



# Random Genetic Drift: A Non-directional Force of Evolution

B. N. Singh\*

Genetics Laboratory, Department of Zoology, Institute of Science, Banaras Hindu University, Varanasi-221005, India.

E-mail: bnsinghbhu@gmail.com

**Abstract.** Evolution is a corner stone of biology. In terms of genetics, it is defined as a change in genetic composition of populations. A population has two attributes: Gene frequency-proportion of different alleles of a gene in a population; Gene pool- sum total of genes in the reproductive gametes of a population (considered as gametic pool). When the population is evolving and under-going microevolutionary changes, different elemental forces operate to bring about these changes: mutation, natural selection, migration and random genetic drift. The first three forces have one quality in common, they usually operate in directional fashion to change allele frequencies progressively from one value to the other. When other factors are not opposing, these factors can lead to fixation of one allele and elimination of others. In case polymorphism is balanced, they can lead to equilibrium between two or more alleles. On the other hand, there is another factor that brings about the changes in allele frequency in non-directional manner and has no predictive constancy from generation to generation. It is known as random genetic drift which arises from variable sampling of gene pool in each generation. It operates in small populations and causes allele frequency changes due to chance events causing random fluctuation in allele frequency occurring because of sampling errors. It may lead to fixation or elimination of a particular allele which causes increase in homozygosity. Sewall Wright discussed the role of genetic drift in small populations with particular

reference to non-adaptive variations resulting from neutral gene combinations persisting in populations. That is why random genetic drift is also known as Sewall Wright effect. In relation to random genetic drift, there are certain population phenomena such as bottleneck effect/founder effect during which small number of individuals migrate to other geographical area and establish a new population which evolves independently. There are examples which demonstrate that random genetic drift plays an important role in population evolution.

**Index Terms:** Random genetic drift, non-directional force of evolution, fluctuation in gene frequencies, small populations, founder principle, examples from *Drosophila*.

## I. INTRODUCTION

In 1908, G.H. Hardy and W. Weinberg independently developed relatively simple mathematical solution which is known as Hardy-Weinberg Rule to describe the genetic equilibrium. This law states that in a randomly mating population (panmixia) with a closed gene pool the allele and genotypic frequencies remain constant from generation to generation with genotypic frequencies being determined by allele frequencies. The Hardy-Weinberg law which is based on binomial square rule is used to determine the frequencies of

each allele of a pair or of series of a locus as well as the frequencies of genotypes in populations. Thus for the maintenance of Hardy-Weinberg equilibrium, there are certain requirements such as random mating, absence of mutation, natural selection, random genetic drift and migration. Dobzhansky (1951) states that the maintenance of genetic equilibrium is evidently a conservative factor. Evolution is modification of this equilibrium. Savage (1963) has also stated that “genetic equilibrium is an expression of conservative nature of biological heredity. According to Hartl and Clark (2007), in one locus two allele system, the allele frequency ( $A = p$ ,  $a = q$ ) give directly the genotypic frequencies ( $AA$ ,  $aa$ ,  $Aa = p^2, q^2, 2pq$ ). Under the above conditions, it is easy to demonstrate the following: For a particular population satisfying the requirements of Hardy-Weinberg Equilibrium the allele frequencies are constant in time. The notion of HWE adopted in the Modern Synthetic Theory derives from the above assumption. In a randomly mating population, according to Hardy-Weinberg principle, allele frequencies of a locus are conserved unless external factors such as mutation, natural selection, random genetic drift and migration act on them and the equilibrium of genotypic frequencies ( $p^2 + 2pq + q^2$  with respect to two alleles of a locus) derive from the gene frequencies (Hall & Hallgrimsson, 2008). Thus, when a population remains in equilibrium it remains stable and not evolving. It is apparent that as long as Hardy-Weinberg equilibrium is maintained evolution is not possible. When this equilibrium is modified by any factor/factors evolution has occurred. Thus evolution is defined as any change in the genetic composition of populations (Dobzhansky, 1951). The factors which modify the Hardy-Weinberg equilibrium become important elemental forces of evolution and are important components of Modern Synthetic Theory of evolution (Singh, 2022).

