The Role of Chance in Evolution[1]
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Introduction

Chance is one of the most misunderstood aspects of evolution. On one hand you have those who want to dismiss evolution by claiming falsely that all its mechanisms are dependent entirely on chance and therefore they are totally undirected and could not possibly produce the complexity and organization we see in nature. The other group totally dismisses chance and views evolution as operating entirely to produce adaptations. Neither of these groups is correct.

Regarding the viewpoint of the evolution deniers, we have already seen that natural selection is hardly a matter of chance. Although it is a non-conscious process and so is not directed by intelligence (remember – science is based on materialism), nevertheless it is a mechanism that still manages to select traits that on the average do better than the alternatives. And if the "selection regime" – the environmental factors causing selection, remain similar over an extended period of time selection can, if given enough variability, produce totally new adaptations. The only factor that is truly chance driven in natural selection is the production of genetic variation – most directly by recombination in sexual reproduction and equally importantly but more indirectly by mutation. Natural selection then becomes the mechanism that removes some mutations and recombinations and favors others – it amplifies or attenuates these chance events and results in population genetic and phenotypic structures that are referred to as adaptations. All available evidence suggests that this mechanism, natural selection, is responsible for most of the differences we see – because such differences are usually associated with different ways for organisms to survive and reproduce. In the last set of notes we considered how populations might diverge or gradually change through time as a result of patterns of selection termed dispersive and directed. Likewise, natural selection is responsible for maintaining many systems common to all organisms – systems that are central to the operation of living systems. We considered this under the term normalizing selection.

Evolution by Genetic Drift

There is an alternative mechanism of evolution to natural selection. It is called genetic drift. If natural selection is evolution that produces adaptation, then genetic drift is evolution where change occurs (else there would be no evolution) but where the change does not result in adaptation. On the other hand, do not get the idea that the change that

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results from genetic drift is maladaptive for it is not. Maladaptation is simply the other side of adaptation – both of these terms imply changes that affect the organism's ability to survive in a given environment (one helps, the other implies it makes things worse). Genetic drift is neutrally adaptive evolution. It is sometimes called non-adaptive evolution but I believe that term is easily confused into meaning maladaptive so I want you to use neutrally adaptive to describe drift.

What is genetic drift? Genetic drift is the random variation of allele frequencies that occurs in small populations. Sewall Wright developed the theory of genetic drift in the late 1920s. It is sometimes called wrightian evolution (just like natural selection is often referred to as darwinian evolution). Wright was a theorist – he developed the hypothesis of genetic drift by extending the ideas of Hardy and Weinberg and formally analyzing the conditions under which genetic drift would be predicted. For genetic drift to have a significant effect the following must be true:

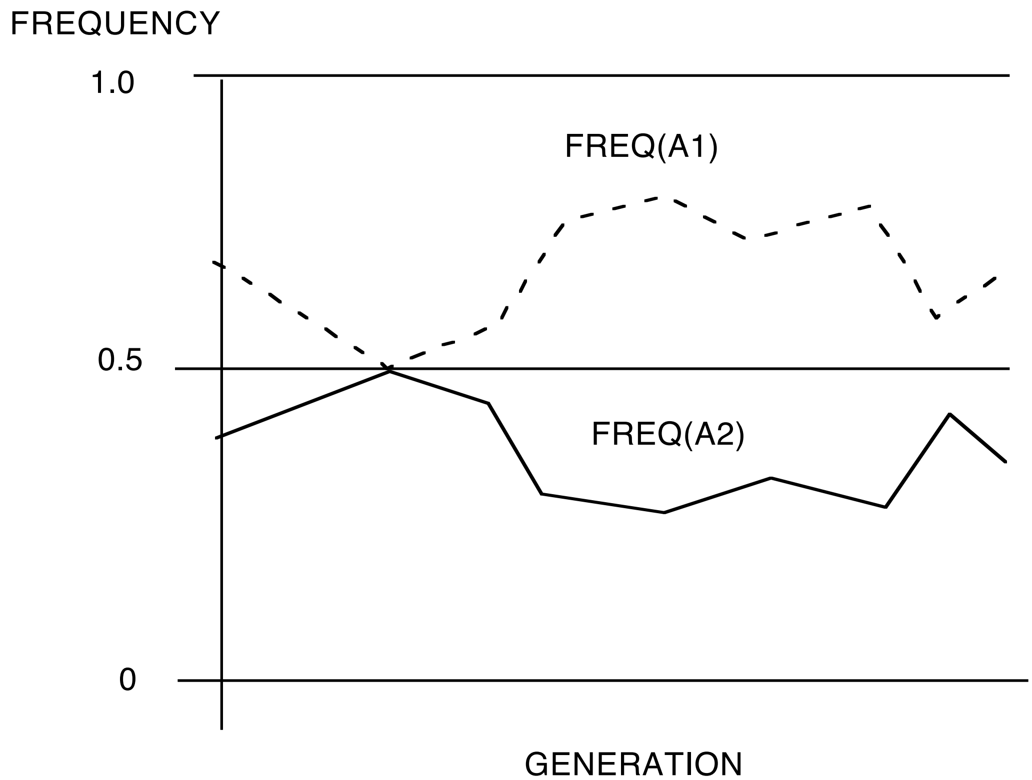
- The population must be sexually reproducing
- There must be little net allele migration
- There must not be significant selection (either natural or sexual)
- The population must be small

