

EVOLUTIONARY BIOLOGY : CONCEPTS OF PUNCTUATED EQUILIBRIUM, CONCERTED EVOLUTION AND COEVOLUTION

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Abstract

For more than a century, evolution has become a corner stone of biology. In the middle of the last century, Ernst Mayr established Evolutionary Biology as a separate field of studies in USA. In 1744, Haller, a Swiss biologist coined the term 'Evolutio' (a Latin word for Evolution) which means to unroll or unfold. It was used to describe the progressive unfolding of structures during development. In the middle of nineteenth century, Herbert Spencer, an English Philosopher popularized the word Evolution. He has also been called as Father of Social Darwinism. His idea about evolution was influenced by both Lamarckism and Darwinism. From time to time, various theories have been proposed to explain the mechanisms of evolution. These theories are: Lamarckism, Darwinism, theory of germplasm, isolation theory, mutation theory, synthetic theory and neutral theory. These theories except synthetic theory explain the mechanisms of evolution by giving more emphasis on single factor. However, the modern synthetic theory which was developed by the contributions of many evolutionary biologists, combines many factors in one theory and is widely accepted theory of evolution. There exists controversy between neutralists vs. selectionists. Further, Lamarckism (theory of inheritance of acquired characters) has been rejected and is of only historical significance. In the last century, a few new concepts of evolutionary biology were proposed by evolutionary biologists. These concepts are punctuated equilibrium, concerted evolution and coevolution which are of considerable evolutionary significance and are briefly described in this article.

Keywords: Evolutionary biology, punctuated equilibrium, concerted evolution, coevolution.

The term evolution is based on Latin verb 'evolvere' for the noun 'evolutio' which means to unroll or unfold. It was coined in 1744 as a biological term by Swiss biologist Arbrecht von Haller to describe the theory of progressive unfolding of structures during development-embryos grow from preformed homunculi in the egg or sperm and simply increases in size during its embryonic development. However, Haller's embryological evolution seemed to preclude Darwin's descent with modification. Thus Haller's term 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 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 Herbert Spencer (1857), an English philosopher who has been called as father of social Darwinism and not specialist in biology. He also popularized the word evolution in the sense of progress of life from larva to higher forms and also as a description of organic change.

Herbert Spencer (1852) was an enthusiastic exponent of evolution and he wrote about evolution before Darwin did. He developed the concept of evolution as progressive development of the physical world, biological organisms, human mind, and human culture and societies. He is best known for coining the expression of the survival of the fittest after reading the book of Darwin. This term strongly suggests natural selection. He also used Lamarckism while explaining evolution in the sense of society and ethics. He also believed in Lamarckism and suggested that the primary mechanism of species transformation that he recognized was based on Lamarckism. The organs are developed or diminished by use or disuse and the resulting changes may be transmitted to future generations. His influence sharply declined during the last part of the nineteenth century.

Theories have been proposed from time to time to explain the mechanisms of evolution by evolutionary biologists. In middle of the twentieth century, Ernst Mayr in U.S.A. established evolutionary biology as a separate field of study (Singh, 2012a). Dobzhansky integrated genetics with evolution and established the new field as evolutionary genetics and the basis for this integration was provided in his book "Genetics and the origin of species" which was published in 1937. The modern synthetic theory as a generally accepted way of approaching the problems of evolution was born with the publication of Dobzhansky's book in 1937 although the modern synthetic theory was proposed by Julian Huxley in 1942. Further, Mayr and Dobzhansky contributed significantly in the development of biological species concept which was initiated by the contributions of naturalists and taxonomists of nineteenth century (Singh, 2012b).

The theories which have been suggested from time to time by evolutionary biologists to explain the mechanisms of evolution are: Lamarckism (theory of inheritance of acquired characters), Darwinism (theory of natural selection), germ plasm theory, isolation theory, mutation theory, modern synthetic theory and neutral theory of molecular evolution. The theory proposed by Lamarck in 1809 which is known as theory of inheritance of acquired character or use and disuse, has not been accepted and is of historical significance. The natural selection theory of Darwin (1859) is really an important theory of evolution but it has a demerit that it could not explain the cause of variations on which natural selection operates and brings about evolutionary changes. Natural selection suggested by Darwin as an important factor of evolution is also an important component of modern synthetic theory of evolution which combines different factors into one hypothesis. These factors are: mutations, natural selection, random genetic drift, migration and reproductive isolation which is a prerequisite for speciation (Singh, 2010). The modern synthetic theory is most widely accepted theory of evolution. In 1968, Kimura proposed the neutral theory of

molecular evolution which is also known as neutral mutations and random drift hypothesis because it concerns mutations that are nearly selectively neutral in their effect and their fate is largely determined by random genetic drift. Still the controversy exists between selectionists and neutralists. Evidences are there to explain the evolutionary changes at molecular level through natural selection (Singh, 2013).

