Indira Gandhi
National Open University
School of Sciences

BZYCT-137
GENETICS AND EVOLUTIONARY BIOLOGY

Block

4

SPECIATION AND SPECIES EXTINCTION

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BLOCK 4: SPECIATION AND SPECIES EXTINCTION

In Block 3 you have learnt the basic principles underlying the evolutionary phenomenon. We outlined the origin of life, history of the evolutionary thought, listed the evidence in favor of the occurrence of evolution and discussed the significance of the natural selection as a process in bringing about the evolutionary change.

In this block you will study the role of natural selection in formation of a species. With the major evolutionary events, there is existence of multiple life forms at present. These life forms are categorized as “species”.

In Unit 14, you will study the important concept of species and mode of speciation. Species is a basic taxonomic unit of biological classification. Also, it is considered as a basic unit of evolution. There are a dozen of species concepts discussed in the unit. However, the most accepted species concept is the one given by Mayr in 1969 which states that species is a group of interbreeding natural population that is reproductively isolated from other such groups. After introducing you to the concept of species the unit describes the artificial, allopatric and sympatric modes of speciation.

You already read about process of natural selection as the major event of evolutionary change. In the Unit 15, you will learn that apart from the natural selection, genetic drift, gene flow and mutation also play vital role in the evolution of species. Thus, allele frequencies in a population may change due to four fundamental forces of evolution: Natural Selection, Genetic Drift, Mutations and Gene Flow.

You will learn about the three important factors governing evolution are **Isolation**, **Adaptation** and **Variation**. Isolation is a kind of physical or environmental barrier that prevents promiscuous breeding. It may be called as a phenomenon due to which a single population of a species gets divided into two or more subpopulations or groups without interbreeding between them through some internal or external factors. Thus, isolation is simply the prevention of gene flow and is a major cause of speciation. The isolating mechanisms are further classified as pre-mating and post-mating isolating mechanisms.

Other major concept discussed in this unit is genetic drift. Usually in a large population the process of Natural selection predominates whereas genetic drift does so in smaller population. The process of genetic drift involves the migration of some individuals from a population and merging into different population of same genus, this eventually leads to a change in the population genotype.

You will also learn that mutations are the ultimate source of new alleles in a gene pool.

Since the origin of life there is an increase in the biodiversity on the Earth, however, it has not been steady and characterized by the fast pace of speciation being followed by periods of negligible change and then episodes of mass extinction.

In Unit 16, you will learn that extinction is actually a very common feature throughout the existence of life on earth when viewed over geological timescales. The concept of extinction was first proposed by Georges Cuvier. Extinction is one of the most common of all ecological/evolutionary processes and information on extinction can be obtained from many sources, including laboratory experiments, field studies and the fossil records. You will be acquainted with the fact that extinction includes the loss of a taxon and the environment associated with it.

You will be introduced to the concept of Mass extinction which occurs due to rapid environmental changes and exposure to harsh conditions during a short period of time where species do not have sufficient time to adapt to the changes. There have been five major mass extinctions in the past which you will study in detail in this unit.

Objectives

After studying this block you should be able to:

- describe the importance of species concept, different definition of species and mode of speciation,
- discuss the role of natural selection evolution among the members of a species with specific examples,
- comprehend the different isolating mechanisms, the role they played in rising of a species and the concept of genetic drift, and
- describe the big five mass extinction events in history.

UNIT 14

EVOLUTIONARY CHANGE, SPECIES CONCEPT AND SPECIATION-I

Structure

14.1 INTRODUCTION

In the present unit you will deal with the concept of species and speciation together with its mechanisms. In the previous unit you have studied the process of evolutionary changes that have led to genetic repatterning during isolation and caused premating and postmating isolation and genetic drift as well. A species is defined as a group of similar individuals that are interbreeding in nature. The species is the principal natural taxonomic unit, ranking below a genus and denoted by a Latin binomial nomenclature e.g. *Homo sapiens*. Where *Homo is genus* and *sapiens* represents species (Fig. 14.1).

