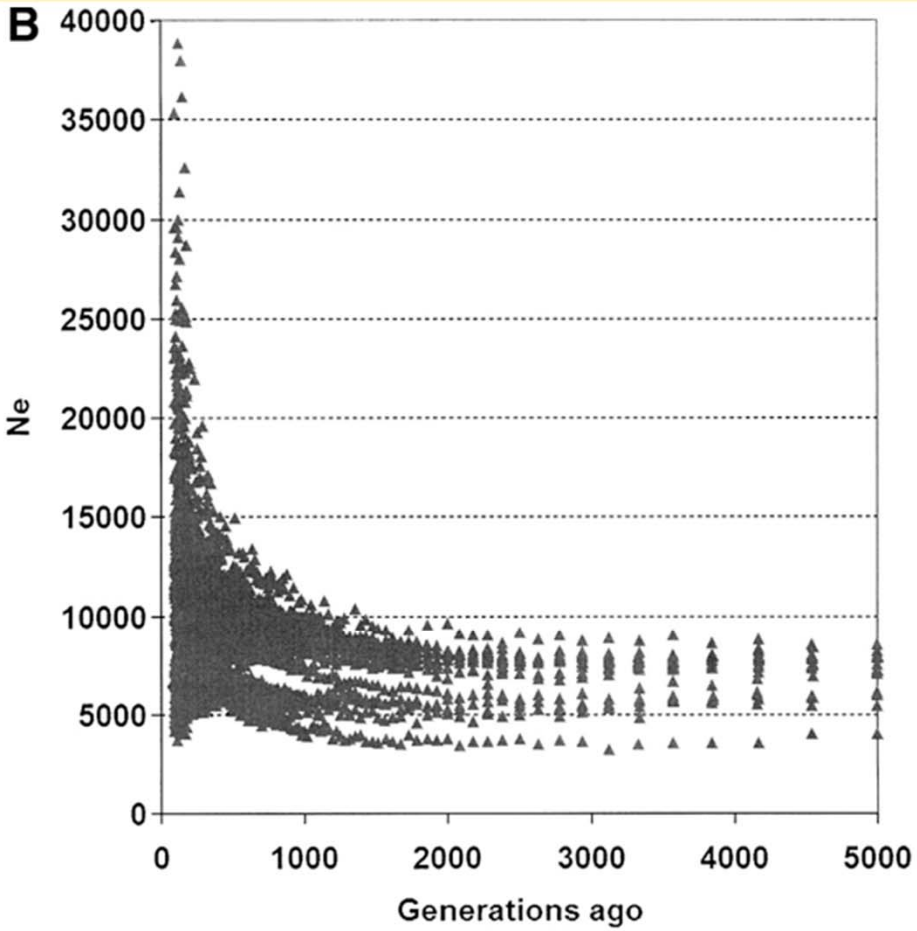
Glenn et al. (1999) Conservation Biology 13: 1097-1107.