Imagine that in such a population you have two alleles at locus A – we'll use our usual names, A_1 and A_2. The three possible genotypes A_1A_1 A_1A_2 and A_2A_2 have not selective advantage over each other in the present environment. Let's also assume that the frequency of A_1 which I'll symbolize as p is 0.5 and so the frequency of A_2 (symbolized as q) is also 0.5. Finally, let's assume that this essentially isolated deme (remember that there is no significant net migration) has a total population of size of 10 individuals, 5 of each sex. Let's also assume that a total of 10 offspring are produced, 2 by each female and male (in other words, no individual has a selective advantage). The most likely outcome for the next generation is that $p = q = 0.5$ and no evolution will have occurred. But is that the only possible outcome? Clearly not There is a just slightly lower chance that in the next generation the frequencies could change to $p = 0.45$ and $q = 0.55$ or vice versa. There is a slightly lower chance yet that p would go to 0.4 and q to 0.6. In fact, there is even a chance that either allele A_1 or A_2 could be totally lost due to the chance events involved in sexual reproduction (in our example, the chance that in the next generation $p = 1.0$ and $q = 0$ would be $0.25^{10} = 9.54 \times 10^{-7}$.

How did I get this? The overall chance of getting an A_1A_1 individual in this population is the chance that two A_1 alleles can come together. Since the frequency of $A_1 = 0.5$, then the overall chance of an A_1A_1 is 0.25. Then, since there are 10 total offspring produced, the overall chance is 0.25^{10}.

In fact the possible outcomes fit a normal distribution with the most likely single outcome being no change in allele frequencies but with the overall chance of some change in allele frequencies (the sum of the chance of all other outcomes) being far greater – so it is likely that some change will occur. On the other hand, the exact direction of change cannot be predicted in this case (an increase in A_1 or A_2 are equally likely) although the chance of a given size of change can be predicted. Notice that if changes occur in one direction one year they can easily occur in another direction in the next reproductive season. Furthermore, there is no reason that the size of the change will be the same each year. In fact, it might vary considerably from one year to the next.

The pattern of evolution that results has been called a "random walk" and it might look something like this:



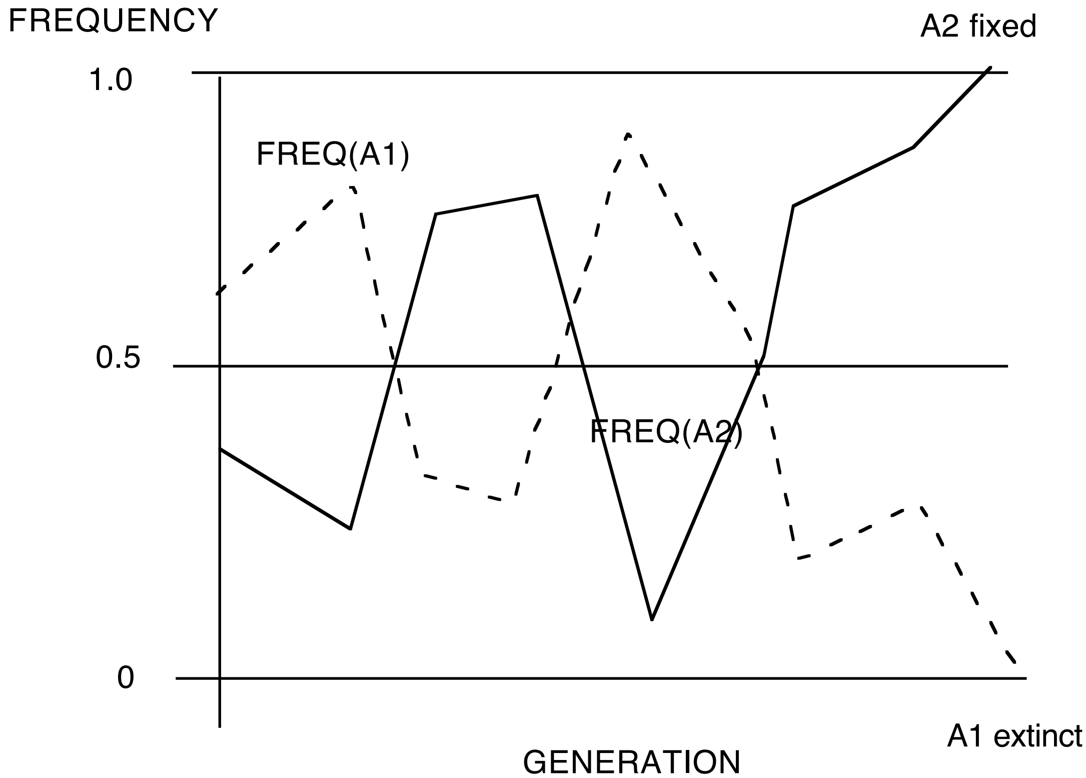
Notice that as one allele increases, the other decreases – the curves are mirror images of each other.