In biological science species is a smallest independently dynamic evolving basic unit of biological classification and a taxonomic rank. A species is often defined as the largest group of organisms in which two individuals can produce fertile offspring, typically by sexual reproduction.

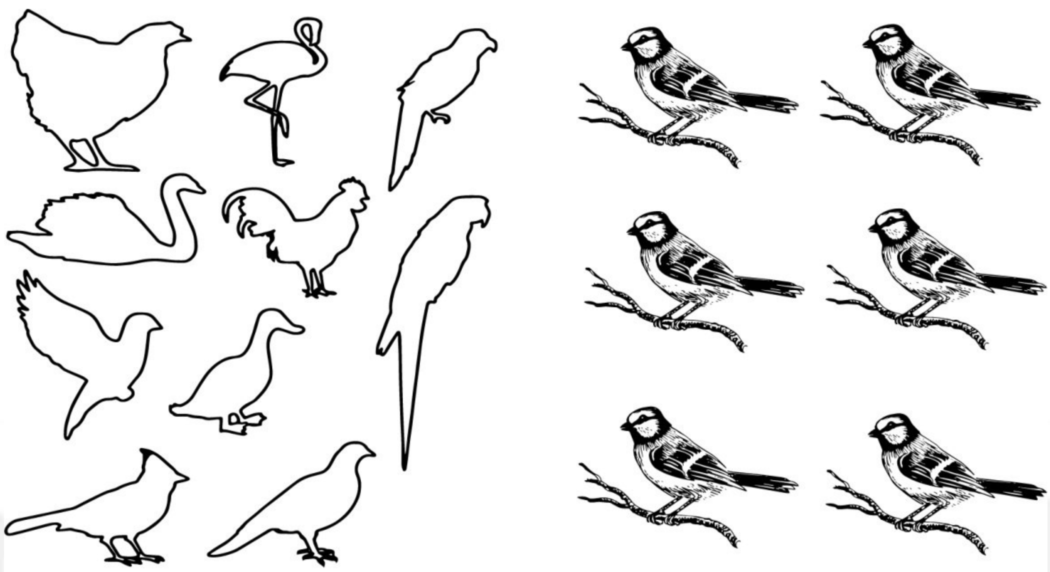


Fig. 14.1: Diversified species are reproductively isolated.

Objectives

After having read this unit you should be able to:

- ❖ define various species concepts, their merits and demerits,
- ❖ explain biological species concept-most acceptable species concept, and
- ❖ discuss mechanism of speciation.

14.2 IMPORTANCE OF A SPECIES CONCEPT

1. Species is a basic taxonomic unit of biological classification. The species should be able to recognize all types of living things existing in nature that participate in evolution. Mayr and Ashlock (1991) stated that one cannot explain the evolutionary process and trend as well as most aspects of philosophy of biology without understanding the meaning of species.

2. It is a fundamental unit used for comparison in all the fields of biology from systematic to taxonomy, anatomy, ecology, evolutionary biology, genetics, molecular biology, physiology and paleontology (De Queiroz,

2005). Most of the ecological, taxonomic, systematic, physiological, biochemical as well as other studies on animals are conducted at species level.

3. The species concept is extremely important to understand and estimate the biodiversity as well as to understand the flow of gene within a population.

4. The species is considered as a unit of evolution, so species is the primary unit of biogeography, selection, adaptation, speciation, etc.

14.3 DEFINING SPECIES: A MAJOR PROBLEM

Defining a species is one of most difficult task for a taxonomist (Garnett and Christidis, 2007). Even after a thousand of years, the concept of species remains central to biology but yet remained at times ill defined and controversial. The main purpose of defining a species is to make it a historical, temporal and spatial entity (Mayr and Ashlokc, 1991). From time to time various definitions have been proposed by a number of workers but still the uncertainty exists. A number of concepts were proposed by various taxonomists from time to time to define a species. A review of some of the important species concepts in the history of defining a species are presented below.