Effective population size of humans

Tenesa et al., Genome Res. 2007. 17: 520-526



Northern and Western Europe

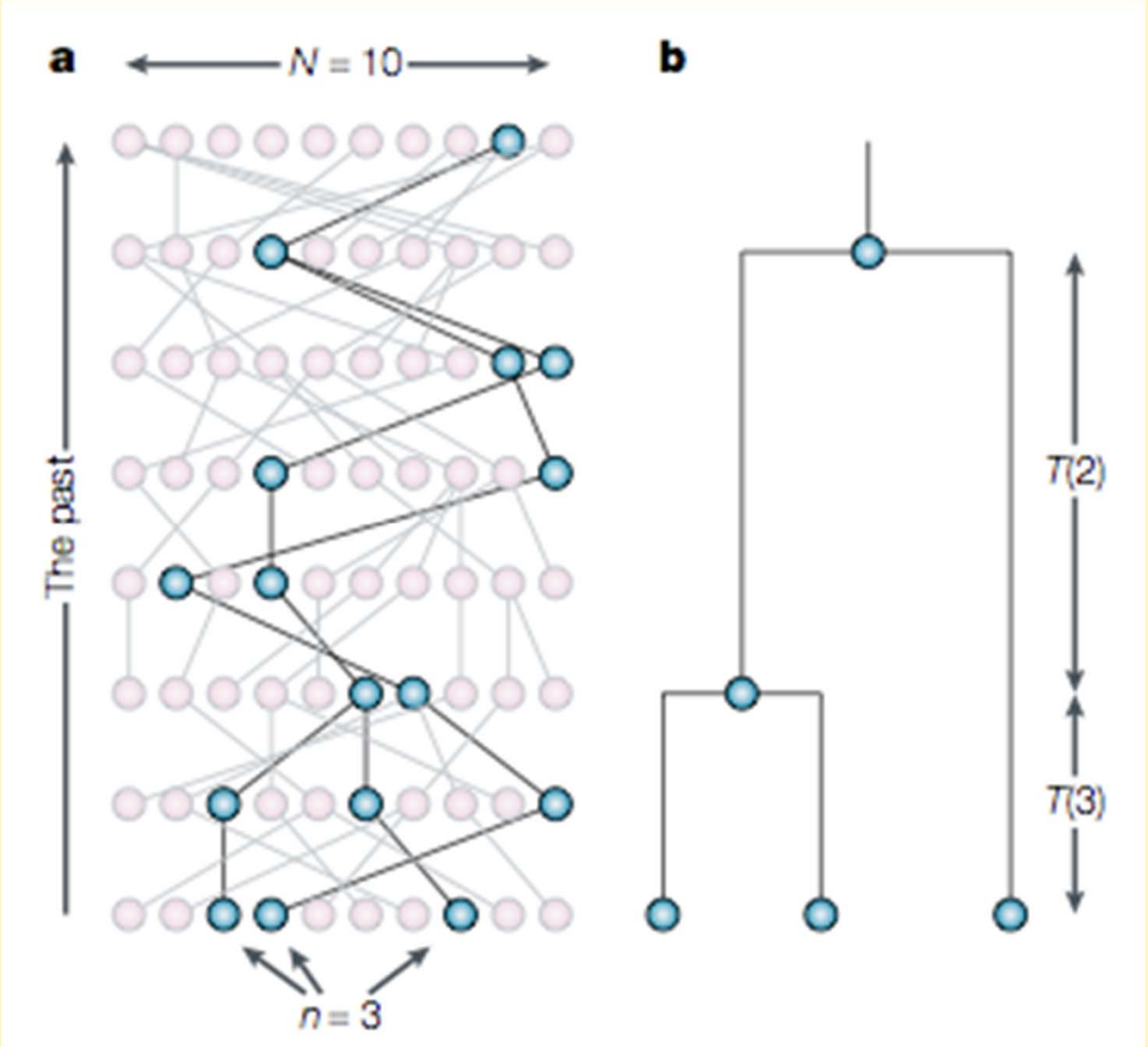


Yoruba, Nigeria

How can we know about past effective population size?

