

Genetic Drift

A common conception about evolution is that the features of an organism have evolved due to random (undirected) change.

Some processes in biology are random – like mutation.

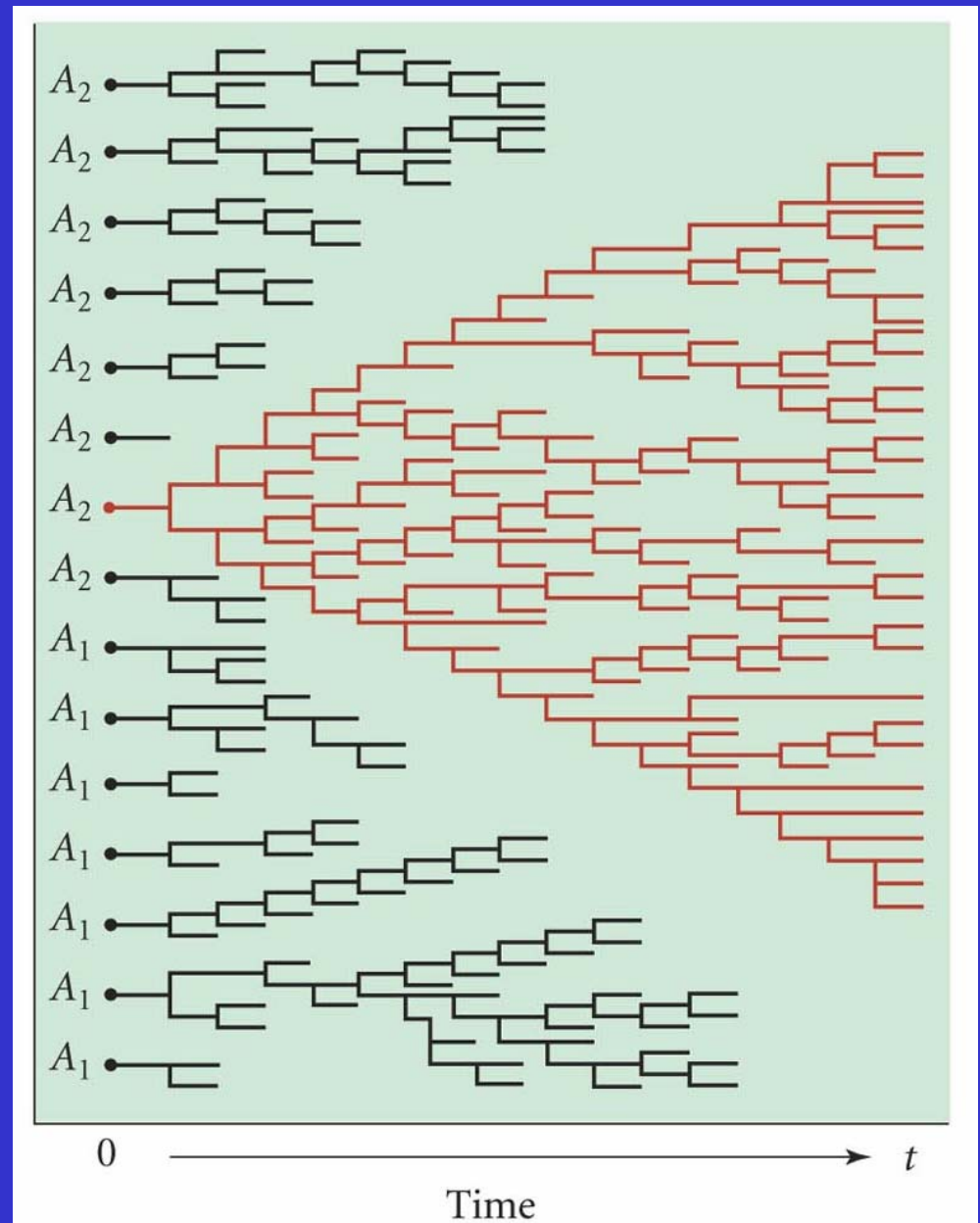
Natural selection is not random. Natural selection is the nonrandom preservation of random variation.

