

Drift: Introduction

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Genetic drift is the random change in allele frequencies by the chance success of some alleles relative to others.

Introductory article

Article Contents

- What Is Random Genetic Drift?
- The Properties of Drift
- The Importance of Population Size
- Genetic Drift and Natural Selection

What Is Random Genetic Drift?

Each gene may have several versions of itself, which differ in DNA sequence and perhaps other properties. These versions are called alleles. A major task of evolutionary biology is to understand how the frequencies of these alleles within populations might change. Allele frequencies can change as a result of selection, mutation, or migration from other populations, as well as by the random changes due to the chance success of some alleles relative to others. This random process is called 'genetic drift'.

When a generation reproduces itself to form the next generation, some individuals may by chance have more offspring than others. When a population produces offspring, that set of offspring may by chance have more of one of the alleles from the parents than the other allele. The result of this sampling of alleles from one generation to the next is that the resulting population will not necessarily have the same genetic composition as its parents.

The 'Sewall Wright Effect'

Random genetic drift was introduced to population genetics through the work of Sewall Wright, who, with R. A. Fisher and J. B. S. Haldane, was one of the three founders of theoretical population genetics. Wright believed that the random properties of allele frequency change were important not only in understanding the exact changes from one generation to the next, but also in the way drift allowed evolution to proceed in novel directions which might otherwise be opposed by direct selection. Drift was largely introduced to evolutionary biology in the context of Wright's arguments and was therefore called the 'Sewall Wright effect' for several decades.

An example

As an extreme example, imagine a small population constrained to allow only two individuals to be present at any given time. If we establish that population with two heterozygotes (genotype Aa) and allow them to cross, the rules from Mendelian genetics can be used to figure out what the next generation will look like. However, we cannot determine exactly what the composition of the population will be because the final outcome depends on

random assortment and union of gametes during meiosis and mating. Instead, what we find is the probability of the population having a particular set of genotypes. For instance, one sixteenth of the time ($\frac{1}{4} AA \times \frac{1}{4} AA$) there will be two AA homozygotes in the population. There is an equal probability that we will end up with only aa homozygotes in the population. In this example there is thus a one eighth chance that we will lose one or the other of the two alleles even though the alleles themselves may not affect the organism either positively or negatively. Indeed, there is only a one-quarter chance ($\frac{1}{2} Aa \times \frac{1}{2} Aa$) that the population will look exactly the same the next generation as it did in the current generation. How large these random changes are depends on how large the population is (see below).

In a direct test of these ideas, in 1956 Peter Buri raised 107 separate populations of the fruit fly, *Drosophila melanogaster*, using eight males and eight females as parents for each generation. Keeping track of the frequency of a mutation causing brown eyes, he found that, although all of the populations were started with the same 50:50 mix of brown versus normal alleles, the populations rapidly diverged from one another over the course of a few generations (**Figure 1**). Within 20 generations most of the populations had completely lost either the mutant allele or the normal allele. Subsequent experiments demonstrated that there was no detectable natural selection operating in these populations, leaving the conclusion that the observed evolutionary change was caused by genetic drift.

The Properties of Drift

The change in allele frequency due to genetic drift, while unpredictable in individual populations, on average causes populations to change in a predictable way. Drift on average causes there to be fewer alleles within populations, more differences between populations, and variable allele frequencies over time. Each of these properties can be seen in the example in **Figure 2**.

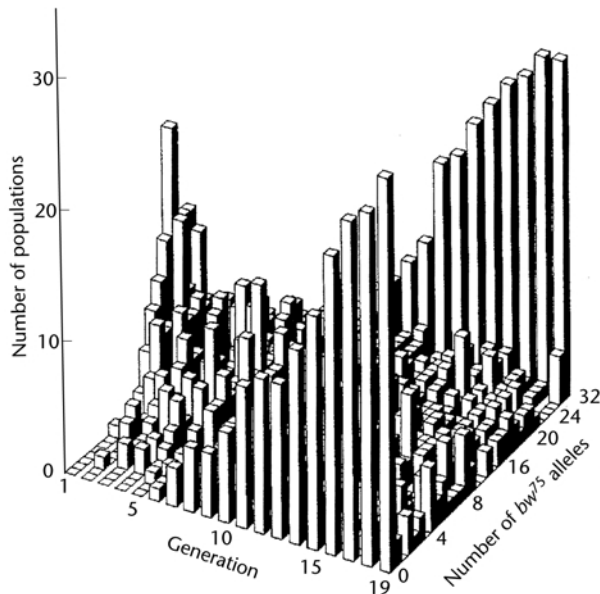
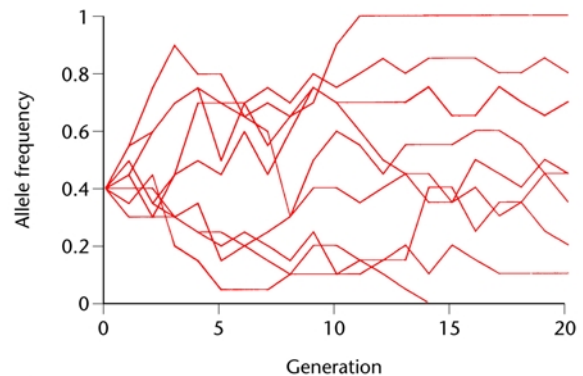