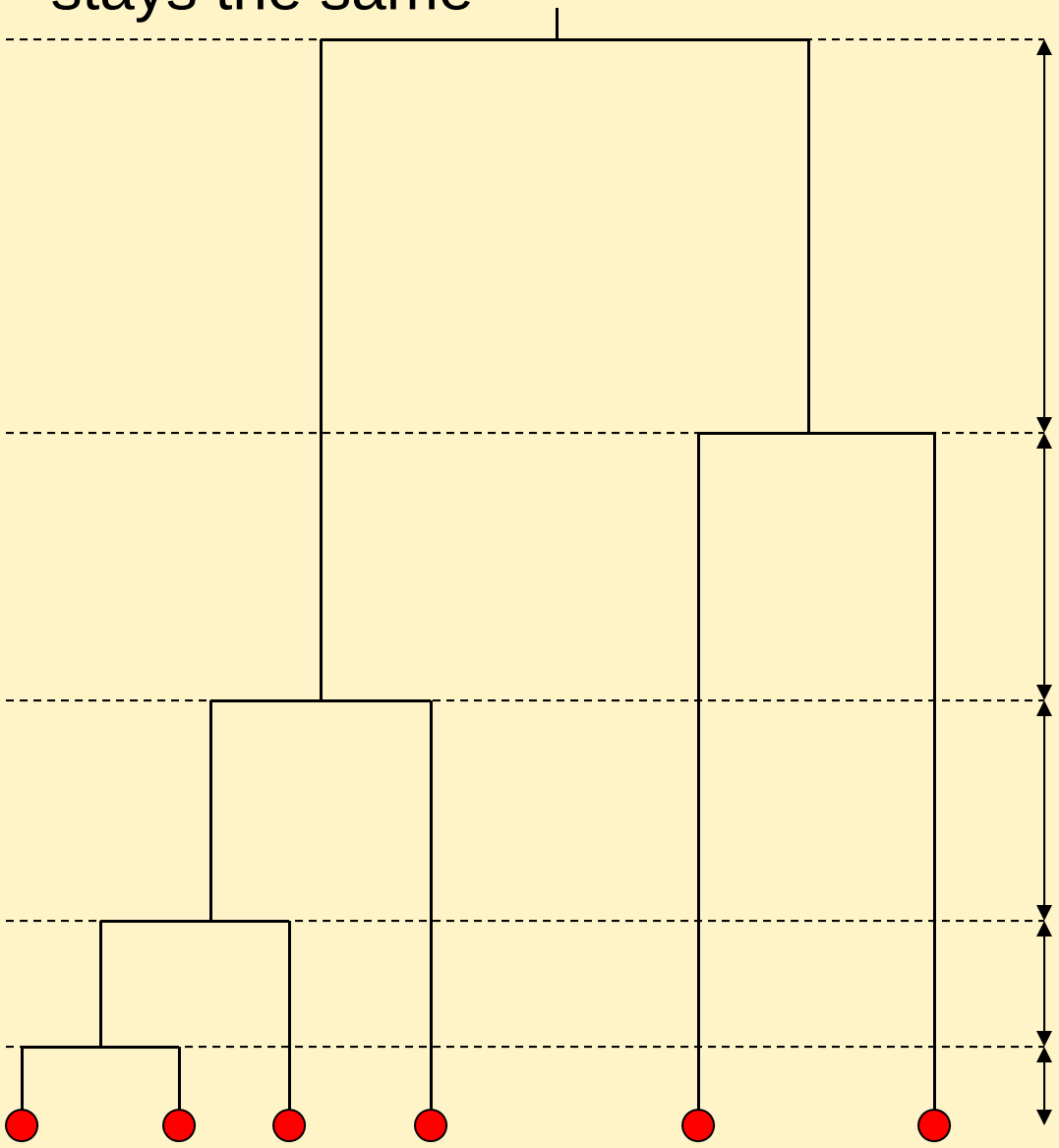
What is the chance that two random alleles share an ancestor in the previous generation?