In previous century, two important theories, synthetic theory and neutral theory were suggested to explain the mechanisms of evolution. In spite of these theories of evolution, three new concepts in the area of evolutionary biology were also suggested in the previous century. These concepts are: punctuated equilibrium, concerted evolution and co-evolution which are of considerable importance. Out of these three concepts, punctuated equilibrium is considered to be controversial because of certain criticisms. All these concepts are briefly described in this article.

Punctuated equilibrium

In 1972, palaeontologists, Eldredge and Gould suggested the concept of punctuated equilibrium which was elaborated by Gould and Eldredge in 1977 and by Stanley in 1979. According to this concept, biological evolution takes place in terms of intermittent bursts of activity separating relatively long period of stasis and was proposed as a criticism of traditional theory of evolution explained by Darwin' theory of gradualism . Thus the punctuated equilibrium concept explains the mechanism of evolution in the opposite of gradualism. Evolution of a lineage follows a pattern of long intervals during which there is a relatively little change (stasis or equilibrium) punctuated by short bursts of speciation and macroevolutionary events in which new taxa arise. This concept was primarily based on fossil records because some of the fossil data for vertebrates, molluscs and other animals show such periodic bursts of evolutionary activity. There is a long period of fossil uniformity of populations punctuated by geologically short periods of rapid evolution (Strickberger, 2000). However, it has been argued that because fossil records have gaps, punctuated equilibrium is only apparent and not real. What seems rapid in geological time scale involves thousands of generations during the period of change. Thus, under this concept evolution seems to be characterized by long period of stasis (standstill or equilibrium) punctuated by episodes of very fast development of new morphological types (species) instead of slow continuous movement. The punctuated equilibrium theory of Eldredge and Gould is based on three important factors of fossil records:

- (i) Extreme rarity of transitional forms (missing links)
- (ii) Stasis or equilibrium as the most prominent feature of the fossil record
- (iii) Sudden appearance of new species

During the sudden appearance of new species, the basic mechanism of speciation was borrowed from others particularly, the geographic speciation (or allopatric mode of speciation) suggested by Mayr (1942, 1963) as a mechanism of evolutionary change.

Phillips (2006) suggested that there is genetic evidence in favour of punctuated equilibrium on the basis of analysis of phylogenetic trees generated from genetic sequences of closely related organisms. On the basis of number of speciation events and nucleotide differences between species in each tree and statistical test, he has shown that there is strongly significant evidence supporting the idea of punctuated equilibrium in 30-35% of phylogenetic trees which were observed. Kimura (1983) suggested that there may be long period of stabilizing selection interspersed with periods of rapid directional selection to track environmental changes which is consistent with the concept of punctuated equilibrium of Eldredge and Gould (1972). Thus the gap may be filled between the mode of evolution at the morphological level and that at molecular level by arguing a preponderance of stabilizing selection at the phenotypic level and a very large number of nucleotide sites involved at the molecular level (Kimura, 1983). The theory of punctuated equilibrium is based on two components: a pattern and a process that explains the pattern (Freeman and Herron, 1998). The sudden appearance of new morphospecies is the most prominent pattern in the history of life. Even Charles Darwin was aware of this fact and it was a problem for his theory of gradual evolution (Kimura, 1983). Rapid morphological changes occur during the creation of new species which is followed by long period of stasis or no change in a particular lineage which results in the occurrence of majority of evolutionary changes during speciation events. This pattern results from the process of peripatric speciation which is a type of allopatric speciation characterized by random genetic drift as suggested by Mayr (1942, 1963). Interestingly, punctuated equilibrium theory is supported by the neutral theory of molecular evolution proposed by Kimura (1983) who suggested that changes at molecular level is influenced by random genetic drift.