14.3.1 Nominalistic Species

The Nominalistic species concept was proposed by Occam and practised by his followers. According to this theory nature can produce individuals and nothing more. Later on one of his followers, Bassey (1908) stated that "Species" has no actual existence in nature and this is a mental concept of human mind and nothing more than that. The name species refers to a great number of individuals collectively existing in nature.

14.3.2 Typological/Morphological/Essentialist Species (Linneaus, 1751)

This concept is actually a philosophy of Plato and was extended by Linneaus (1751) and his followers to define a species. The concept says that a group of individuals that differ from other such groups by possession of constant diagnostic (morphological) characters. According to this theory (i) all the members of a species should exhibit the same morpholocial characters (essence) and due to this reason the concept is also known as essentialistic species concept (ii) each species group is separated from all other such groups by a sharp discontinuity (iii) the species remain completely constant through the time and (iv) there are strict limitations on the possible variation within the species. The species named in this manner are called Morphospecies.

This concept has been universally rejected due to following reasons. (i) If this concept is followed, each variant of a species will be called a different species. Different phena that belong to a particular population cannot be regarded as single species. If a particular species consists of two phena, male and female shall be considered as two different species. Similarly a four winged *Drosophila* born to a two winged mother shall be considered as different species (ii) according to this concept there is no space for intra-population variation due to individual genetic variations, sexual dimorphism and different stages (eg. Caterpillars, pupa, adult) in the life history (iii) all the sibling species, which are reproductively isolated from one another has to be considered as a single species because of morphological similarity, but the individuals of the same species with a longer or shorter tail shall be considered as different species.

This concept is still defended by some taxonomists. When there is lack of biological information at the initial stage of recognizing a species, a taxonomist has no other option than to describe it on the basis of available or observed morphological characters. However, such species are subject to correction at the later stage when more biological information about the species is available and evaluation of intra-population variation has been done properly.

14.3.3 Phenetic Species (Sneath and Sokal, 1973)

The phenetic concept is upgraded, modified and numerical presentation of Typological species concept based upon morphological characters and can be defined as populations distinguished by discrete clusters of phenotypic characters. It may be defined loosely as set of organisms that cluster at a certain distance from other such clusters. This concept has its basis in numerical taxonomy. All the morphological characters are evaluated quantitatively, analyzed statistically and recorded for classifying species. So, the species are defined on the basis of overall statistically measured and evaluated morphological characters. More simply, this approach specifies some exact degree of phonetic similarity in a population and is measured by phenetic distance statistics. A species is then a group or set of organisms which is “X” times phenotypically different or distant from such other groups. A population is defined as a species by a cluster of phonetic characters sufficiently different so that it can be differentiated from such other populations.

There are some problems with this concept also. (i) It lacks a sound theoretical basis which may lead to subjective and arbitrary decisions, (ii) Neo-Darwinians have dismissed this concept because there is no reason to suppose that any ideal pattern of morphological type exists in nature, (iii) The phenetic species will require a modified definition if it undergoes a significant evolutionary change without speciation.

14.3.4 Recognition Species (Paterson, 1985)

The concept states that species have a specific mate recognition system. According to this concept the species can be defined as a population sharing common fertilization system in which the individuals recognize one another as their potential mate. The mate recognition system includes compatibility between reproductive organs and gametes (sperm and egg), courtship behavior, common reproductive timings and various reproductive events, utility of different signals like use of sex pheromones in attracting opposite sex for mating etc. The recognition concept is different from biological species concept (reproductive isolation) in that individuals of a population look for a successful mating attempt. For example, even if the frogs are prevented from mating due to the presence of a barrier, they will recognize each other as their potential mate and this makes them to be recognized as the same species under recognition species concept.

The problems with this concept are (i) the concept connot be applied on asexual species, (ii) it cannot be applied on fossils, (iii) it is difficult to know whether geographically isolated populations can potentially interbreed or not (iv) the concept fails when species fail to recognize their own mate or mate with other species leading to hybridization.