1/2N



Chances for coalescent event get smaller with fewer lineages sorting

Branches get longer with fewer remaining lineages, even though N stays the same



Expected times for coalescent events with 6 to 2 lineages remaining

E(T2)=2N/1

E(T3)=2N/3

E(T4)=2N/6

E(T5)=2N/10

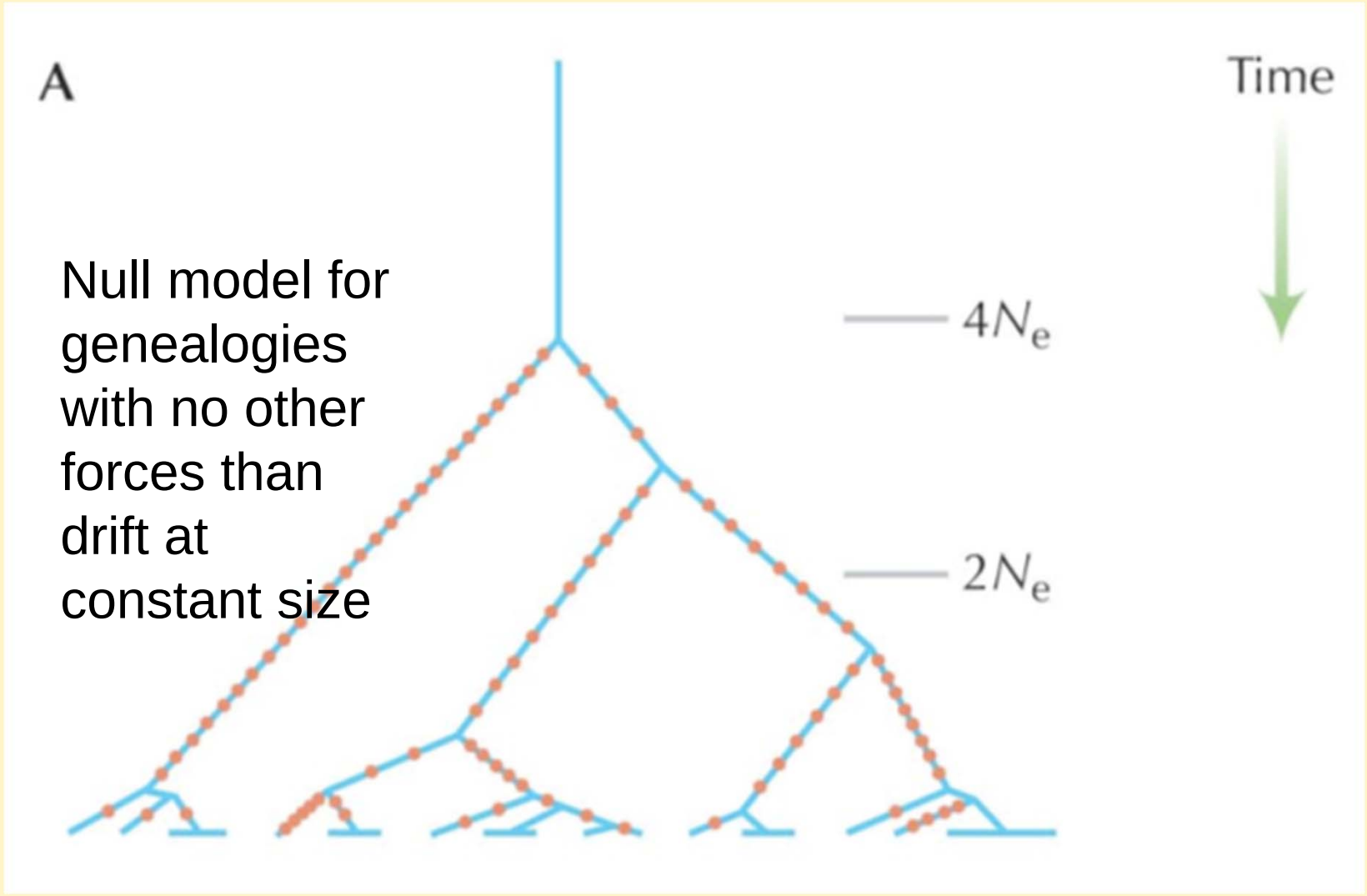
E(T6)=2N/15

We can make predictions about the average and variance of coalescent times - but not about specific genealogies

Figure 2 | **Random genealogical trees.** The trees were generated using the same model — the standard coalescent for sample of size ten. Therefore, the variation among the trees reflects chance alone.

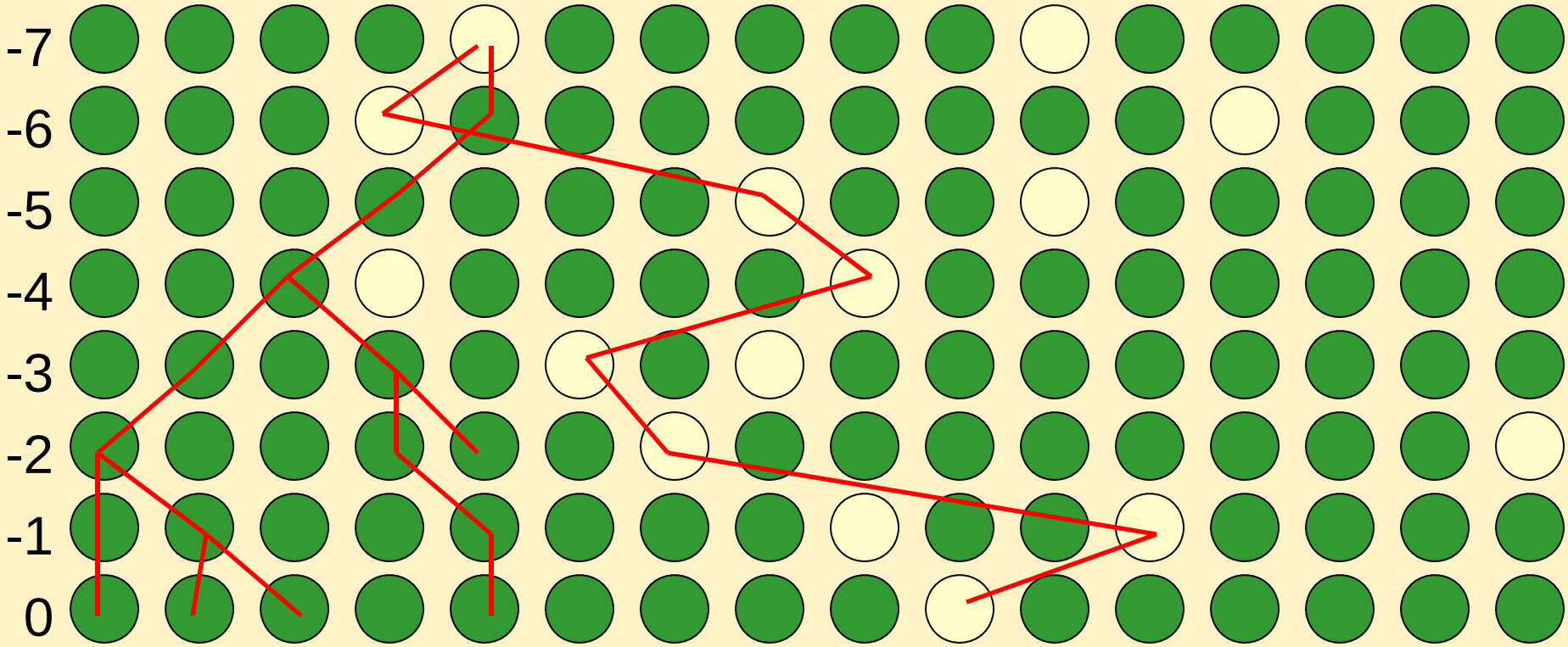
- Some potential outcomes of evolution in a Wright-Fisher population