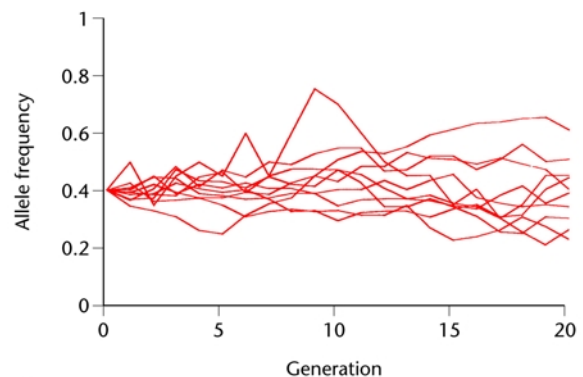
Figure 1 The effects of genetic drift on 107 laboratory populations of the fruit fly, *Drosophila melanogaster*. The populations were maintained at a size of 16 individuals, giving a total of 32 possible different alleles (two per individual). The two horizontal axes respectively give the number of generations since the populations were all started (initial allele frequency of 0.5) and the number of mutant brown eye alleles in the population. The vertical axis reports how many of the populations possess that many alleles at a given time period. Looking across all 107 populations shows that genetic drift generates variation among the populations that increases with time, eventually ending in fixation of one or the other of the two alleles. Data from Buri (1956); figure from Hartl and Clark (1997).

Fixation of alleles

When one allele becomes so common in a population that no others exist, that allele is said to have ‘fixed’ in that population. One of the consequences of genetic drift is that, if there is no other source of new genetic variation such as mutation or migration from other populations, allele frequencies will randomly increase and decrease until one or another of the alleles in the population is fixed, and the others lost. The probability that a particular allele is fixed, when there are no other factors operating on the population, is equal to its initial frequency in the population. Thus a new neutral allele introduced to a diploid population as one copy has an initial allele frequency of $1/2N$, where N is the number of diploid individuals in the population (with two copies per individual). Therefore that allele would also have a $1/2N$ chance of ultimately fixing in the population as well, if there were no selection, migration or mutation also affecting allele frequencies.



(a)



(b)

Figure 2 The effects of time and population size on populations undergoing genetic drift. Each line shows the allele frequency from generation to generation of a separate population of size either 10 (a) or 100 (b). Each population was started at the same initial allele frequency (0.4). Note that the populations diverge from one another over time as genetic drift takes them in different directions. Also note that the rate of divergence is much less in the larger population. Given enough time, however, even these larger populations will diverge as much as the smaller populations. Thus, population size affects the rate of drift but not necessarily its eventual outcome.

Divergence of populations

Just as drift can cause the fixation of a particular allele in a population, it is of course also responsible for the loss of other alleles. Because drift is a random process, the fixation of an allele in one population is independent of its fixation in another population. As a result, over time populations will become more and more different from each other due to the effect of genetic drift. This effect is not merely the result of fixation of alternate alleles in different populations, but also happens earlier as the result of the random change in one population not being exactly the same as that somewhere else, such that different populations become different from one another. Natural populations that are isolated from one another because they rarely exchange migrants would be expected to diverge from one another solely on the basis of genetic drift unless some other

evolutionary force, such as natural selection, is acting to maintain the populations in a similar state.

Fluctuations in allele frequency

The most immediate consequence of genetic drift is that the allele frequencies in one generation are not likely to be the same as those in the previous generation. This creates many difficulties for the study of evolutionary processes, because the change in allele frequency over time is ultimately the best measure of evolution. Many interesting evolutionary processes, such as selection, are demonstrated in particular cases by changes in allele frequencies; in each case the investigator is required to demonstrate that the changes which have been observed are larger than would be expected by genetic drift, as a null model.

The Importance of Population Size

The most important predictor of the magnitude of genetic drift is the number of breeding individuals in a population – its population size. As the number of breeding individuals gets smaller, the magnitude of genetic drift increases. This effect can be seen in **Figure 2**. Thus genetic drift can be very important in populations which have only a small number of individuals.

Effective population size

In fact, the population size alone is not enough to predict the amount of genetic drift. Other properties of the species, in particular variation in the amount of reproductive success among individuals of that population, also affect the amount of genetic drift. These effects are often encapsulated into the concept of the ‘effective’ population size, which is often written as N_e . The effective population size of a population is the number of individuals that would be in an ideal population, with equal probabilities of reproduction of each individual in the population, which would have the same amount of genetic drift as the population under study. Variation in reproductive success decreases the effective population size; for example, individuals that breed very little contribute very little to the next generation, and therefore do not count for much in terms of slowing drift. In general, most natural populations have effective population sizes that are much smaller than their actual population sizes, and therefore genetic drift is more important than the large apparent population size of many species would seem to indicate.