14.3.5 Cohesion Species (Templeton, 1989)

This concept can be considered as a modified or upgraded recognition concept and is closer to Biological species concept. Cohesion species are most inclusive population of individuals with potential for phenotypic cohesion through intrinsic cohesion mechanism. According to this concept the species can be defined as "The most inclusive group of organisms having the potential for genetic and/or demographic exchangeability". The genetic exchangeability limits the spread of new genotype through gene flow and is intimately linked to pre-mating and pre-zygotic barriers to sexual barriers because two groups of organisms are genetically exchangeable if the gene flow is free between the representatives of two groups. Demographic exchangeability refers to those factors that define the fundamental ecological niche of each entity. The cohesion species concept therefore defines species as an evolutionary lineage and classify them through the mechanism that limits the boundary of population under micro-evolutionary forces like gene flow, genetic drift and natural selection. If a mutation occurs within a population, it will be either fixed or discarded because genetic drift and natural selection determine the fate of a mutation. So, Cohesion species concept recognizes two sets of micro-evolutionary forces whereas Biological species concept recognizes only one (gene flow).

Problems with Cohesion species concept are (i) the concept emphasizes the presence of gene flow but cannot distinguish the internal and external barriers to gene flow, (ii) it emphasizes cohesion through gene flow and at the same time claims its applicability to species reproducing asexually where there is no gene flow, (iii) It defines the species as evolutionary lineage but fail to explain how to delimit the open ended lineage (iv) It does not specify which kind of gene flow affects genetic exchangeability.

14.3.6 Phylogenetic Species (Cracraft, 1983)

There are several versions of this concept. It essentially delineates species as a group of organism by a unique ancestry. According to this concept species can be defined as "a smallest diagnosable monophyletic group of populations within which there is a parental pattern of ancestry and descents". So, a diagnosable geographic form of the same basic kind of bird shall be recognized as a distinct species, because other forms have evolved separately and have unique evolutionary histories. For example, a population of mynas exhibiting a unique heritable character would be considered as a separate species from those in which this particular character is missing or absent. This concept attempts to define species on the basis of their relationship to other species and involve uncovering their genealogical relationship. The concept is applicable also to those species which do not reproduce sexually.

Problems with phylogenetic concept are (i) it is just another form of morphological species concept, (ii) connot explain which character or characters should be taken into consideration while delineating a species, (iii) it cannot explain at what level of divergence a species is constituted, (iv) In uniparental species in which there is no or little gene exchange, each clone with a mutation have to be designated as a different species.

14.3.7 Ecological Species (Van Valen, 1976)

Ecological species concept is a concept of species in which a species is a set of organisms adapted to a particular set of resources called a niche (adaptive zone) in the environment. Coninvaux (1986) explained the ecological species as “A number of related populations, the members of which compete more with their own kind than with the members of other species”. The ecosystem tends to remove the overlapping species to avoid competition between them so that no two species occupy a single niche. The concept suppose that ecological niche in nature are discrete zones with gaps between them. This concept draws support from “two or more species cannot occupy the same”. Either one will be better and beat out the other in competition or a drift in the relative population size will eventually eliminate one of them. In character displacement, similar species that share a common niche will diverge from one another and this will effectively divide the shared niche and reduces competition. This concept emphasizes that selection for efficient niche utilization is the primary cause that leads to speciation.

Problems with Ecological species concept are (i) it denies the existence of cryptic species, (ii) prevalence of niche is assumed theoretically and not well defined, (iii) a number of species have local populations which occupy different niche, but according to this concept all such population have to be recognized as different species, (iv) according to this concept all sympatric species which occupy the same niche have to be designated as same species.

14.3.8 Genetic Species (Baker and Bradley, 2006)

The morphological species concept is based upon the morphological characters. Similarly, an attempt was made to define species on the basis of genetic similarly or distance. Genetic species was defined by Baker and Bradley as “A group of genetically compatible interbreeding natural population that is genetically different from any other such population.” In this concept emphasis is on the genetic isolation which makes it different from the Biological species concept where emphasis is on reproductive isolation. It was stated that defining species on the basis of genetic isolated will lead to better understanding of biodiversity, evolution and speciation. There may be some advantages of Genetic species concept : (i) with the automated sequencing and available data base, it will be easy to analyze DNA quickly, (ii) this concept will be very useful and save a lot of time for bacteria and small organisms and (iii) it will address the problem of recognition of cryptic species that cannot be explained on the basis of morphological studies.

