

Volume 66, Issue 3, 2022

Journal of Scientific Research

of

The Banaras Hindu University



Perspectives on Modern Synthetic Theory of Evolution

B. N. Singh

Genetics Laboratory, Department of Zoology, Institute of Science, Banaras Hindu University, Varanasi- 221005, India. bashisthsingh2004@rediffmail.com, bnsingh@bhu.ac.in, bnsinghbu@gmail.com

Abstract: For the past more than a century, evolution has become a corner stone of biology. Different theories have been proposed to explain the mechanisms of evolution such as Lamarckism, Darwinism, germ plasm theory, isolation theory, mutation theory, modern synthetic theory and neutral theory. Among these theories, emphasis is mostly given on single factors. However, modern synthetic theory combines different factors into one theory, particularly natural selection and Mendelian genetics that is why the word synthetic theory is used. Presently, it is the most widely accepted theory to explain the mechanism of evolution although it owes more to Darwin than to any other evolutionary biologist and is essentially built around the concept of natural selection. However, it incorporates much that is post-Darwinian. This theory offers the most widely accepted explanation for the mechanism of evolution and is based on factors such as gene mutations, structural and numerical alterations in chromosomes, genetic recombination, natural selection, random genetic drift, migration, hybridization and reproductive isolation. Further, some recent work in the field of molecular biology have thrown light on the mechanisms of evolution. The new biology goes beyond the modern synthesis, it integrates together genomics, bioinformatics, evolutionary genetics and molecular biology to provide novel explanations, and in the light of these findings, the OMS should be modified or extended. Even there is a suggestion to propose a new theory of evolution as a coherent alternative to modern synthesis.

Index Terms: Mechanisms of evolution, theories of evolution, modern synthetic theory, different factors, H-W equilibrium, reproductive isolation, and recent molecular data.

I. INTRODUCTION

Evolution is a corner stone of biology. Theodosius Dobzhansky who integrated genetics with evolution, remarked that "Nothing in biology makes sense except in the light of evolution" (Singh, 2021). Dobzhansky has also been called Darwin of the twentieth century. The term evolution means unrolling or unfolding of events and it is based on the Latin verb "evolvere" for the noun "evolutio". In 1744, Haller, a Swiss biologist coined this term to describe the theory of progressive unfolding of structures during development. However, Haller's embryological evolution seemed to preclude Darwin's descent with modification. Thus, the term suggested by Haller was transformed into a nearly opposite meaning and with the publication of Darwin's book in 1859 the term used by Haller became available for other purposes. Thus, evolution in Darwin's days had become a common English word with a meaning quite different from Haller's technical sense. Darwin did not use the noun "evolution" to describe his theory in his book "Origin of Species" but he used the word "evolved" once in his book. Evolution entered the English language as a synonym for descent with modification through the idea of Spencer (1857), an English philosopher who popularized the word evolution and was called father of social Darwinism but he was not specialized in biology. He realized the progressive change in life forms from larva to higher forms and believed in organic change. The idea of organic evolution is not of recent origin. Essentially it appeared in Greek writings (600 BC) and occurred to many naturalists, philosophers and others but it was very vague and rather unacceptable. An interesting suggestion was given by Aristotle (384-322 BC), a well known philosopher and biologist about evolution that organisms constitute a series (ladder of life) in which they could be arranged in order of increasing complexity. For many centuries, it was believed that everything was created by God and the living world is unchangeable. However, in medieval period evolutionists like Bacon, Bonnet, Kent, Oken, and others revived the idea of evolution. Later, the contributions of Linnaeus, Buffon and Erasmus, Darwin are considered important as far as shaping the very idea of evolution is concerned.

From the beginning of nineteenth century, biologists recognized the importance of evolution and started thinking about the mechanisms and role of different factors in evolutionary changes. It was believed that the different forms of life existing on earth are the result of evolution. There was clear recognition and demonstration of the facts of evolution. To explain the mechanism of evolution, various theories were proposed by different evolutionary biologists and according to their views, different factors play a role in evolution which varies in different theories. The theories to explain the mechanism of evolution proposed by different evolutionary biologists incorporating the role of different factors are: Lamarckism, Darwinism, germ plasm theory, isolation theory, mutation theory, modern synthetic theory and neutral theory of molecular evolution. In 1900s, rediscovery of Mendel's laws, mutation theory of De Vries in 1901 and suggestion of Hardy-Weinberg law (1908) are considered important for providing genetical basis of evolution. Further, genetical basis of evolution and operation of natural selection was also provided by the leading population geneticists such as Fisher, Haldane and Wright when the discipline of population genetics was initiated in 1920s (Hall & Hallgrimsson, 2008).