Genetic drift is a random process that can be important in the evolution of some populations.

One of the requirements for the maintenance of allele frequencies in populations is a very large population size. Genetic drift is the consequence of finite population size.

Alleles that do not affect fitness fluctuate randomly in frequency. Random fluctuation eventually results in the loss of alleles (allelic extinction) from populations. One allele becomes fixed – the only allele in the population.

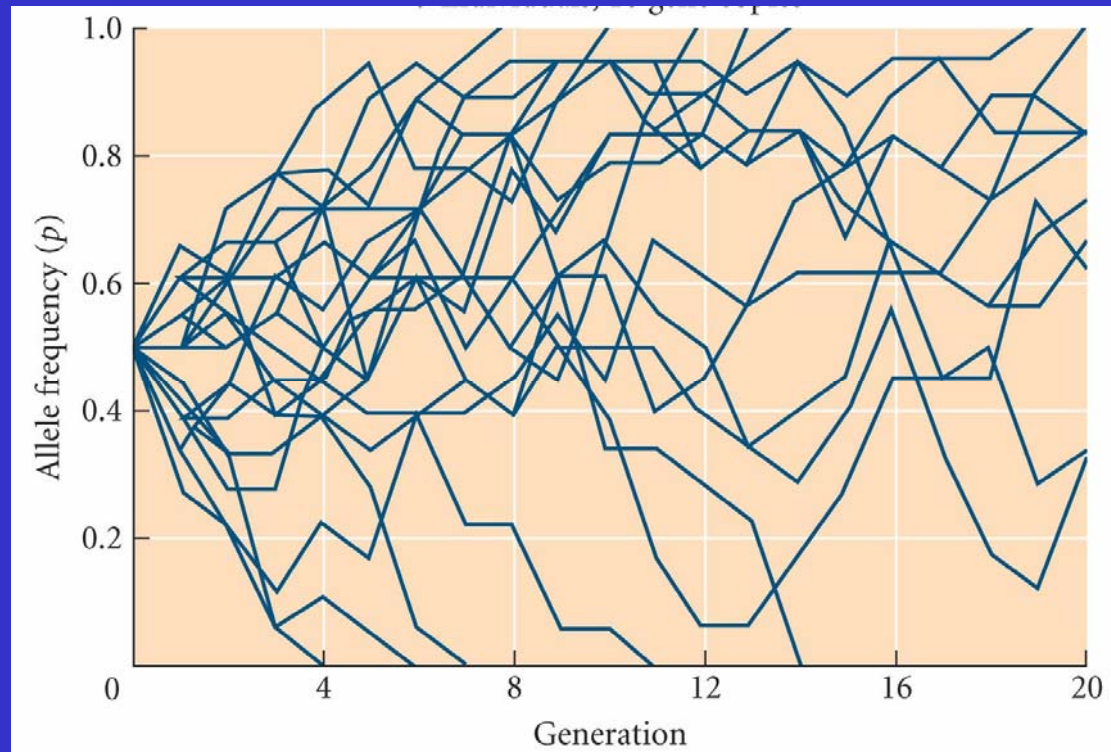
Sampling error (random chance) results in some gene copies being lost and others continuing.