Problems with Genetic species concept are (i) the decision of a person will determine if the genetic difference is enough to recognize a new species, however may conclude that genetic differences are not enough to give a population the status of a species, (ii) there may be a situation when DNA samples of the host may get contaminated with DNA sample of parasite, (iii) the services of expert in DNA taxonomy will be required in such case.

14.3.9 Genic Species (Wu, 2001)

Wu in the year 2001 emphasized that it is not whole genome but a gene is the unit of species differentiation. According to this concept speciation depends upon genes, the speciation genes. Speciation genes are those genes that exhibit a higher frequency of differentiation during the process of speciation compared to other genes which are responsible for differential adaptation to different environment. On the basis of this Wu defined Genic Species as "Group of individuals which are differentially adapted and upon contact fail to share genes controlling adaptive characters either by direct exchange or through intermediate hybrid population." As per this concept differential adaptation is a form of divergence in which alternative alleles of a gene have opposite fitness effect in two groups of individuals. This concept is applicable to both biparental as well as uniparental organisms.

Problems with Genic species Concept are (i) the concept was criticized by Orr (2001) because of excessive and exclusive focus on differential adaptation caused by mutation in genes. (ii) even if differential adaptation is considered as a frequent process during speciation, other processes like genetic drift cannot be excluded in speciation (Noor, 2002).

14.3.10 Evolutionary Species (Simpson, 1961)

Simpson described the species on the basis of evolutionary changes in a population and defined the species as "A series of ancestor dependent populations passing through time and space independent of other populations each of which processes its own evolutionary tendencies and historical fate." So, an evolutionary species is a population that has a common ancestor and has a lineage that maintains its integrity with respect of other such lineages through time and space. In such a population at a particular time some members diverge from parental population and when this divergence become sufficient time some members diverge from parental population and when this divergence become sufficient, the members which diverged are regarded as new species. To estimate the degree of divergence a wide range of characters are evaluated before assigning the status of a species to a population diverged from ancestral population. It is the most popular concept among the paleontologists and used frequently in comparative biology and phylogenetic systematic. However, Mayr and Ashlock, 1991) criticized this concept. The major problems with this species concept are (i) it is silent about the reproductive isolation between the different species (ii) it cannot explain what is evolutionary tendency and historical fate (iii) it cannot explain the new species formed from the ancestral population maintains its identity (iv) Its main aim is to delimit the species taxa on the time dimension. It ignores the core problem of defining a species and cannot explain the causes and maintenance of discontinuities between contemporary species (v) the definition of species describes the phyletic lineage and cannot answer if the species is a equivalent to a phyletic line, according to this concept not only each phyletic line but all its geographic isolates have to be treated as new species (vi) in case of fossils, the evolutionary tendency and historical fate cannot be observed.

14.3.11 Biological Species (Mayr, 1969)

It is the most widely accepted species concept at present. According to Biological species concept **"A species is a group of interbreeding natural population that is reproductively isolated from other such groups. This concept emphasizes three aspects of species."**

1. A species is a reproductive unit and for the purpose of reproduction the individuals recognizes each other as potential mate. In other words a species is a population of interbreeding individuals,

2. A species is an ecological unit that interacts with other species with which it shares its environment, and

3. It is a genetic unit and protective gene pool consisting of a large inter-communicating gene pool in which the individual holds only a small portion of this gene pool for a shorter period. Genes of the same gene pool from harmonious combination because they have been co-adapted by natural selection. Mixing the genes of two different species usually leads to high frequency of disharmonious gene combinations and natural selection favors any mechanism that prevents it. These properties show that species are biological populations.