(Typical) constant population size genealogy



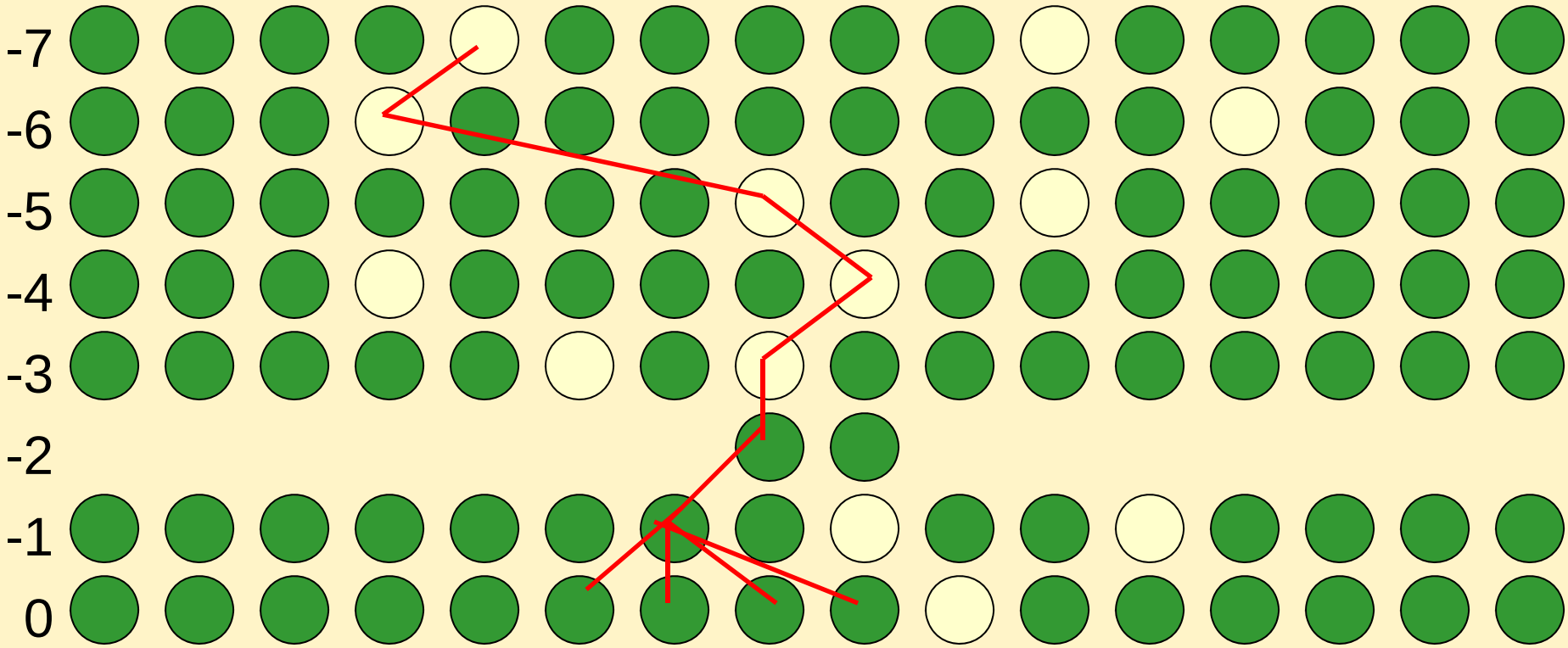
Null model for genealogies with no other forces than drift at constant size