Thus there are evidences in favour of the theory of punctuated equilibrium suggested by Eldredge and Gould in 1972. This theory was also strongly emphasized by them in their later publications. They wrote a review article in 1993 entitled "Punctuated Equilibrium: Come of Age" which was published in *Nature* in which they have written that punctuated equilibrium has been accepted by most of their colleagues as a valuable addition to evolutionary theory and many palaeontologists also support this concept. In response to their review, questions have also been asked "Is evolution by punctuated equilibrium a biological absurdity?" Even the opponents of this concept seem to have accepted the concept of stasis and even a brief period of rapid change but they reject the anti-neo-Darwinian concept on non-adaptive, random origin of new species and species selection as the mode of macroevolution (Batten, 1994). According to Saylo *et al.* (2011), both phyletic gradualism and punctuated equilibrium are speciation theory and are valid models for understanding macroevolution. Both evolutionary patterns have played at least some role in the evolution of life. Mayr (1992) has raised some basic questions about punctuationism and comments that this theory makes two basic claims: most evolutionary changes occur during speciation events and that most species usually enter a phase of stasis after the end of speciation

process. According to Mayr (1992), these two claims are to some extent two separate theories. After the proposal of this theory, the controversy revealed that there are considerable conceptual and evidential difficulties in either substantiating or refuting this theory (Mayr, 1992). Gould and Eldredge have done palaeontology a great service by giving the real data of fossil study, that is stasis and abrupt speciation events, theoretical breathing space. We can only hope that there will be similar frankness amongst evolutionary biologists about the lack of any observed biological mechanism for producing appearance of new species (Batten, 1994). Gould and Eldredge (1993) have mentioned that punctuated equilibrium comes of age while emphasizing that intense controversies surrounded the youth of punctuated equilibrium have helped it to mature it as useful extension of evolutionary theory. Although it has been severely criticized by evolutionary biologists because: (i) populations can evolve without speciation, (ii) stable lineages in fossil records not absolutely static, (iii) fossil sequences incomplete, and (iv) evolution of populations by natural selection (Futuyma, 1998), the concept of punctuated equilibrium is important and interesting contribution to the field of evolutionary biology as it has received support from palaeontology, genetics, peripatric speciation and neutral theory of molecular evolution.

Concerted evolution

All genomes particularly of higher species are complex. Multigene families are formed due to increase in the number of genes through duplication and such genes are homologous with related functions. Examples of such genes are r-RNA and histone genes which are often arrayed in tandem along the chromosome. After duplication, the genes may retain similar function or may diverge (Hartl and Clark, 2007). There is enough evidence that members of gene families evolve in a non-independent or concerted manner. The concerted evolution has been defined as:

“Individual repeat units of DNA sequences which are present in multiple copies in the genome are often found to be more similar within a species or population than they are between species or population. This pattern implies non-independence and referred to as concerted evolution” (Majerus *et al.* 1996).

“The process by which a series of nucleotide sequences or different members of a gene family remain similar or identical through time” (Strickberger, 2000).

“Concerted evolution essentially means that an individual member of a gene family does not evolve independently of other members of the family. Rather, repeats in a family exchange sequence information with each other either reciprocally or non-reciprocally, so that a high degree of intrafamilial sequence homogeneity is maintained” (Graur and Li, 2000).

“Maintenance of a homogeneous nucleotide sequence among the members of a gene family, which evolves over a time” (Futuyma, 2005).

“Genes A1 and B1 of one species as well as A2 and B2 of other species may have more similar sequences because the genes of one species evolve together, in

concert, under the influence of mechanisms that operate to homogenize their sequences through such processes as gene conversion and unequal crossing-over. This tendency towards homogenization is known as concerted evolution” (Hartl and Clark, 2007).