The important forces of evolution are mutation, recombination, natural selection, random genetic drift and migration which bring about microevolutionary changes in evolving

populations. Interestingly, the factors, mutation, natural selection and migration bring about changes in population in directional manner and the frequency of alleles increases progressively in the course of evolutionary change which may lead to fixation of favourable allele or establishing balanced polymorphism with equilibrium frequencies. On the other hand, the random genetic drift brings about random fluctuation in allele frequency in every generation without any predictive value in small populations and it is considered as a non-directional force of evolution. Genetic drift results in random fluctuation in allele frequencies due to sampling error and it is just a chance event in small population. As a consequence of the occurrence of genetic drift, genetic variability decreases in populations and there may be an increase in genetic divergence but in non-directional fashion. This may also lead to elimination or fixation of a particular allele causing an increase in homozygosity. Thus random genetic drift has a greater consequence in population composition particularly in small populations and in this way it is entirely different from natural selection as far as the operation of elemental forces on genetic variability in population is concerned. Some times there may be an interaction between natural selection and genetic drift. Sewall Wright (1931) discussed in detail the effect of random genetic drift in small populations which may cause elimination or fixation of a particular allele in small populations and he stressed on non-adaptive variations resulting from neutral gene constitutions persisting in populations. Such variations cause puzzling difficulty when natural selection is considered as the only guiding force of evolution in populations. Thus random genetic drift or Sewall Wright effect plays an important role in populational evolution. When the number of parents of a population is consistently large in every generation, there is a strong likelihood of obtaining a good sample of genes of previous generation. However, the gene frequency will deviate considerably when compared with previous generation in case small number of parents are chosen to start the new generation.

With the help of calculation of standard deviation (SD), the degree of deviation in allele frequency may be measured.

$$SD = \sqrt{\frac{pq}{2N}}$$

p= frequency of one allele

q=frequency of other allele

N= Total number of genes sampled

For diploid parents, each carrying two alleles, N is the number of actual parents. For example, if a large diploid population is perpetuating and the number of parents in each generation is 5000 and p=q=.5, then

$$SD = \sqrt{\frac{(0.5) \times (0.5)}{2 \times 5000}} = 0.005.$$

So allele frequency will deviate around  $0.5 \pm 0.005$  (between 0.495 and 0.505). On the other hand, a choice of only two parents to start the new generation, the value of SD is 0.25

$$(SD = \sqrt{\frac{(0.5) \times (0.5)}{2 \times 2}} = 0.25).$$

Thus the allele frequency will fluctuate between 0.25 and 0.75 ( $0.5 \pm 0.25$ ). This shows that sampling error because of small population size will lead to random fluctuation in allele frequencies and consequently, an allele may be fixed or eliminated from the population due to random genetic drift in the absence of directional forces. When the population size is large, the rate of fixation or elimination will be slow. Wright (1931) has demonstrated the effect of population size on the fluctuation in allele frequency, fixation or elimination of an allele and maintenance of polymorphism in populations depending upon the size of populations (see Hall & Hallgrímsson, 2008).

Wright-Fisher model of random genetic drift has clearly demonstrated that the comparison of oscillations in allele frequency and elimination/fixation of allele depends on population size while considering two populations with  $2N=18$  and 100. In 20 generations there is elimination/fixation of a

particular allele with population size of  $2N = 18$ . In seven populations, A allele became fixed ( $p=1.0$ ), in five populations A became lost ( $p=0$ ). The remaining eight populations remained polymorphic (unfixed) carrying both the alleles (A and a). However, during the same number of generations, there is neither fixation nor elimination of any of two alleles in the population when population size is  $2N = 100$  and prediction of allele frequency is very difficult because allele frequency behave erratically. This clearly demonstrates the operation of random genetic drift in small populations (see Hartl and Clark, 2007). Associated with random genetic drift, there is another important aspect that is effective population size for the determination of genetic drift. It is different from the actual population size because all individuals of a population are not necessarily parents for the next generation. This concept was given by Sewall Wright (1951). For example, there are 1000 individuals in a population but only 300 mating pairs contribute equal amount of progeny to the succeeding generation. So there will be effective population size of 600 only. A formula was suggested by Wright (1951) to estimate the effective population size which is mentioned below:

$$N_e = 4N_f N_m / (N_f + N_m)$$

$N_e$ = Effective population size

$N_f$ = number of parental females

$N_m$ = Number of parental males

(For details see Hall and Hallgrímsson, 2008).