A. Hardy-Weinberg equilibrium

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.

Figure 1 shows how Hardy-Weinberg Law is derived from Mendel's laws.

Sperm

Allele	Α	а	
Frequency	р	q	
р	AA P ²	Aa pq	
q	Aa pq	Aa q ²	
	Allele Frequency P q	Allele A Frequency p P P P P P P P P P P P	Allele A a Frequency p q p AA P2 Pq q Aa Aa pq Q ²

Summed frequencies in zygotes: p2 + 2pq +q2

Figure 1. Punnett square showing Hardy-Weinberg equilibrium frequencies derived from random mating with two alleles, A and a with frequencies p and q, respectively.

It is basically derived from Mendel's laws and has become a foundation of population and evolutionary genetics. 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 (panmixia), 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 Clarke (2007) and Brosco et al. (2012), in one locus two allele system, the allele frequency (A-p, a-q) gives directly the genotypic frequencies (AA, aa, Aa=(p2,q2, 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 $(p_2 + 2p_q + q_2)$ 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(s) evolution has occurred. Thus, evolution is defined as any change in the genetic composition of population. The factors which modify the Hardy-Weinberg equilibrium become important elemental forces of evolution and are important components of Modern Synthetic Theory of Evolution. Other theories of evolution lay emphasis on single factors but the modern synthetic theory integrates different factors in one theory. This theory, as a generally accepted way of approaching the problems of evolution, was born in 1937 when "Genetics and the origin of species" was published by Theodosius Dobzhansky although the term Modern Synthesis was coined by Huxley in 1942. The other evolutionists who contributed to the development of this theory were Mayr (1942), Simpson (1942) and Stebbins (1950). The restoration of Darwin's natural selection as the primary guiding factor in evolutionary change was initiated with the birth of population genetics in 1920s mainly due to the work of Chtverikov, Fisher, Haldane, Wright and others. The term Neo-Darwinism has also been used for synthetic theory of evolution (Hall & Hallgrimsson, 2008). The modern synthetic theory of evolution has been briefly described by Mayr (1963), Stebbins (1979) and Hall and Hallgrimsson (2008). Caplan (1978) has discussed the modern synthetic theory of evolution and has made an elaborate comments on it. It is well known that Darwinian evolutionary theory was characterized by the absence of an accurate understanding of genetics and of genetic mechanisms of recombination and replication. With rediscovery of Mendel's laws and rise of classical Mendelian genetics, it became possible for synthetic evolutionary theorists such as Haldane, Fisher,

Wright and Chetverikov to supplement the Darwin account of evolution with an account of basic mechanisms of generating genetic variability within population- mutations, recombination and genetic drift. The synthesis of Darwinian selection theory with classical genetics led the synthetic evolutionary theorists to construct idealized models of gene flow, fluctuations in the mechanisms of genetic variations, population size and selectional factors (Caplam, 1978). He has also mentioned that "One final comment on the content of modern synthetic theory is in order". However, Saslisbury (1971) has expressed doubts about the modern synthetic theory of evolution while citing inheritance of acquired characters by Lamarck and instant new species by mutations (De Vries) and he has also expressed problems about genetic variability acted upon by natural selection. Mayr (1996) has remarked that "It is no exaggeration to claim that the evolutionary synthesis was one of the most remarkable and successful events in the history of biological science". The Modern Synthesis (MS) is the current paradigm in evolutionary biology (Mayr, 1993 see the commentary by Pigliucci, 2007).