The definition of concerted evolution provided by different authors differ to some extent but the essence of all definitions remains similar in the sense that the members of the same gene family evolve in a non-independent or concerted manner. It is an interesting topic of molecular evolutionary genetics. Concerted evolution is a universal biological phenomenon. Most repetitive gene families thus far investigated in species ranging from bacteria to mammals undergo concerted evolution (Liao, 1999). The foundation of this concept was laid down by the work of Brown *et al.* (1972) in which they made comparison of ribosomal RNA genes from the two species of *Xenopus*. In *Xenopus* and many other vertebrates, the genes specifying 18S and 28S ribosomal RNA are present in hundreds of copies and are arrayed in one or a few tandem arrays (Pardue, 1974; Long and David, 1980). The transcribed repeats are separated from each other by a non-transcribed spacer (NTS). Brown *et al.* (1972) reported an interesting observation that 18S and 28S genes of the two species of *Xenopus* are identical but the NTS regions differ greatly between the two species. However, the NTS regions are very much similar in all the individuals of the same species. They concluded that NTS regions have evolved together but they have diverged rapidly between the species. Concerning this phenomenon of molecular evolutionary genetics, different terms were used such as horizontal evolution, sequence coevolution and coincidental evolution. The term concerted evolution was coined for the first time by Zimmer *et al.* (1980) and is most commonly used in literature. Dover (1982) also extended evidence for this phenomenon by suggesting a term molecular drive to describe the evolutionary processes that change the genetic composition of a population through DNA turnover mechanisms which operate independently of natural selection and random genetic drift. The best known such process is the concerted evolution of genes present in many tandem copies such as those of ribosomal RNAs. The concept has been proposed to extend to the diversification of multigene families (Dover, 1986). The concept of concerted evolution was developed due to the main work of Brown *et al.*, Zimmer *et al.* and Dover. Since then numerous studies on this topic have been published which lend support to the concept of concerted evolution. A large body of data has proved the generality of this phenomenon in multigene families (Ohta, 1980; Elder and Turner, 1995; Ganley and Kobayashi, 2007; Morris-Pocock *et al.*, 2010). Although it is an important biological phenomenon in evolutionary context at molecular level, concerted evolution does not homogenize all multigene families. Depending upon the balance of forces of mutation, gene conversion and unequal crossing-over, the pair of genes may remain active and very similar or these genes may diverge functionally or one gene may lose its function and may become a pseudogene (Hartl and Clark, 2007). Basically there are two important mechanisms of concerted evolution: unequal crossing over and gene conversion which is followed by fixation of

a homogenized array by the operation of selection or random genetic drift. During gene conversion which is a nonreciprocal recombination process, two sequences interact in such a manner that one is converted by the other. Unequal crossing over is a reciprocal recombination process that creates a sequence duplication in one chromosome or chromatid and a corresponding deletion in the other. This may occur either between two homologous chromosomes at meiosis or between the two sister chromatids of a chromosome during mitosis in germ cell. The most important evolutionary significance of concerted evolution is suggested for the striking cases of gene families such as those encoding histones and ribosomal RNA in which a large amount of gene product are required (Futuyma, 1998).

Coevolution

The term coevolution was originally coined by Charles Mode in 1958 while giving the main emphasis on the development of mathematical models for understanding the mechanisms of continuous evolution of host and parasite to the evolutionary change in other. In 1964, this concept of coevolution was given more emphasis in ecological context by Paul Ehrlich and Peter Raven. In biology, coevolution is the change of a biological object triggered by the change of a related object (Yip *et al.*, 2008) and it can occur at various biological levels. There is evidence for coevolution at the level of populations and species. The concept of coevolution was briefly described by Charles Darwin in *Origin of species* and developed in detail in *Fertilization of Orchids* (Darwin, 1859, 1877; Thompson, 1994). In a coevolutionary relationship, each species exerts selective pressure on the other by which affecting each other evolution. Coevolution of different species includes the evolution of a host and its parasites (host-parasite coevolution) and cases of mutualism evolving through time. Pair-wise coevolution exists such as predator and prey, host and symbiont or host and parasite. Coevolution may also be responsible for genetic diversity exhibited in normal populations including blood plasma polymorphism, protein polymorphism, histocompatibility systems etc. (Anderson and May, 1982). Although coevolution is a primarily biological concept, by analogy it has been applied to other fields such as computer science, sociology, astronomy and International political economy (Jessop, 2004). To explain this phenomenon of coevolution, various examples have been given and also different types have been described (Thompson, 1989, 1994, 2005; Futuyma, 1998, 2005; Yip *et al.*, 2008; Hall and Hallgrímsson, 2008). The specific interesting examples are: Hummingbirds ornithophilous flowers, agraecoid orchids and African moths, old world swallowtail and fringed rue, garter snake and rough-skinned newt, California buckeye and pollinators, acasia ant and bullhorn acacia tree and yucca moth and the yucca plant.