In a population of 3 males mated to 300 females, the effective population size will be more than six but less than 303. In this case the effective population size will be  $4 \times 300 \times 3 / 300 + 3 = 11$ . Random genetic drift in populations with small effective size will produce significant variation in allele frequency. Genetic drift may also operate in the presence of directional forces such as natural selection and migration from other

populations. Some times natural selection and random genetic drift may interact and produce changes in allele frequency.

Associated with Sewall Wright effect, there are population phenomena like bottleneck effect, founder effect and flush-crash cycle which are of considerable significance in changing allele frequencies drastically and also playing role in speciation (White, 1978; Powell, 1978; Hedrick, 2005; Hartl & Clark, 2007; Hall & Hallgrímsson, 2008; Singh, 2021). Bottleneck effect- this phenomenon shows severe temporary reduction in population size resulting in change in allele frequency due to random genetic drift. Genetic variability is reduced and it leads to genetic bottleneck. This also leads to increase in homozygosity and decrease in heterozygosity. A severe population bottleneck often occurs in nature when a small number of individuals from the parental population migrate to new area (in extreme cases a single gravid female) and start a new population, the accompanying random genetic drift is known as founder effect which has been called as founder principle by Mayr (see Hartl and Clark, 2007; Singh, 2021). Kimura (1983) proposed the neutral theory to explain the mechanism of evolution at molecular level which is primarily based on random genetic drift. At morphological, physiological and behavioural levels, evolutionary changes are governed by natural selection, but at the molecular levels (proteins and nucleic acids), most evolutionary changes are not governed by natural selection rather by random fluctuations of adaptively neutral variants. The frequency of adaptively neutral mutations would change from generation to generation due to sampling accidents or random genetic drift. Kimura also suggested that variations at molecular level are neutral and have no effect on fitness. There is controversy between neutralists and selectionists as far as evolution at molecular level is concerned because selectionists have presented evidence in favour of operation of natural selection maintaining protein polymorphisms: strong correlation between particular alleles (allozymes) and particular environmental conditions, non random allele frequencies in enzyme polymorphisms, enzyme

function and degree of polymorphism and polymorphism for DNA coding sequences. Thus selective forces unquestionably affect polymorphism at molecular level and help to maintain it. However, some genetic variants may be neutral at certain period of time or certain environmental conditions but may have selective value when genetic background or environmental conditions change (Hall and Hallgrímsson, 2008).

## II. EXAMPLES DEMONSTRATING THE OPERATION OF RANDOM GENETIC DRIFT

A. Kerr and Wright (1954) conducted laboratory experiments for sixteen generations by maintaining 96 lines of *Drosophila melanogaster* with initial frequency of 50% of two alleles (*forked*<sup>+</sup> and *forked*) and breeding 4 females and 4 males randomly in every generation. It was known that there was small selection against *f* allele. After 16 generations, it was found that 29 lines were fixed for *forked* allele, 41, lines fixed for *f*<sup>+</sup> and remaining 26 lines remained unfixed. Although less number of lines remained fixed for *f* allele because of small selection occurring against it, the results clearly indicate that genetic drift played an important role in causing fixation/elimination of an allele in the laboratory populations as lines were maintained by randomly selecting 4 females and 4 males in every generation to maintain these lines.

B. In *D. melanogaster*, similar experiments were conducted by Buri (1956) who maintained 107 lines with initial equal frequency of two alleles at brown locus (*bw* and *bw*<sup>75</sup>) and 8 females and 8 males were randomly selected as parents in every generation. By generation 19, more than 50% of the populations reached fixation for either *bw* or *bw*<sup>75</sup> alleles which clearly demonstrated that random genetic drift may lead to elimination or fixation of a particular allele very quickly if population size is small.