Difficulties in applying Biological species concept are : (i) assignment of status of species is often difficult when sufficient information is not available about a population. For e.g. Individual variations within a species always have a doubt whether they represent a separate species or a phenon within a species. Sexual dimorphism, differences due to age variation, polymorphism etc. can be studied through a study of life history or through population analysis but problem arises when a taxonomist is working with a preserved animal, (ii) Species have been defined as interbreeding population. This definition cannot be applied on populations which reproduce by amitosis, automixis, self fertilization, parthenogenesis and other modes where only females or hermaphrodites are involved. Such parental lineage are sometimes called as agamospecies or binoms or paraspecies but these entities cannot be the subdivisions of biological species. In some group of animals like aphids, bisexual generations alternate with parthenogenetic generations. In such cases neither kind of generation shall qualify for a separate species. There are about 1000 species in which male sex is either absent or non-functional. These species reproduce by **Thelotoky (parthenogenesis in which only females are produced,** (iii) Geographically isolated populations exist that are in the process of becoming separate species, have acquired some but not all the attributes of distinct species (incipient species). It is difficult to decide at what stage of divergence such a population be called as a species. It is difficult to assign species taxon to populations that have acquired reproductive isolation without equivalent morphological change. It is also difficult to assign species taxon to populations that have acquired strong morphological differences without reproductive isolation, (iv) reproductive isolation may breakdown occasionally even between two good species. This leads to the production of hybrids which are either sterile or have low viability, hybrids have sometimes been described as new species, but as soon as it was discovered they lost the status of a species. Only populations are recognized as species and the hybrids are not the population. But rarely there is complete breakdown of isolation the results in the production of hybrid Swarm. In such case the species status of parental was upheld and the explanation was given that two parental species fused together into a single species, whereas in some cases no taxonomic recognition was given to hybrid populations that were fully fertile.

14.3.12 Ring Species

A ring species is a connected series of neighbouring populations, each of which can sexually interbreed with closely sited related populations, but for which there exist at least two "end" populations in the series, which are too distantly related to interbreed, though there is a potential gene flow between each "linked" population. Such non-breeding, though genetically connected, "end" populations may co-exist in the same region thus closing the ring. Ring species thus presents a difficult concept for any species that relies on reproductive isolation. However, ring species are at best rare. Proposed examples include the herring gull-lesser black-backed gull complex around the North pole, the *Ensatina eschscholtzii* group of 19 populations of salamanders in America, and the greenish warbler in Asia, but there is evidence that none form genuine rings.

14.3.13 Genetic Similarity and Barcode Species

In microbiology, genes can move freely even between distantly related bacteria, possibly extending to the whole bacterial domain. As a rule of thumb, microbiologists have assumed that kinds of Bacteria or Archaea with 16S ribosomal RNA gene sequences more similar than 97% to each other need to be checked by DNA-DNA Hybridisation to decide if they belong to the same species or not. This concept was narrowed in 2006 to a similarity of 98.7%. **DNA barcoding has been proposed as a way to distinguish species suitable even for non-specialists to use. The so-called barcode is a region of mitochondrial DNA within the gene for cytochrome c oxidase**. A database, Barcode of Life Data Systems (BOLD) contains DNA barcode sequences from over 190,000 species. However, scientists such as Rob DeSalle have expressed concern that classical taxonomy and DNA barcoding, which they consider a misnomer, need to be reconciled, as they delimit species differently. Werner Kunz observes that DNA barcoding cannot distinguish new, rapidly-created sympatric species, as they will have almost identical genomes, differing in just those few genes that fit them to their new habitats. This means, Kunz argues, that several **species concepts disagree with the barcode species concept.**

SAQ 1

a) What is a species?

b) What is your preferred species concept, and why?

c) Are species real units in nature or are they man-made constructions? Explain your answer.

d) Fill in the blanks:

   i) Species adapted to ecological type is known as ………………. Species.

   ii) Herring gull-lesser black-backed gull complex around the North pole are examples of ………………. Species.

   iii) The term species is coined by ………………. .

   iv) Species are mainly ………………. physically/ reproductively/ ecologically isolated from other species.