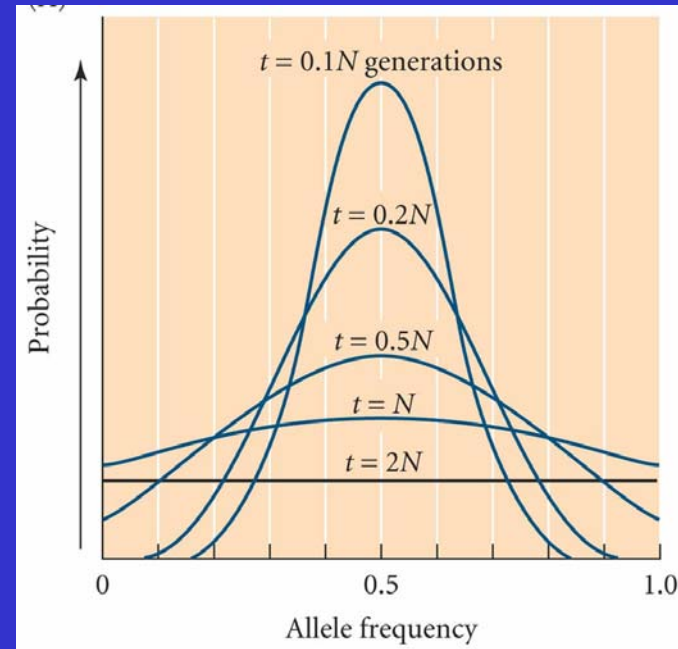
Different populations will lose different alleles.

The probability that a particular allele will be fixed in a population in the future equals the frequency of the allele in the population. If there are two alleles in a population, A and a , with frequencies p and q . The probability that the allele a will be lost at some point in the future is p and the probability that allele A will be lost is q .

If a large number of populations is considered, each drifting, the total heterozygosity overall will decrease.

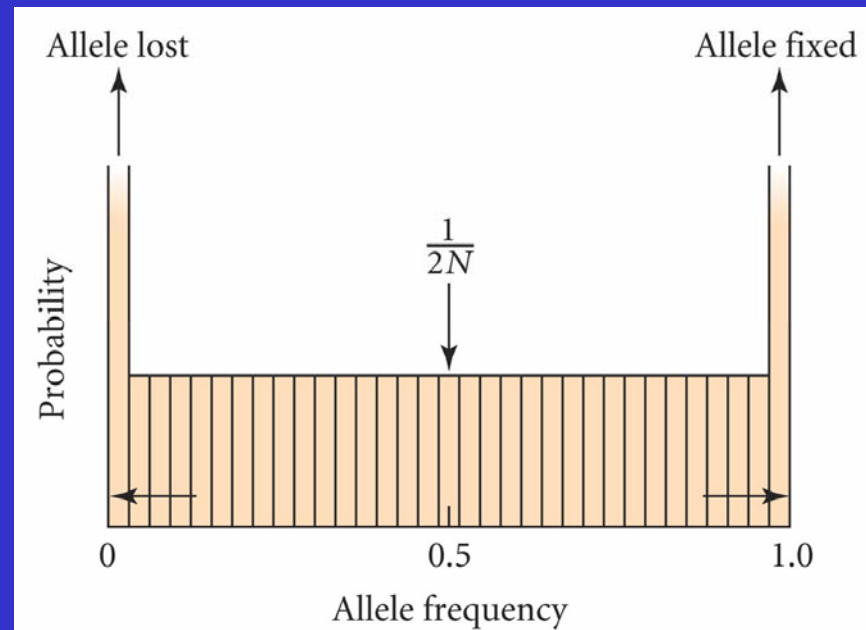


Starting with a population size of N with two alleles in equal frequencies p and q , the likely magnitude of divergence from the initial frequencies increases with time.