C. Hawaiian Species of *Drosophila*

There are more than 500 species of *Drosophila* reported from Hawaiian Islands. Carson and others have made extensive study on cytogenetics, behavior and evolutionary aspects of these species. Out of these species, about 100 species are picture winged and have been studied in detail. Speciation of a large number of *Drosophila* species on Hawaiian Archipelago has been explained by founder principle of Mayr (1942). Carson (1971) has suggested that a few individuals (in extreme cases a single gravid female) migrated to another island and established a new colony which evolved into a new species. Primarily, founder principle is based on random genetic drift (with narrow population bottleneck). Due to the effect of random genetic drift, the new population becomes genetically different from the original population. Based on this principle and behavioural differences, Kaneshiro (1976) suggested that ancestral females discriminate against the derived males. He suggested the evolutionary sequence among certain picture winged species: *D. differens*-----*D. planitibia*-----*D. silvestris*. Thus, new species originates due to founder effect (random genetic drift/bottleneck effect/Sewall Wright effect/flush crash cycles). Thus random genetic drift plays important role in the process of speciation although it is a non directional force of evolution.

D. The role of genetic drift via founder effect was demonstrated in experimental populations of *D. pseudoobscura* using different chromosome gene arrangements in the third chromosome and maintaining the populations for several generations (Dobzhansky & Pavlovsky, 1957). Interestingly, variation in the frequency of gene arrangements was more when less number of flies were employed to start the population. However, the variability in the gene arrangement frequencies was less when higher number of individuals were used to start the populations. These results reported by Dobzhansky and Pavlovsky (1957) in *D. pseudoobscura* clearly demonstrated that the variation in chromosome arrangement frequencies depended upon the number of individuals used to start the experiments.

E. *Drosophila ananassae* is a cosmopolitan and domestic species and is of common occurrence in India. Further, it is characterized by several unusual genetic features (Singh, 2000). Population genetical studies on inversion polymorphism has clearly demonstrated that Indian populations are genetically differentiated at the level of three cosmopolitan inversions (Singh, 1998; Singh and Singh, 2007, 2008). Two homozygous lines (ST/ST and AL/AL) were crossed and maintained for 12 generations in the food bottles (10 lines) in the laboratory by transferring 50 flies (males and females in equal number) in each generation. After 12 generations, the chromosomal analysis of all the 10 lines revealed that polymorphism persisted in all the lines due to superiority of inversion heterozygotes but there was much fluctuation in the frequencies of two gene arrangements (standard - ST and alpha -AL) when different lines were compared. Fluctuation in chromosome arrangement frequencies were caused due to random genetic drift. However, persistence of polymorphism was due to superiority of inversion heterozygotes (Singh, 1988). Thus, there was interaction between random genetic drift and natural selection.

F. Nanda and Singh (2011) demonstrated that sexual isolation may originate due to founder effect in laboratory populations of *D. ananassae*. Three mass culture stocks of different geographic origin showing no sexual isolation with each other, were used to initiate drift lines differing in the number of founders (one pair, five pairs and 10 pairs-3+3+3). These drift lines were passed through flash-crash cycles at every generation with same initial number of founders. All the lines were maintained for 27 generations and then the pattern of sexual isolation was tested involving 36 crosses. In 23 crosses sexual isolation was observed but it was asymmetrical (in only one direction). These findings in *D. ananassae* clearly indicated that sexual isolation was induced due to founder effect. Thus random genetic drift may cause the origin of reproductive isolation and thus plays an important role in speciation. It has been said that origin of reproductive isolation

is pre-requisite for speciation (Singh, 2014). Sawamura (1999) has remarked that based on biological species concept, the question how new species evolve should be substituted by a more answerable question "how reproductive isolating mechanism are established between the populations".

G. Powell (1978) provided evidence for flush-crash cycles in experimental populations of *D. pseudoobscura* in which at every crash (founder effect) bottleneck population was small and genetic drift was strong which caused the development of ethological isolation between different populations resulting from founder effect. Thus bottleneck effect/founder effect/flush crash cycles lead to the origin of ethological isolation extending evidence for the role of random genetic drift in speciation.