Coevolution may occur in any interaction involving different species:

- (i) interspecific competition for food or space
- (ii) parasite/host interactions

- (iii) predatory/prey interactions
- (iv) symbiosis
- (v) mutualisms

Biological factors stimulate mutual evolutionary responses and foster diversity of adaptations. In response to biological factors, organisms tend to diversify. Coevolution refers to reciprocal evolution between interacting populations. Ehrlich and Raven (1964) emphasized the empirical patterns after their observation that closely related butterflies tend to feed on closely related species of tropical vines which provides evidence for a long evolutionary history together. During coevolution the butterflies developed abilities to tolerate the specific chemical defenses of their hosts. Some times coevolution may reveal genotype-genotype interactions. Population may contain genetic variations for specific traits that influence the interaction between two populations. An interesting example showing this phenomenon is provided by coevolution between wheat and wheat pathogens (telomycetid fungi causing rusts) in which genotype-genotype interactions affecting fitness of host and pathogen has been observed. It is likely that viruses and their hosts may have coevolved in various scenarios. Interactions between species that benefit each other is known as mutualism. It can also lead to coevolution for example, lichens, partnership between algae and fungi.

Coevolution may be of different types: specific coevolution, guild coevolution or diffuse coevolution and escape and radiate coevolution.

In specific coevolution, one species interacts closely with another and changes in one species induces adaptive changes in the other and vice-versa. During adaptation there may be involvement of polygenes or gene for gene interaction. It may also lead to cospeciation. In some cases which may be regarded as true coevolution, speciation in one lineage (a parasite) induces speciation in the other (host). In guild or diffuse or multispecies coevolution, whole groups of species interact with other groups of species leading to changes which can not really be identified as specific examples of pairwise coevolution between two species. Examples are available in a group of plant species and a family of insects (hosts and parasites). In escape and radiate coevolution which was proposed by Thompson (1989), a plant species which is host to diverse herbivorous insects, evolves a new defense to get rid of most of its enemies. This evolving escape from most herbivores enable the host species to diversify into numerous species that share the novel defense evolved. At later stage, one or more species of herbivorous insects become adapted to one or more species of these plants which gives rise to clades of specialized species associated with various of the species in the diverse clade of plants. A similar hypothesis could apply to other groups of parasites (or mutualism) and their hosts (Futuyma, 1998). It is known that evolutionary changes in one species may induce evolutionary changes in other species with which it is interacting ecologically. There is palaeontological evidence suggesting competition between herbivorous and carnivorous mammals during which size and speed seemed to increase

sequentially in members of both the groups (Hall and Hallgrímsson, 2008). A very good example showing the involvement of genes in coevolution is provided by Thompson (2005) who has shown that 27 genes in the flax plant confer resistance against a fungal rust pathogen which in turn has similar number of genes allowing it to overcome resistance these host genes confer (Hall and Hallgrímsson, 2008). Thus, coevolution has occurred in many cases but some times it may be complex. In this phenomenon, genetics, ecology and phylogeny interact and diversity of life and life forms is not just due to adaptation to static environments, biotic interactions are much more important.

Conclusion

During the last century, two important theories to explain the mechanisms of evolution were proposed. (i) modern synthetic theory by Huxley (1942) for which the basis was provided by Dobzhansky (1937) in his book “Genetics and the origin of species” which incorporates various topics integrating genetics and evolution and in this theory also natural selection is an important guiding force of evolution and (ii) Neutral theory of molecular evolution proposed by Kimura (1968) which is based on neutral mutations and random genetic drift. The controversy between selectionists and neutralists still exists. However, three new concepts of evolutionary biology also emerged during more or less same period which are considered important. These are: coevolution, punctuated equilibrium and concerted evolution.

In coevolution each species exerts selective pressure on the other by which affecting each other evolution. Coevolution of different species includes the evolution of a host and its parasites (host-parasite coevolution) and cases of mutualism evolving through time. Pair-wise coevolution exists such as predator and prey, host and symbiont or host and parasite. There are numerous examples demonstrating this phenomenon which also involves the role of genetic factors. Punctuated equilibrium suggested by two palaeontologists to explain the mechanism of evolution is opposite to gradualism. Although this concept is considered as controversial due to several criticisms, it has received support from palaeontology, genetics, peripatric speciation and neutral theory of molecular evolution. Concerted evolution means the members of the same gene family evolve in a non-independent or concerted manner. It is an interesting topic of molecular evolutionary genetics and is a universal biological phenomenon. A large body of data has proved the generality of this phenomenon in multigene families. Most repetitive gene families thus far investigated in species ranging from bacteria to mammals undergo concerted evolution Basically there are two important mechanisms of concerted evolution: unequal crossing over and gene conversion which is followed by fixation of a homogenized array by the operation of selection or random genetic drift. It has been suggested that concerted evolution has evolutionary significance because there are striking cases of gene families in which a large amount of gene product is required. Although it is an important biological phenomenon in evolutionary context at molecular level, concerted evolution does not homogenize all multigene families.

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