B. Aspects of molecular genetics, epigenetics and some other

recent work

Since the modern synthesis, a great deal of research has been done in the areas of advanced genetics and molecular biology and the results of these studies have revolutionized the study of evolution (Futuyma, 2005). After modern synthetic theory, one more theory of evolution was proposed by Kimura (1983) which is known as Neutral Theory. Kimura (1983) proposed the neutral theory to explain the mechanism of evolution at molecular level which is primarily based on random genetic drift. According to his theory, at the levels of proteins and nucleic acids most evolutionary changes are not governed by natural selection but by random fluctuation of adaptively neutral variants. However, this theory recognizes that most morphological, physiological and behavioural features of organisms evolve chiefly by the action of natural selection. Recently, modern synthesis has been discussed by certain evolutionary biologists, naturalists and philosophers and different views have been presented. Sarkar (2004, 2017) is one of the most prolific contributors on philosophy of biology and allied disciplines. He has argued that Haldane's "The causes of evolution" was the most important founding document in the emergence of an evolutionary theory which is typically referred to as the Modern Synthesis. Further, he suggested that there is conceptually no question of synthesis of biometry and Mendelism. The appropriate philosophical description of the relation of biometry and Mendelism is reduction. In Nature under the section "Comment" a question was raised "Does evolutionary theory needs rethink? Laland and colleagues commented: Yes, urgently, without an extended evolutionary framework, the theory neglects key processes. However, Wray and colleagues replied: No, all is well, theory accommodates evidence through relentless synthesis. Laland et al. (2015) suggested the concept of extended evolutionary synthesis (EES) pointing out the structure, core assumptions and novel predictions of the EES and showed how it can be deployed to stimulate and advance research in those fields which study evolutionary biology. On the other hand, Stoltzfus (2017) has explained in detail why we do not want another synthesis. He explained high level debate in evolutionary biology often treats the modern synthesis as a framework of population genetics or as an intellectual lineage with a changing distribution of beliefs. Gould (1977) concludes "The essence of Darwin lies in the claim that natural selection creates the fit and directs the course of evolutionary change. That is, the original modern synthesis (OMS) is the synthesis of genetics and Darwinism, not the synthesis of genetics and selection. Stoltzfus (2017) is of the view that OMS failed as a master theory in 1960s when the results of comparative sequencing prompted the biochemists to invoke the type of mutation-driven view which was excluded by Fisher and architects of OMS. According to molecular evolutionists, we require new rules to understand the dynamics and pattern of evolution at molecular level (King and Jukes, 1969). Kutschera and Niklas (2004) have discussed the explanation of modern synthesis touching all branches of biology and concluded that the basic tenets of the synthetic theory have survived but in a modified form. Further, they have also suggested that different sub-theories need continuous elaboration particularly in the light of findings of molecular biology to answer the questions regarding mechanisms of evolution. The new biology goes beyond the modern synthesis and it integrates together genomics, bioinformatics, evolutionary genetics and molecular biology to provide novel explanations (Rose & Oakley, 2007). Danchin et al. (2011) opine that many biologists are calling for an extended evolutionary synthesis which will modernize the modern synthesis of evolution. According to these authors, there is accumulating evidence indicating that both genetic and non-genetic inheritance and the interactions between them have important effects on the evolutionary outcomes. Muller (2017) has discussed why an extended evolutionary synthesis is necessary. The extended framework overcomes many of the limitations of traditional gene-centric explanation and entails a revised understanding of the role of natural selection in the process of evolution. The features of extended evolutionary synthesis stimulates research into new fields of evolutionary biology. The rise of molecular biology and evolutionary developmental biology, recognition of ecological development, niche construction and multiple inheritance systems, the genomics revolution, the science of biology, epigenetic inheritance among system other developments have provided a wealth of new knowledge about the factors responsible for evolutionary change (Muller, 2017). It has also been argued that gene-centric interpretations of evolution and more particularly the selfish gene expression of those interpretations form barriers to the integration of physiological science with evolutionary theory (Noble, 2011). Perez et al. (2010) have suggested that a new evolutionary theory is needed since modern synthesis lacks some major elements such as endosymbiosis, reticulate evolution, modern synthesis of embryonic development, and evolution (evo-devo), epigenetics, phenotypic plasticity, evolvability which involve several evolutionary mechanisms such as functions of genomes

and gene fragments, methylation of DNA, regulatory *cis*elements hybridization and polyploidy. It is also necessary to include different sources of genetic variability and not only mutations (Perez et al. 2010). The knowledge of these areas requires the necessity to develop a new evolutionary theory, as a coherent alternative to modern synthesis (Perez et a., 2010).