Wright-Fisher Genealogy



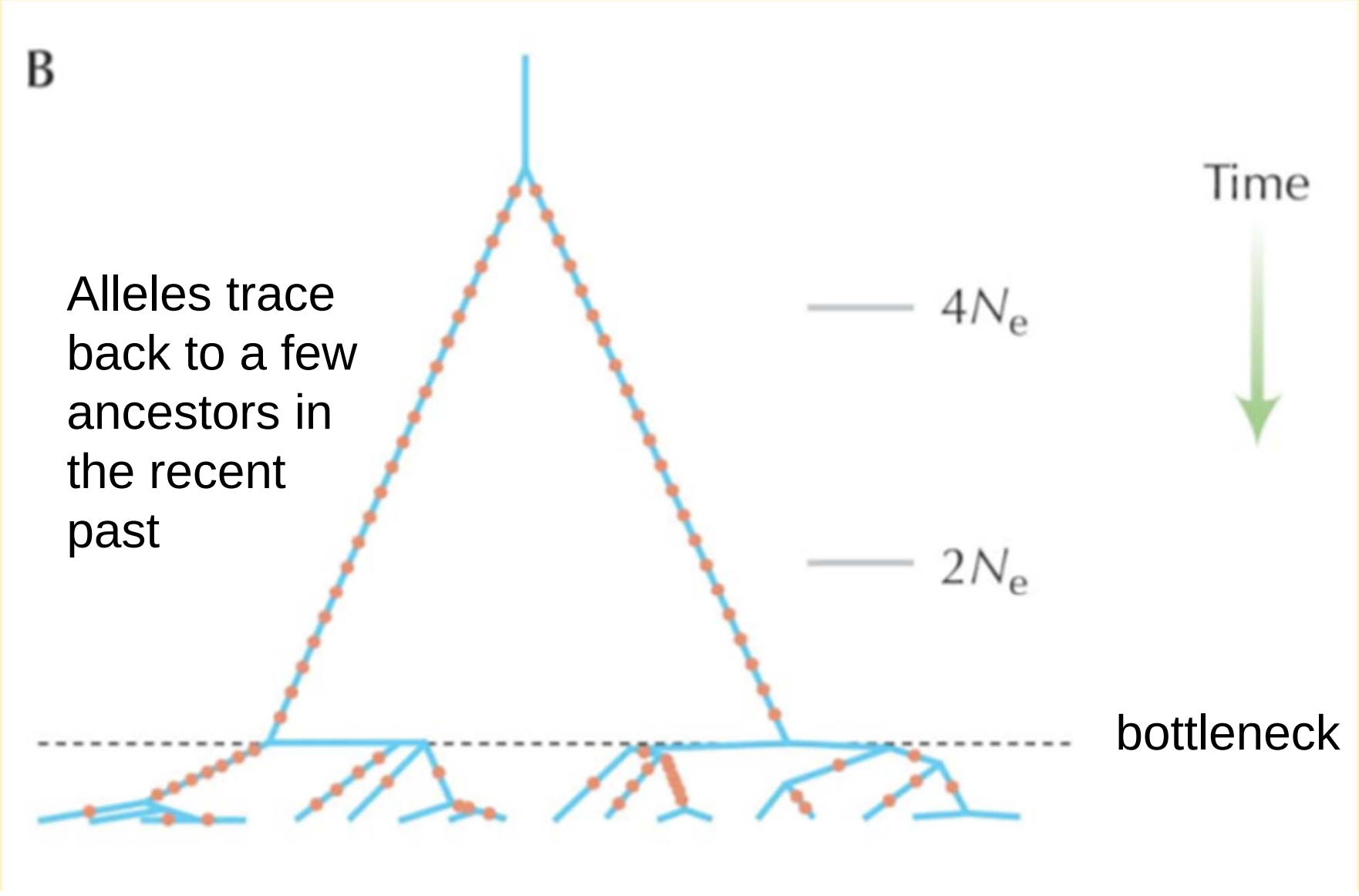
Null model for our expectations about the age of common ancestors