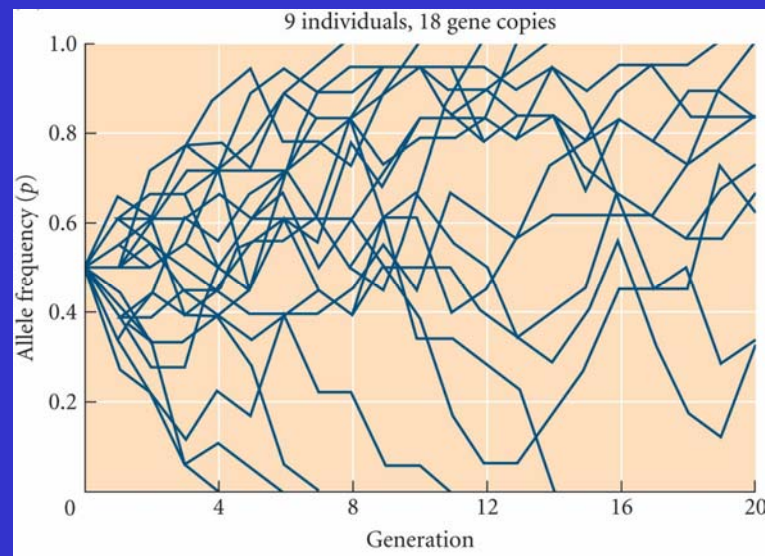
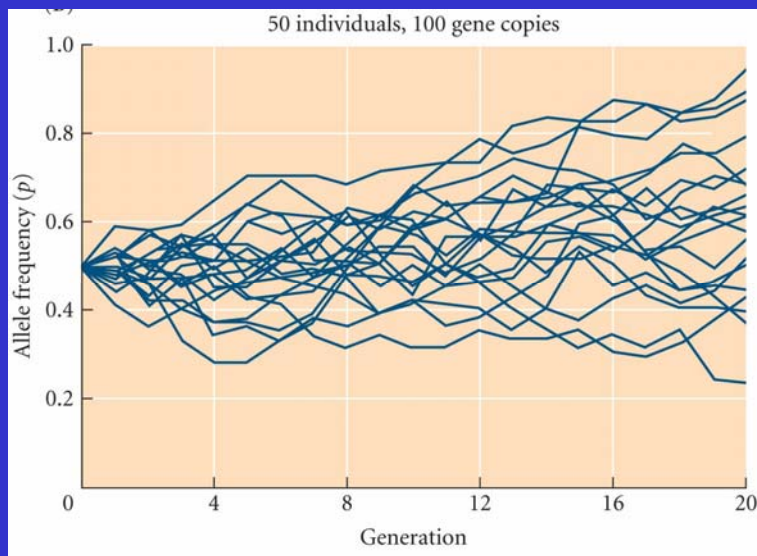
After $2N$ generations, all allele frequencies are equally likely.

The average time to fixation of one of the alleles is $4N$ generations.



The effective population size is the number of individuals in the population that successfully pass genes to the next generation. This is usually smaller than the actual number (census number) in the population.

The smaller the effective population size, the faster a population will drift, and the faster one of the alleles in the population will become fixed.



The effective population size (N_e) is affected by biological parameters other than the number of individuals in the population.

Variation in offspring number among individuals can reduce N_e . If some individuals produce more offspring than others their alleles, even those that have no effect on fitness, will be passed on at higher rates.

