

LECTURE 9. Genetic drift

In population genetics, **genetic drift** (or more precisely **allelic drift**) is the evolutionary process of change in the allele frequencies (or gene frequencies) of a population from one generation to the next due to the phenomena of probability in which purely chance events determine which alleles (variants of a gene) within a reproductive population will be carried forward while others disappear. Especially in the case of small populations, the statistical effect of sampling error during random sampling of certain alleles from the overall population may result in an allele, and the biological traits that it confers, to become more common or rare over successive generations, and result in evolutionary change over time. The concept was first introduced by Sewall Wright in the 1920s, and is now held to be one of the primary mechanisms of biological evolution. It is distinct from natural selection, a non-random evolutionary selection process in which the tendency of alleles to become more or less widespread in a population over time is due to the alleles' effects on adaptive and reproductive success.^[1]

Basic concept

Genetic drift is the process of change in allele frequencies that occurs entirely from chance. As an analogy, imagine representing organisms in a population with a large number of marbles, half of them red and half blue. These two colors correspond to the two different gene alleles present in the population. Put 10 red and 10 blue marbles in a jar; this represents a small population of these organisms. Each generation the organisms in this population will reproduce at random and the old generation will die. To see the effects of this, imagine randomly picking a marble from the jar and putting a new marble of the same color as the one you picked into a second jar. After your selected marble has "reproduced", put it back, mix the marbles, and pick

another. After you have done this 20 times, the second jar will contain 20 "offspring" marbles of various colors. This represents the next generation of organisms.

Now throw away the marbles remaining in the first jar - since the older generation of organisms eventually die - and repeat this process over several generations. Since the numbers of red and blue marbles you pick out will fluctuate by chance, the more common color in the population of marbles will change over time, sometimes more red: sometimes more blue. It is even possible that you may, purely by chance, lose all of one color and be left with a jar containing only blue or red offspring. When the jar only contains one color (allele), say red, the other allele, in this case the blue, has been removed or "lost" and the remaining allele (red) becomes fixed. Given enough time, especially in a small population, this outcome is nearly inevitable. This is genetic drift - random variations in which organisms manage to reproduce, leading to changes over time in the allele frequencies of a population.

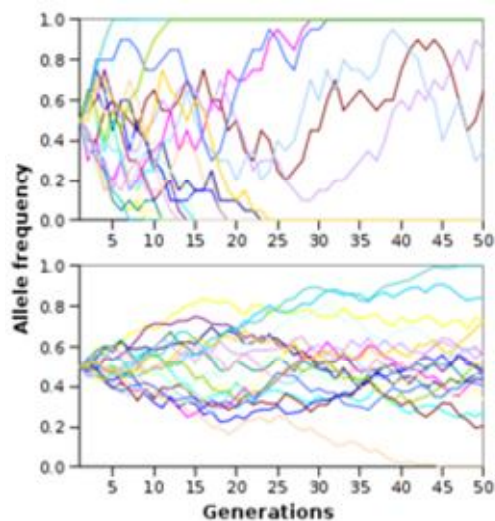
Probability and allele frequency

Chance events can affect the allele frequency of a population because within that population any organism's reproductive success can be determined by factors other than adaptive pressures. When chance events preserve the survival of randomly selected organisms of a given population, and the resulting allele frequency of the descendant group differs statistically from the allele frequencies in the ancestral group, evolution can result from probabilistic phenomenon rather than selective pressures. A shift in the frequency distribution of alleles over time which occurs as a consequence of sampling error is called genetic drift.

Genetic drift depends strongly on small population size since the law of large numbers predicts weak effects of random sampling with large populations. When the reproducing population is

large, the allele frequency of each successive population is expected to vary little from the frequency of its parent population unless there are adaptive advantages associated with the alleles. But with a small effective breeding population, a departure from the norm in even one individual can cause a disproportionately greater deviation from the expected result. Therefore small populations are more subject to genetic drift than large ones.^[2]

By definition, genetic drift has no preferred direction, but due to the volatility stochastic processes create in small reproducing populations, there is a tendency within small populations towards homozygosity of a particular allele, such that over time the allele will either disappear or become universal throughout the population. This trend plays a role in the founder effect, a proposed mechanism of speciation.^[1] With reproductively isolated homozygous populations, the allele frequency can only change by the introduction of a new allele through mutation.



Simulations of genetic drift for 20 alleles with initial frequency 0.5, for populations of size $N=10$ and 100, respectively. In general, alleles drift to fixation (frequency of 0 or 1) significantly faster in smaller populations.

When the alleles of a gene do not differ with regard to fitness, probability law predicts the number of carriers in one generation will be relatively unchanged from the number of carriers in the parent generation, a tendency described in the Hardy-Weinberg principle. However, there is no residual influence on this probability from the frequency distribution of alleles in the grandparent, or any earlier, population--only that of the parent population. The predicted distribution of alleles of the offspring is a memory-less probability described in the Markov property. In large populations, where sampling error is a weak factor, the allele frequencies will change little from one generation to another over time unless there are selective pressures acting on those alleles. However, in small populations where sampling error is more likely to result in greater change in an allele frequency from one generation to the next, the allele frequencies in a population can vary considerably from those further back in their lineage.

The lifetime of a neutral allele is governed by the effective population size. In a very small population, only a few generations might be required for genetic drift to result in fixation. In a large population, it would take many more generations.

Drift versus selection

Genetic drift and natural selection do not act in isolation; both forces are always at play in a population. However, the degree to which alleles are affected by drift and selection varies according to population size.

In a large population, where probability predicts little change in allele frequencies over many generations will result from sampling error, even weak selection forces acting upon an allele will push its frequency upwards or downwards (depending on whether the allele's influence is beneficial or harmful). However, if the population is very small, drift will predominate. In small

populations, weak selective effects may not be seen at all as the small changes in frequency they would produce are overshadowed by drift.^[3]

Evolution of maladaptive traits

Drift can have profound effects on the evolutionary history of a population. In very small populations, the effects of sampling error are so significant that even deleterious alleles can become fixed in the population, and may even threaten its survival.

In a population bottleneck, where a larger population suddenly contracts to a small size, genetic drift can result in sudden and radical changes in allele frequency that occur independently of selection. In such instances, the population's genetic variation is reduced, and many beneficial adaptations may be permanently eliminated.

Similarly, migrating populations may see a founder effect, where a few individuals with a rare allele in the originating generation can produce a population that has allele frequencies that seem at odds with natural selection. Founder's effects are sometimes held to be responsible for high frequencies of some genetic diseases.