Danchin et al. (2011) in their article "Beyond DNA: integrating inclusive inheritance into an extended theory of evolution" have expressed their view that there is evidence for such effect of epigenetic, ecology and cultural inheritance as well as parental effects and they have outlined the methods which quantify the relative contributions of genetic and nongenetic heritability to the transmission of phenotypic variations across generations. These issues have implications for diverse areas including major evolutionary transitions (Danchin et al. 2011).Thus these recent work pertaining to molecular genetics, epigenetics and other areas has posed challenges to modern synthetic theory as it was proposed originally by integrating Darwinism with Mendelian genetics.

In this article, the different factors of Modern Synthetic Theory of evolution are briefly described: Mutation, recombination, natural selection, random genetic drift, migration, hybridization and reproductive isolation. Further, the perspectives of this theory are also discussed in the light of some aspects of molecular genetics, epigenetics and other recent work.

II. MUTATION

Mutations are inheritable change(s) which occur(s) in all living organisms. Mutations are primary source of genetic variability. A very good example of spontaneous mutation detected by T H Morgan in 1909 in Drosophila melanogaster was white eye which is a recessive and sex-linked mutation. Point mutations have been extensively studied in a variety of organisms starting from bacteria to humans. Mutations are generated spontaneously in natural populations but the rate of mutation may vary in different organisms as well as for different loci. Mutations may be induced also by different external factors such as X-Ray, chemicals and temperature. Thus, mutations may be spontaneous or induced. Further, mutations may be recessive or dominant, autosomal or sex linked, harmful (deleterious) or beneficial; even mutations may cause lethality. If such mutations are recessive, they may persist in populations in heterozygous conditions. Mutations may occur due to slight change in DNA molecules which are capable of replication to be inherited by succeeding generations. However, a single mutation may not have much effect but interaction of genes, pleiotropism, epistasis, and other phenomenon enhance the role of mutations in evolution because an individual is the result of interactions involving his total genotype, and every gene plays a part in the process.

Apart from point mutations, chromosome mutations also play role in increasing the level of genetic variability in populations. There are two types of chromosomal mutations: change in the number of chromosomes (aneuploidy and euploidy) and change in the structure of chromosomes (deletion, duplication, translocation and inversion). Such chromosomal aberrations have been reported in a variety of animal and plant species but they are more common in plants than animals. For example, polyploidy has played a more important role in the evolution in plants than animals and a large number of species of plants are the result of polyploidy (White, 1978). Thus, different kinds of mutations are the primary source of genetic variability in populations on which different elemental forces of evolution such as natural selection, genetic drift and migration operate and bring about the microevolutionary changes.

III. RECOMBINATION

Recombination is also considered an important source of genetic variation because it produces new combinations of already existing genes in populations. The process of mixing or recombining the available genes into a variety of genotypes becomes important in generating genetic variability in populations. There are two kinds of recombination: production of gene combinations containing in the same individual two different alleles of the same locus and formation of heterozygous individuals and the production of new combinations when homologous chromosomes pair during meiosis, known as crossing over, to generate new combination of genes. Both these processes are important in generating new genotypes thus increasing the genetic variability. Thus both the processes, mutation and recombination are important in generating raw materials for evolution but it has been suggested that recombination is the principal source because mutation alone has relatively less effect on variation without the pervasive impact of recombination (Savage 1963). Evolution is based on variation and changing gene frequencies. Mutation may modify gene frequencies and produce evolutionary change. However, recombination cannot be regarded as elemental force of evolution as it never changes allele frequencies. Basically, the effect of mutation is enhanced by recombination through the process of assembling a broad spectrum of new combinations of genes. Thus, recombination modifies and intensifies the contribution of mutation (Savage, 1963). Both these factors, mutation and recombination, develop the genetic variability which is required for evolutionary forces to operate because without the availability of genetic variability, there is no role of natural selection and random genetic drift.