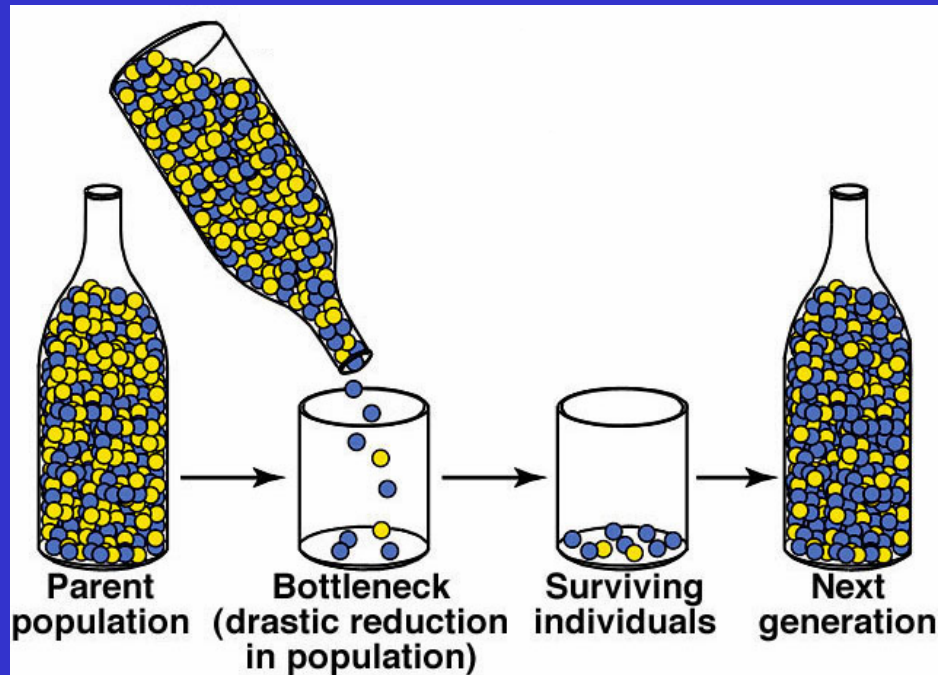


A sex ratio other than 1:1 produces a similar reduction in N_e

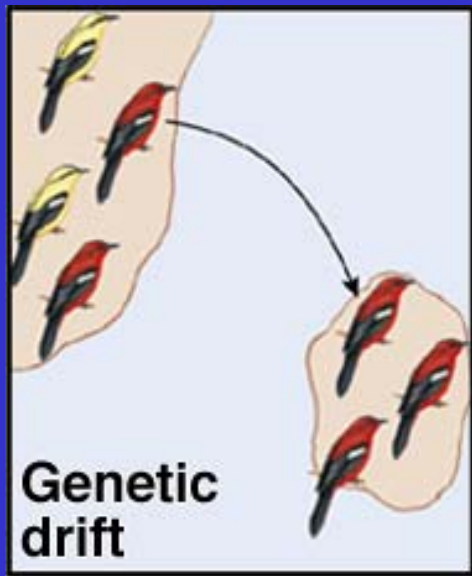
Natural selection at one gene can produce differences in offspring number among individuals and reduce N_e

Inbreeding within or between generations reduces the number of different copies of a gene passed to the next generation and effective reduces N_e

Fluctuations in population size reduce N_e . Temporary decreases in population size have greater effects than temporary increases in population size.



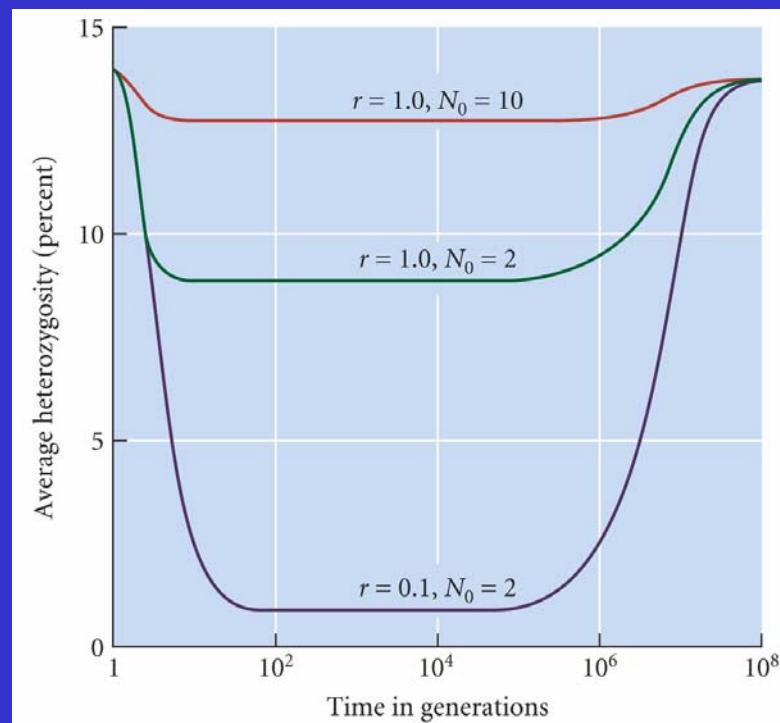
A temporary reduction in population size is called a **bottleneck**.



When a small number of individuals from a source population establish a new population genetic variation can be lost. The loss of genetic variation due to such an extreme bottleneck is called the **founder effect**.

Simulations of founder effects suggest that a small number founders and a small population growth rate (r) result in greater loss of genetic diversity.