Founder events and population bottlenecks

The long-term patterns of genetic drift are also very sensitive to periods of small population size. A single

generation where the population size drops to a low value can cause more change in allele frequency than many generations at a large population size. When a population goes through a period of unusually small size, this is referred to as a ‘population bottleneck’. If the population goes through this period of small population size at a time when it arrives to a new, uncolonized area, this is referred to as a ‘founder event’. In both cases, much genetic drift can occur over a short period of time. Many biologists have suggested a special role for population bottlenecks or founder events in the evolution of new species; most evolutionary biologists now view these theories with some scepticism. However, many species are likely to go through population bottlenecks from time to time, and the relative importance of genetic drift may be increased dramatically by these periods. The current population size of a species may be only a weak guide to the amount of evolutionary change caused by genetic drift in that species’ history.

Conservation genetics

The reductions in the population sizes of many species that have resulted from the destruction of habitat by humans and other insults to the natural world have led to increased concern about genetic drift in more species. In particular, scientists are concerned that because of small population sizes genetic drift will eliminate much of the genetic variation required for future adaptation of natural populations; and they are also concerned that mildly deleterious new mutations will drift to high frequencies and lower the fitness of these populations. As a result, it has been suggested that species should never be allowed to decrease below a minimum effective population size of 5000–10 000 in order to ensure the genetic health of that species. While it is widely believed that other, more ecological processes determine the immediate success of populations, these effects of genetic drift can be very important in determining the ultimate success of endangered species.

Genetic Drift and Natural Selection

Natural selection is ultimately the most important evolutionary force. The effects of drift on genetic loci affected by selection are those which matter most to the outcome of the evolutionary process. Drift affects the evolutionary response to selection in a variety of ways. First, drift, being nondirectional, causes the frequencies of selected alleles sometimes to increase more than expected by selection alone, and sometimes even to decrease the frequency of more fit alleles, contrary to the effects of selection. Deleterious alleles can increase in frequency as a result of drift, which is not possible if selection alone were acting on a population.

Weak selection allows more drift

The effects of genetic drift on gene frequency change are more pronounced, relative to selection, if the differences in the fitness of different alleles are small. In other words, drift becomes more important as selection becomes weaker. As a rule of thumb, if the fitness differences between two alternative alleles is less than the reciprocal of four times the effective population size, then the alleles change in frequency largely independently of the effects of selection, and act according to the effects of drift. If the selective difference between alleles is much greater than this, then selection becomes most important.

As a result of this relationship between the strength of selection and the impact of drift, smaller populations have more possibility of deleterious alleles increasing in frequency.

Drift is nonadaptive and nondirectional

Drift in itself, although it causes the change of allele frequencies in populations and therefore is a process of evolution, does not increase the adaptedness of a population. Drift changes allele frequencies without regard to their adaptive properties and therefore is nonadaptive.

Furthermore, drift is as likely to increase allele frequencies as to decrease them, and is therefore nondirectional. Moreover, drift is not correlated across generations; an increase in an allele frequency in one generation is as likely to be followed by a decrease in the next generation as another increase. While in a particular time series of one population drift can by chance cause consecutive directional changes in allele frequency, there is no correlation expected on average across generations.

Selection, in contrast, is by definition adaptive, and is quite likely to be directional. These properties of selection can allow scientists to discriminate selection from genetic drift in natural populations.

Molecular evolution

It is thought that the strength of selection between alternative alleles with effects on the morphology, physiology, or behaviour of organisms are greater than the minimum required for selection to be the most important determinant of evolutionary change for these alleles. In contrast, much of the genetic variation at the DNA level,

changing not the protein-coding regions of DNA but rather the sequences of other regions of the genome, is thought to be under much weaker selection. Evolution at the level of the DNA is called molecular evolution, and it is at this level that genetic drift plays a large role in determining evolutionary patterns.

For example, the genetic code is redundant, which means that in most cases more than one codon can code for the same amino acid. As a result, the fitness differences between an allele that codes for an amino acid with one codon, and another that codes for the same amino acid but with a different codon, are likely to be very small indeed. As a result, genetic drift can play a large role in determining which codons are used. Many other parts of the genome have no obvious molecular function, and their evolution may also be dominated by the effects of genetic drift rather than selection. The rate of molecular evolution via drift and mutation in the absence of selection is equal to the mutation rate to new alleles, suggesting that evolution in this case should proceed at a constant, clock-like, pace (a molecular clock). This result is one of the foundations of the neutral theory of molecular evolution formulated by Motoo Kimura and others.

Modern molecular analysis of natural populations has revealed that there is a great deal of genetic variation at the molecular level – probably too much for it all to be explained by natural selection. One of the major current research efforts in evolutionary genetics is to identify methods of distinguishing the relative importance of drift versus selection in describing DNA sequence variation. These issues will continue to grow in importance in many areas of biology as more DNA sequence data become available and biologists attempt to distinguish functionally meaningful variation, such as that leading to genetic disease, from random background variation.

Further Reading

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