IV. NATURAL SELECTION

Charles Darwin (1859) explained the mechanism of evolution in his book "On the origin of species by means of natural selection". His theory has two components: Descent with modifications-all species living and extinct descended from one or few original forms of preexisting species, and natural selection is a causative agent of evolutionary change. The total environment which includes all those kinetic forces introduced by biotic and physical factors operate as selective forces sorting out the better adapted variants to the particular environmental conditions and eliminating those variants which are not fit for survival. The original concept of natural selection proposed by Darwin was unsophisticated and applicable to individuals but not the populations. However, it definitely provided the basis of evolutionary process. The modern synthetic theory of evolution owes more to Darwin than any other evolutionary biologist and developed around the basic concept of natural selection proposed by Charles Darwin. Certainly, it includes much that is post-Darwinian. The idea of selection is based on differential mortality which may result in differential reproduction. Due to the extensive work done in the area of population genetics, it has been demonstrated that there is genetic basis of evolution and natural selection operates on genetic variability produced by mutations and recombination in the populations. Thus natural selection operates in the form of differential reproduction of genotypes in a population which brings about differential contribution of progeny to the next generation. In this way, it may be concluded that the wide varieties of mechanisms responsible for changing the reproductive success of a given genotype is collectively known as selection. The term artificial selection is also used for those situations when parents of each generation are chosen consciously by animal and plant breeders. The adaptive value or Darwinian fitness may be defined as "the relative capacity of carriers of a given genotype to transmit their genes to the gene pool of succeeding generations". The factor which acts to reduce the fitness of the genotype is known as selection coefficient. When on a particular locus, the heteozygotes show superiority over corresponding homozygotes, polymorphism is maintained and it leads to the maintenance of genetic variability in the population. This phenomenon is known as balanced polymorphism. The genotypes remain in equilibrium and superiority of heterozygotes is known as heterosis.

There are different types of selection: 1. Stabilizing selection (centripetal or normalizing), 2. Directional selection, and 3. Disruptive selection. In stabilizing selection, intermediate phenotypes are selected and extreme variants falling towards both the ends of a bell shaped curve are eliminated. It causes reduction in the level of genetic variability. In directional selection, extreme phenotypes are favoured. When experiments by plant and animal breeders are conducted for a particular trait, it comes under directional selection and genetic variability is reduced under this type of selection. Purifying selection is simply directional selection in favour of advantageous homozygous genotypes. Disruptive (diversifying) selection helps to sustain the genetic variability. Within a single generation, population may be subjected to different environments to which different genotypes are most suited. It may be closely related to frequency dependent selection. There are a large number of examples from natural populations and laboratory experiments which demonstrate the action of natural selection. Some examples are mentioned below:

- i. Industrial melanism in Biston betularia (peppered moth)
- ii. Resistance to DDT in house fly
- iii. Resistance to streptomyc in *E. coli*
- iv. Inversion polymorphism in Drosophila

- v. Competition experiments in the laboratory involving wild type and mutant types showing superiority of wild type allele.
- vi. Demonstration of balanced polymorphism involving different chromosome arrangements showing superiority of inversion heterozygotes in *Drosophila*.
- vii. Ecological niche hypothesis which states that "Inversion polymorphism in *Drosophila* is a device to cope with the diversity of environments".
- viii. North-south clines in inversion frequencies in certain species of *Drosophila* (Singh, 2013).