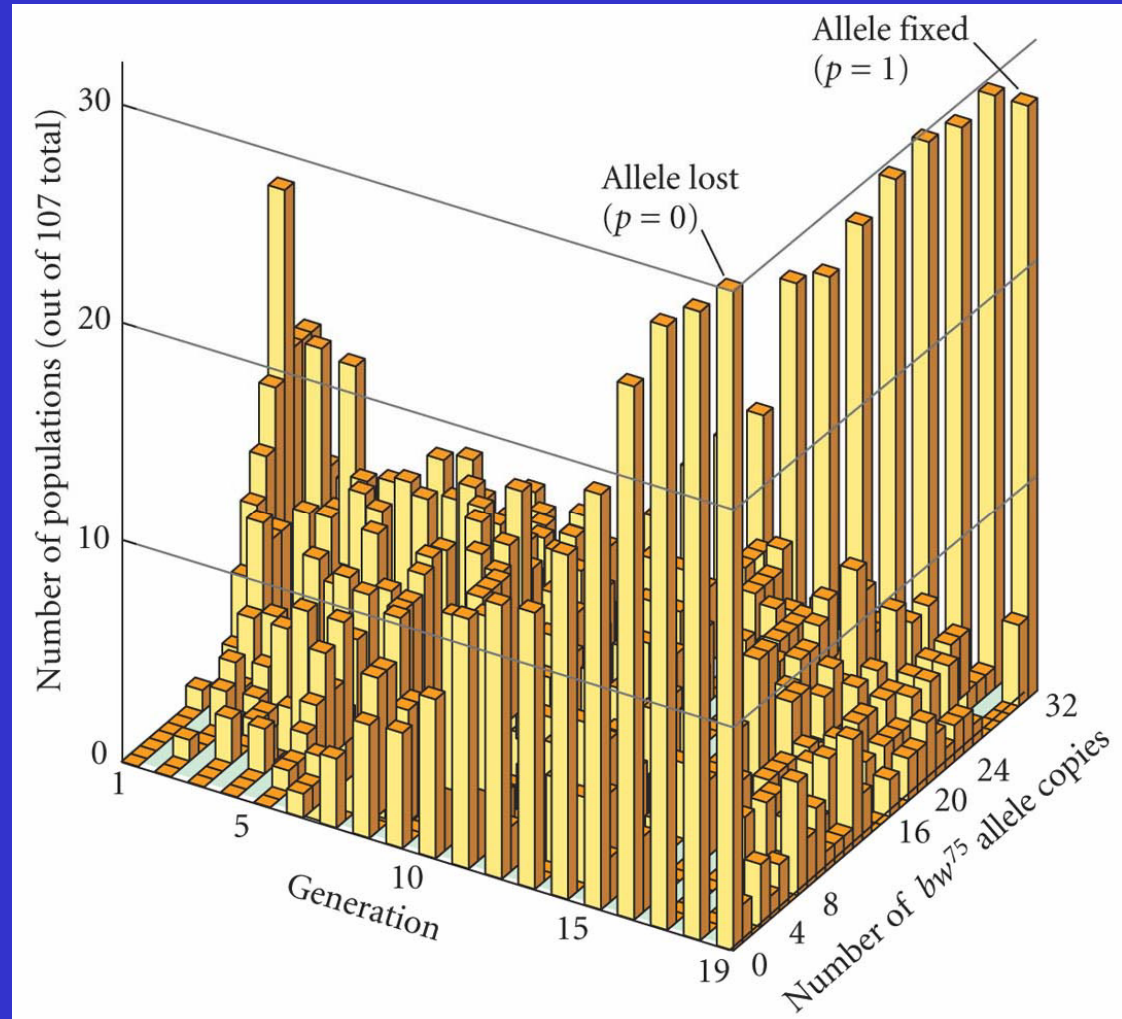
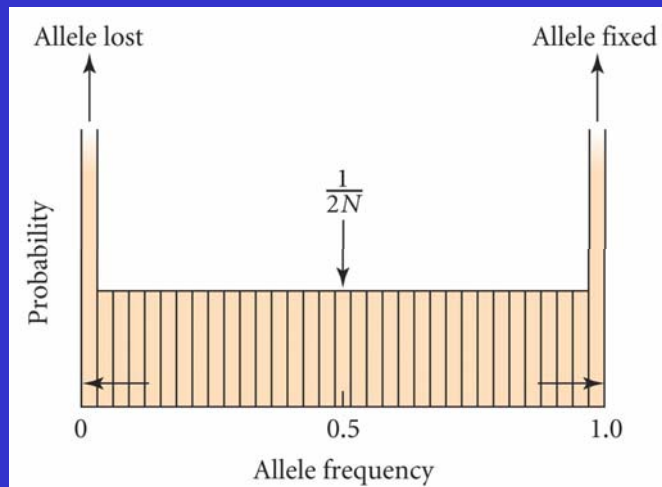
Eventually mutation will restore genetic variation in a founding population.