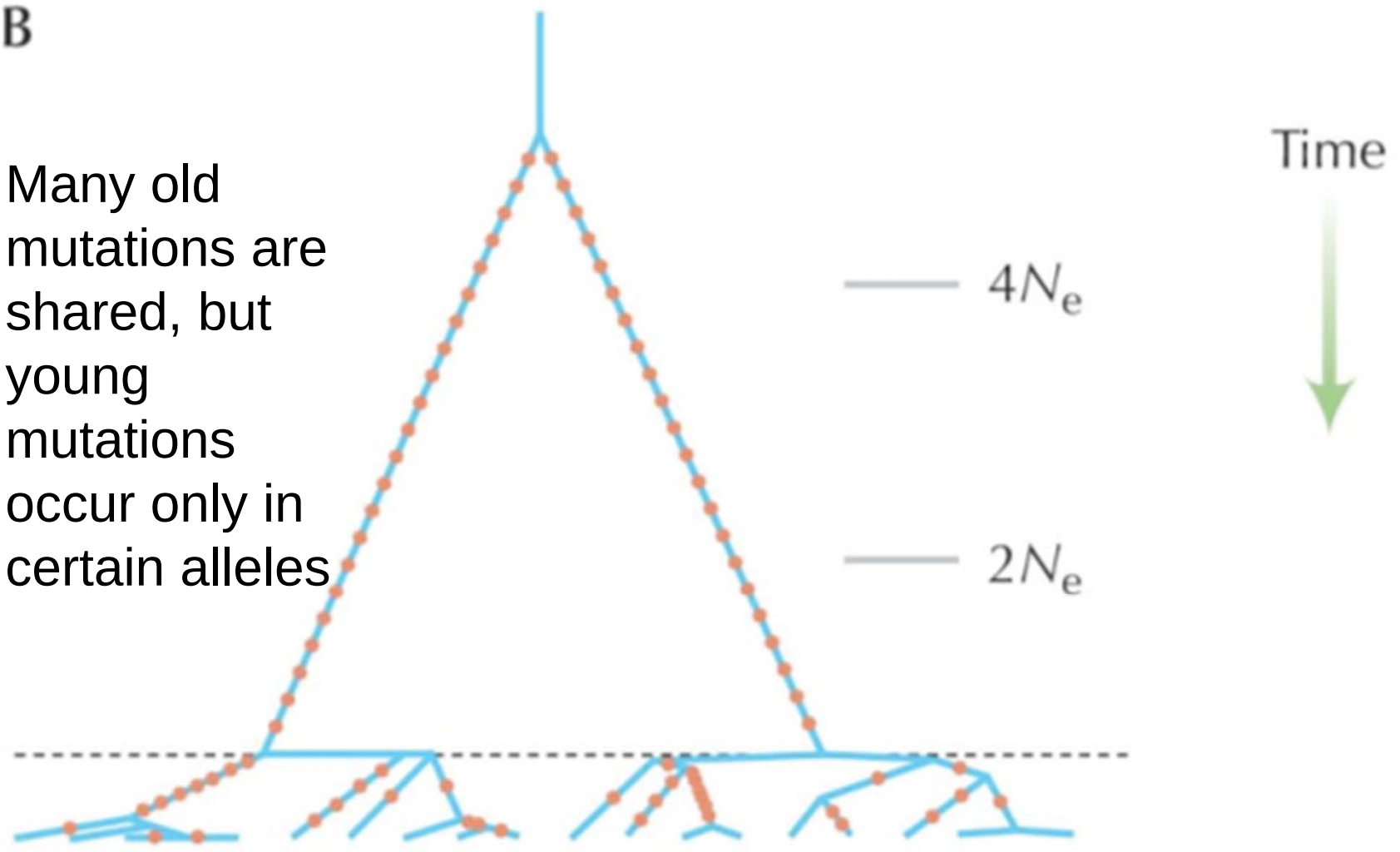
Genealogy of a bottleneck



The most recent common ancestor of a random set of alleles is younger than it would be without a bottleneck

Bottleneck genealogy



Alleles trace back to a few ancestors in the recent past

The distribution of mutations in alleles can be used to estimate past population size