V. RANDOM GENETIC DRIFT

The frequency of alleles in small populations may change due to chance events arising from variable sampling of gene pool (sampling error). It was explained in detail by Sewall Wright (1931). It is known as random genetic drift or Sewall Wright Effect. It is a non-directional force of evolution. Due to the occurrence of random genetic drift, a particular allele may be fixed or eliminated. In Drosophila, the occurrence of genetic drift has been demonstrated for mutant alleles (Kerr & Wright, 1954; Buri, 1956) and chromosomal polymorphism (Carson, 1983; Singh, 1988). Dobzhansky and Pavlovsky (1957) conducted experiments in laboratory populations using different chromosome gene arrangements in the third chromosome of D. pseudoobscura keeping the frequency of one gene arrangement 50%. When the populations were maintained for several generations, variation in the frequency of chromosome arrangements was more when less number of founding individuals were used to initiate the population. On the other hand, variability in the frequency of chromosome arrangements was less when the number of founding flies was more. Thus, variability in the frequency of chromosome arrangements depended upon the number of founding individuals demonstrating the role of genetic drift in these experimental populations. The founder principle of Mayr (1942) is also based on random genetic drift. Sometimes a few individuals may migrate from the original population to a new place and may establish a new population which differs from parental population in genetic composition. Carson and others (Carson, 1971; Carson & Templeton, 1984) have explained the evolution of Hawaiian species of Drosophila on the basis of founder principle which is caused due to Sewall Wright Effect or random genetic drift. Powell (1978) has discussed founder-flush speciation theory based on experimental evidence in D. pseudoobscura. He maintained different populations of D. pseudoobscura in population cages in laboratory which were passed through flush-crash cycles. At each crash, the bottleneck population was small and genetic drift was strong. In certain populations, some degree of reproductive isolation could evolve rapidly following flush-crash cycles which demonstrated that founder-flush cycles may lead to the development of reproductive isolation. Thus the role of random genetic drift

although it is a non directional force of evolution, is of considerable importance in speciation.

VI. MIGRATION

Migration is also considered as a factor of modern synthetic theory of evolution because it may bring about changes in gene frequency. When very closely located populations having similar genetic composition exchange migrants, migration will have very little effect. Certainly, when populations are geographically distantly located and having differences in gene frequencies exchange migrants, will lead to greater consequences. The most obvious effect of migration is to make the populations homogeneous. Two factors are important for recipient population when migration occurs: the differences in gene frequencies between the populations and the proportion of migrant genes that are incorporated in every generation. Migration is also known to occur in human populations. The relationship between the two factors can be expressed mathematically (Strickberger, 1985).

VII. HYBRIDIZATION

Hybridization is known to occur in plants and animal species. It may involve different genera, species, subspecies and populations. As a consequence of hybridization, there is increase in the degree of genetic variability. It can also increase the size of gene pool with respect to genes having different adaptive values provided hybrids are fertile and can give rise to offspring in later generations. There are numerous examples of hybridization in plants and animals. It may promote the origin of new characters and variability.

VIII. GEOGRAPHICAL AND REPRODUCTIVE ISOLATION

When the populations are fragmented geographically, they undergo microevolutionary changes in the course of time and acquire genetic differences due to the action of mutation, recombination, selection, genetic drift, migration and hybridization. These differences accumulate in the population and lead to the origin and development of reproductive isolating mechanisms which are prerequisite for speciation (Singh, 1997, 2010, 2014, 2022). Finally, reproductive isolation which includes all the barrier to gene exchange between populations, has a canalizing effect. Since the richness and organizational complexity of the gene pool make possible many different responses to the same kind of environmental change, those populations which are reproductively isolated from each other are almost certain to evolve in different directions. On the other hand, those populations which are not so isolated because of gene exchange, will evolve in the same direction (Stebbins, 1979). There are different kinds of reproductive isolating mechanisms: premating and postmating/pre zygotic and post zygotic. These mechanisms prevent interbreeding between the populations even though the allpopatric populations become

sympatric due to removal of geographic barrier. Thus, isolation or prevention of interbreeding between the populations is essential for maintaining their integrity as a separate gene pool.