One important thing to note about genetic drift is that the smaller the population, the more likely that we can get very large genetic changes in one generation.

One way to envision this is to think about the two sides of a coin as representing two competing alleles. A coin flip represents a reproduction. If you imagine that a population only has two individuals, then you would represent reproduction as the result of two coin flips.

There is a 50% (25%+25%) chance that you will get either two heads or two tails – the equivalent of removing one allele or the other from the population. On the other hand, if your population size is 10, the chance of removing one or the other (i.e., of getting 10 H or 10 T) is $2*0.5^{10}$or about 0.02.

Thus, in small populations, allele frequencies can shift rapidly. It is especially possible in a small population for one allele to be lost and the other "fixed" (a term that means that it is the only allele present at this locus in this population). This obviously becomes more and more likely as the allele frequencies become more skewed –as one allele becomes rare in a small population, the chance that it will be lost becomes greater and greater.



Selection vs. Drift:

For genetic drift to occur, it is not a requirement for there to be absolutely no selective advantage of one allele over another. Genetic drift is most powerful when populations are extremely small. In these cases, even if one allele has some advantage over another, by chance, we could lose the better allele or lower its frequency.

Note: we assume here that both are functional but that one on the average is associated with somewhat higher reproduction than is the other.

Thus, selection and drift could oppose each other or, in other cases they could work together.

Is Genetic Drift Real?

Genetic drift is as well documented, as is natural selection (meaning that it is far better documented than most things in biology – including those associated with treatments of disease). Many examples could be cited but perhaps the most famous one deals with a type of human blood group (another set of red blood cell antigens called M and N). A famous population geneticist, Luigi Luca Cavalli-Sforza showed that in the distributions of these blood groups in northern Italian villages fit the predictions of genetic drift. The frequencies varied from village to village in a random manner. The populations in these historically isolated villages have been very small over the last 1500 years (we have records for most of this time) and there has been relatively little intermarriage until recently (no migration) and finally, there is no known selective advantage of the M, MN or N blood types. The bottom line is that whenever we look in appropriate places for evidence of genetic drift, we find it.

The bigger and more difficult question is the relative significance of genetic drift and natural selection in the evolution of various populations. We may have time to discuss this after we have considered speciation.

Other Chance Events and Evolution

Many other chance events can impinge on evolution. One of the most important is something called the founder effect. This idea was first put forward by the great evolutionary biology Ernst Mayr in the 1950s. The idea is simple. When new habitats are invaded by a species, typically only a few individuals do the colonizing. This is often because of distance and danger associated with the colonization. These same factors may make repeat colonizations rare. Imagine an island if you need and example and then imagine how most plants and animals would get there. If the colonizers succeed, notice that they are but a small sample of the entire genetic diversity of the parent population. Their characteristics will determine the future the population heavily and to a large degree the exact genes that make it to this new habitat may be a matter of chance. Notice also that there will initially be a lot of opportunity for genetic drift.

Mutation, Sex and Chance

Mutations are truly chance events and they are rare – normally about 1 in 1,000,000 copies of an allele is a mutant. However, they are the ultimate source of diversity that the two evolutionary mechanisms operate on. Without mutation, at some point you can have no evolution. However, just because these are chance events, it is not the same thing as saying that all of evolution is chance. Again, the reason is simple – natural selection is not random.

Likewise, sexual reproduction involves chance recombinations and is very important in evolution. As linkages of alleles are broken up, some of the new combinations confer more advantage and others less than the previous ones. So, once again, chance is central but what makes the ultimate outcome very different from chance is natural selection.

Questions

1. How are founder effect and genetic drift similar and different from each other?
2. Which one(s) of the Hardy-Weinberg postulates is/are violated in order for genetic drift to occur.
3. What does genetic drift tend to do genetic variation within a population, given enough time?
4. What is meant by a random walk in genetic drift? Imagine taking a "random walk" on a pier – how does this analogy -- especially the prospect of falling off the edge – relate to the previous question?