Studies of laboratory and natural populations confirm the theoretical expectations of genetic drift models.

107 populations of fruit flies each started with 16 heterozygotes, 8 males and 8 females.

8 randomly chosen males and females were used to start each generation.

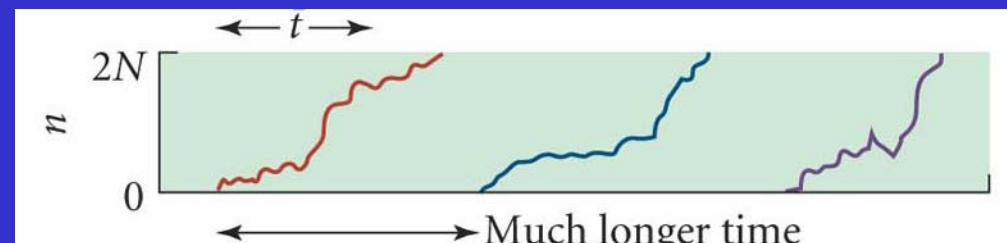
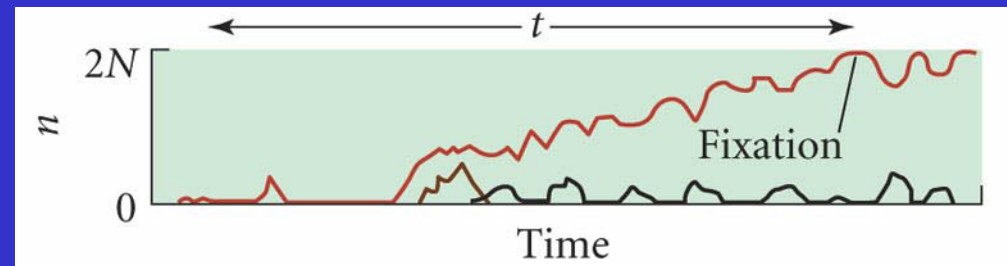


The **neutral theory of molecular evolution** holds that although some genetic variation is selectively advantageous or disadvantageous and can result in natural selection, most genetic variation is effectively neutral.

Neutral genetic variation can be expected to evolve according to the mathematical expectations of genetic drift models.

Neutral alleles arise by mutation and many are lost but some increase and become fixed.

Over long periods of time more alleles become fixed.



Since there are $2*N_e$ copies of a gene to mutate in a population the number of new alleles in a population in each generation should be $\mu*2*N_e$

The probability that an new neutral allele will eventually become fixed is equal to its initial frequency, $1/(2*N_e)$

So the number of new alleles that arise in each generation that will someday become fixed is

$$\mu*2*N_e * 1/(2*N_e) = \mu$$

Thus the rate of fixation of neutral alleles is equal to the mutation rate. **This is the basis of the molecular clock.**

If we have 2 species that have diverged from a common ancestor t generations ago and have D mutational differences between them, the rate of production of neutral mutations can be estimated as $\mu = D/2t$

Over long periods of time this estimate becomes poorer because of multiple mutations at the same site or “multiple hits.”