CONCLUSION

The Modern Synthetic Theory integrates different factors into one theory. Essentially it shows how different elemental forces of evolution contribute and play role in micro evolutionary changes in the course of time. This theory explains how genetic variability is generated in populations on which different elemental forces operate and populations undergo micro evolutionary changes in the course of time which leads to origin and development of reproductive isolating mechanisms that are considered pre-requisite for speciation. Some recent developments in the field of evolutionary biology with regard to Modern Synthesis are also mentioned particularly in the light of the findings in the field of molecular biology. Further, it is suggested that the modern synthesis may be extended or modified in the light of recent data in the field of molecular biology as it has already been suggested by many biologists who are calling for an extended evolutionary synthesis which will modernize the modern synthesis of evolution. According to these researchers, there is accumulating evidence indicating that both genetic and non-genetic inheritance and the interactions between them have important effects on the evolutionary outcomes. Further, modern synthesis is touching all branches of biology and it has been concluded that the basic tenets of the synthetic theory have survived but in a modified form. Further, it has also been suggested that different sub-theories need continuous elaboration particularly in the light of findings of molecular biology to answer the questions regarding mechanisms of evolution. The new biology goes beyond the modern synthesis and it integrates together genomics, bioinformatics, evolutionary genetics, epigenetics and molecular biology to provide novel explanations. It has been suggested that the knowledge in the areas such as endosymbiosis, reticulate evolution, modern synthesis of embryonic development, and evolution (evo-devo), epigenetics, phenotypic plasticity, evolvability which involve several evolutionary mechanisms such as functions of genomes and gene fragments, methylation of DNA, regulatory ciselements, hybridization and polyploidy and different sources of genetic variability and not only mutations requires the necessity to develop a new evolutionary theory, as a coherent alternative to modern synthesis.

ACKNOWLEDGMENT

I thank Professor J. S. Singh, Emeritus Professor, Department of Botany, BHU for his helpful suggestions during preparation of the manuscript. I also thank the anonymous reviewers for their helpful comments on the original draft of the manuscript, and Prof Rajnikant Mishra, Corresponding Editor for getting my manuscript reviewed by the experts.

References

- Brosco, F., Castro, D. & Briones, M.R.S.(2012). Neutral and stable equilibria of genetic systems and the Hardy-Weinberg principle: limitations of the chi-square test and advantages of auto-correlation functions of allele frequencies. *Frontier in Genetics*, 3, 276 (1-10).
- Buri, P. (1956). Gene frequency in small populations of mutant *Drosophila. Evolution*,10, 367-402.
- Caplan, A. (1978). Testability, disreputability, and the structure of the modern synthetic theory of evolution. *Erkenntnis*, 13, 261-278.
- Carson, H.L. (1971). Speciation and the founder principle. *Stadler Genetics Symposium*, 3, 51-70
- Carson, H.L. (1983). Chromosomal sequences and interisland colonizations in Hawaiian *Drosophila*, *Genetics*, 103, 465-482.
- Carson, H.L. & Templeton, A.R. (1984). Genetic revolution in relation to speciation phenomena: The founding of new populations. *Annual Review Ecology and Systamatics*,7, 311-346.
- Comment (2014). Does evolutionary biology theory need a rethink? *Nature*, 514, 161-164.
- Darwin, C. (1859). On the Origin of Species by Means of Natural Selection. John Murray, London.
- Danchin, E., Charmantier, A., Champagne, F. A., Mesoudi, A., Pujol, B. & Blanchet, S. (2011). Beyond DNA: integrating inclusive inheritance into an extended theory of evolution. *Nature Reviews Genetics*, 12, 475-86.
- Dobzhansky, Th. (1951). *Genetics and the Origin of Species*.ColumbiaUniversity Press, New York.
- Dobzhansky, Th. & Pavlovsky, O. (1957). An experimental study of interaction between genetic drift and natural selection. *Evolution*, 11, 311-319.
- Futuyma, D.J. (2005). *Evolution*. Sinauer Associates, Inc. Publishers, Sunderland, MA, USA.
- Gould, S. J. (1977). Ever since Darwin. W.W. Norton and Co., New York.
- Hall, B. K. & Hallgrimsson, B. (2008). *Strickberger's Evolution*, Jones and Bartlett, Massachusetts, USA.
- Hartl, D.L. & Clark, A.G. (2007). *Principle of Population Genetics*. Sunderland, Sinauer, MA, USA.
- Huxley, J.S., (1942). *Evolution, the Modern Synthesis*. Allen and Unwin, London.
- Kerr, W. E. & Wright, S. (1954). Experimental studies of the distribution of 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.
- King, J.L. & Jukes, T.H. (1969). Non-Darwinian evolution. *Science*, 164, 788-97.