#### CONCLUSION

Although a large number of examples are available in natural and laboratory populations of different species demonstrating the effect of random genetic drift, some examples are mentioned in this article which clearly show that random genetic drift is an important evolutionary force which operates in small populations bringing about random fluctuation in gene frequencies and it may lead to fixation or elimination of a particular allele. It is different from other forces of evolution because it acts in non-directional fashion. The level of polymorphism decreases in population as a consequence of loss or fixation of alleles causing increase in homozygosity. There are examples available which provide evidence for speciation resulting from founder effect. The very good example of this is Hawaiian species of *Drosophila* in which speciation is explained by founder effect (see Carson, 1971).

#### REFERENCES

Buri, P. (1956). Gene frequency in small populations of mutant *Drosophila*. *Evolution*, 10, 367-402.  
Carson, H.L. (1971). Speciation and the founder principle. *Stadler Genetics Symposium*, 3, 51-70.

Dobzhansky, Th., (1951). *Genetics and the Origin of species*, Columbia University Press, New York.  
Dobzhansky, Th. & Pavlovsky, O. (1957). An experimental study of interaction between genetic drift and natural selection. *Evolution*, 11, 311-319.  
Hall, B.K. & Hallgrimsson, B. (2008). *Strickberger's Evolution*, Jones and Bartlett, Massachusetts, USA.  
Hartl, D. L. & Clark, A. G. (2007). *Principles of Population Genetics*, Sinauer Associates, Inc. Massachusetts, USA.  
Hedrick, P.W. (2005). *Genetics of Populations*, Jones and Bartlett Publishers, Boston.  
Kaneshiro, K. Y. (1976). Ethological isolation and phylogeny in the *planitibia* subgroup of Hawaiian *Drosophila*. *Evolution*, 30,740-745.  
Kerr, W. E. & Wright, S. (1954). Experimental studies of the distribution gene frequencies in very small populations of *Drosophila melanogaster*. *Evolution*, 8, 172-177.  
Kimura, M. (1983). *The Neutral Theory of Molecular Evolution*. Cambridge University Press, Cambridge.  
Mayr, E. (1942). *Systematics and the Origin of Species*. Columbia University Press, New York.  
Nanda, P. & Singh, B.N. (2011). Origin of sexual isolation in *Drosophila ananassae* due to founder effects. *Genetica*, 139, 779-787.  
Powell, J.R. (1978). The founder-flush speciation theory: an experimental approach. *Evolution*, 32, 465-474.  
Savage, J.M., (1963). *Evolution*, Holt, Rinehart and Winston, Inc., New York.  
Sawamura, K. (1999). The origin of reproductive isolation: biological mechanism of genetic incapability. In *The Biology of Biodiversity* (ed. Kato, M.), Springer Verlag, Tokyo, pp. 3-19.  
Singh, B.N. (1988). Evidence for random genetic drift in laboratory populations of *Drosophila ananassae*. *Indian Journal of Experimental Biology*, 26, 85-87.

- Singh, B.N. (1998). Population genetics of inversion polymorphism in *Drosophila ananassae*. *Indian Journal of Experimental Biology*, 36, 739-748.
- Singh, B.N. (2000). *Drosophila ananassae*- a species characterized by several unusual genetic features. *Current Science*, 78, 391-398.
- Singh, B.N. (2014). Reproductive isolating mechanisms: a prerequisite for speciation. *Journal of Experimental Zoology, India*, 17, 23-31.
- Singh, B.N. (2021). Allopatric and sympatric modes of speciation: examples from *Drosophila*. *Current Science*, 121, 201-204.
- Singh, B.N. (2022). Perspectives on modern synthetic theory of evolution, *Journal of Scientific Research (BHU)*, 66, (3), 109-116.
- Singh, P. & Singh, B.N. (2007). Population genetics of *Drosophila ananassae*: Genetic differentiation among Indian natural populations at the level of inversion polymorphism. *Genetical Research*, 89, 191-199.
- Singh, P. & Singh, B.N. (2008). Population genetics of *Drosophila ananassae*. *Genetics Research*, 90, 409-419.
- White, M.J.D. (1978). *Modes of Speciation*, W.H. Freeman and Co., San Francisco.
- Wright, S. (1931). Evolution in Mendelian populations. *Genetics*, 16, 97-159.
- Wright, S. (1951). The genetical structure of populations. *Annals of Eugenics*, 15, 323-354.

\*\*\*