- Kutschera, U. & Niklas, K.J. (2004). The modern theory of biological evolution: an expanded synthesis. *Naturwissenschaften*, 91, 255-76.
- Laland, K.N., Uller, T, Feldman, M.W., Sterelny, K., Muller, G.B., Mokzec, A., Jablonka, E. & Odling-Smee, J. (2015). The extended evolutionary synthesis: its structure, assumptions and predictions. *Proceedings of Royal Society*, B, 282, 20151019.
- Mayr, E. (1942). *Systematics and the Origin of Species*. Columbia University Press, New York.
- Mayr, E. (1963). *Animal Species and Evolution*. Belknap Press of Harvard University Press, Cambridge, Massachusetts.
- Mayr, E. (1993). What was the evolutionary synthesis? *Trends* in Ecology and Evolution, 8, 31-33.
- Mayr, E. (1996). The Modern Evolutionary Theory. *Journal of Mammology*, 77, 1-7.
- Muller, G.B. (2017). Why an extended evolutionary synthesis is necessary? *Interface Focus*, 7:2017.0015.
- Noble, D. (2011). Neo-Darwinism, the Modern Synthesis and selfish genes: are they of use in physiology? Journal of *Physiology*, 589.5, 1007-1015.
- Perez, J.E., Alfonsi, C. & Carlos, M. (2010). Towards a new evolutionary theory. *Interciencia*, 35, 862-68.
- Pigliucci, M. (2007). Do we need an extended evolutionary synthesis? *Evolution*,61, 2743-2749.
- Powell, J.R. (1078). The founder-flush speciation theory: an experimental approach. *Evolution*, 32, 465-474.
- Rose, M. R. & Oakley, T. H. (2007). The new biology: beyond the modern synthesis. *Biology Direct*, Doi:10.1186/1745-6150-2-30.
- Sarkar, S. (2004). The evolutionary theory in the 1920s: The nature of the "Synthesis". *Philosophy of Science*, 71 (5), 1215-26
- Sarkar, S. (2017). Haldane's The causes of evolution and the Modern Synthesis in evolutionary biology. *Journal of Genetics*, 96, 753-63.
- Saslisbury, F.B. (1971). Doubts about the modern synthetic theory of evolution. *The American Biology Teacher*, 33, 335-354.
- Savage, J.M. (1963). *Evolution*. Holy, Rinehart and Winston, Inc., New York.
- Simpson, G.G. (1942).*Tempo and Mode in Evolution*. Columbia University Press, New York.
- Singh, B.N. (1988). Evidence for random genetic drift in laboratory populations of *Drosophila ananassae*. Indian Journal Experimental Biology, 26, 85-87.
- Singh, B.N. (1997). Mode of mating preference and the direction of evolution in *Drosophila*. *Indian Journal of Experimental Biology*, 35, 111-119.
- Singh, B.N. (2010). The origin of reproductive isolating mechanisms is an important event in the process of speciation: evidence from *Drosophila*. In *Nature at Work:*

Ongoing Saga of Evolution (ed. Sharma, V.P.), Springer Ltd. (Int.), pp. 159-173.

- Singh, B.N. (2013). Genetic polymorphisms in *Drosophila*. *Current Sci*ence, 105, 461-469.
- Singh, B.N. (2014). Reproductive isolating mechanisms: prerequisite for speciation. *Journal of Experimental Zoology, India*,17, 23-31.
- Singh, B.N. (2021). How Theodosius Dobzhansky integrated genetics with evolution, *Current Science*, 121,201-204,
- Singh, B.N. (2022). Reproductive isolating mechanisms and speciation. *Journal of Scientific Research* (BHU), 66, 179-85.
- Spencer, H. (1857). Progress: its law and causes. *The Westminster Review*, 67, 445-447.
- Stebbins, G.L. (1950). *Variation and Evolution in Plants*. Columbia University Press, New York.
- Stebbins, G. L. (1979). *Process of Organic Evolution*. Prentice Hall of India, New Delhi, India.
- Stoltzfus, A. (2017). Why we do not want another "Synthesis". *Biology Direct*, DOI 10.1186/s 13062-017-0194-1.
- Strickberger, M.W. (1985). Genetics. McMillan, New York.
- White, M.J.D. (1978). *Modes of Speciation*, Freeman, San Francisco, USA.
- Wright, S. (1931). Evolution in Mendelian populations. *Genetics*, 16, 97-159.