14.4 MODE OF SPECIATION

Speciation is evolutionary process by which a biological population becomes a distinct species. In 1906 Orator F. Cook used the term Species for cladogenesis. Charles Darwin was the first to describe the role of natural selection in speciation. Speciation is a key component in the divergence of species and biodiversity. Accordingly the speciation is classified into three major types, Artificial, Sympatric and Allopatric speciation which will be discussed in detail in subsections 14.4.1 & 14.4.2 (Fig. 14.2).

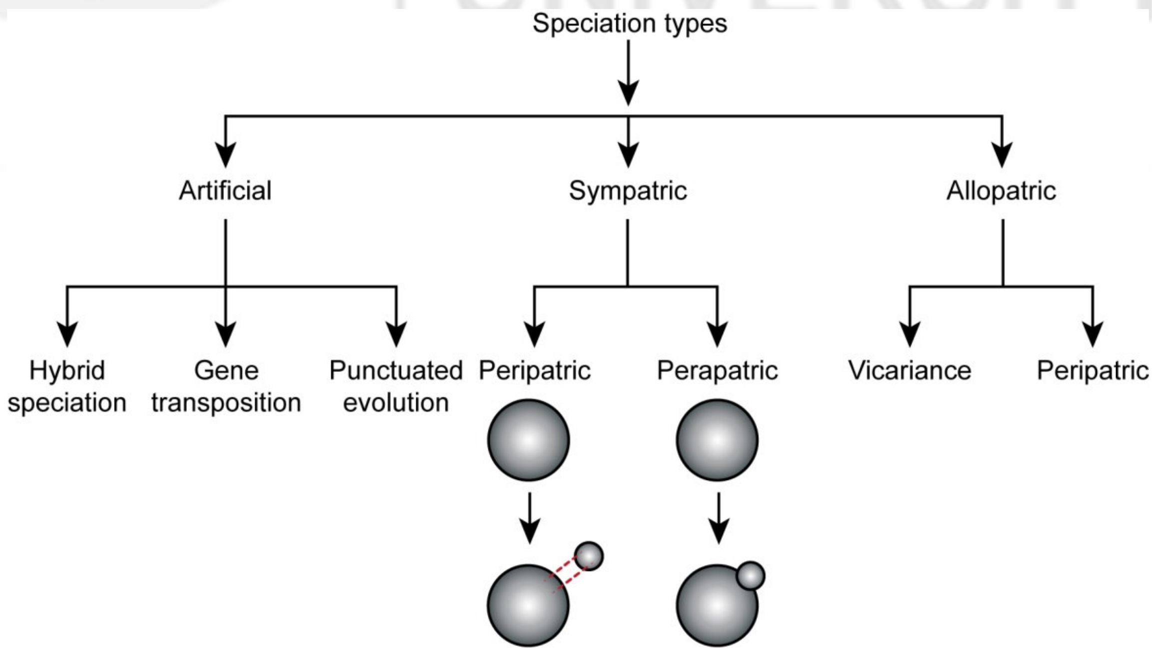


Fig. 14 2: Showing Speciation type.

14.4.1 Artificial Speciation

New species have been created by animal husbandry, but the dates and methods of the initiation of such species are not clear. Often, the domestic counterpart of the wild ancestor can still interbreed and produce fertile offspring as in the case of domestic cattle, that can be considered as same species as several varieties of wild ox, gaur, yak, etc., or domestic sheep that can interbreed with the mouflon. William R. Rice and George W. salt bred *Drosophila melanogaster* fruit flies using a maze with three different choices of habitat such as light/dark and wet/dry. Each generation was placed into the maze, and the groups of flies that came out of two of the eight exits were set apart to breed with each other in their respective groups. After thirty-five generations, the two groups and their offspring were isolated reproductively because of their strong habitat preferences. They mated only within the areas they preferred, and did not mate with flies that preferred the other areas. Dodd used a laboratory experiment to show reproductive isolation can develop in *Drosophila pseudoobscura* after several generations by placing them in different media such as, starch-and maltose-based media. Dodd's experiment has been easy for many others to replicate with other kinds of fruit flies and foods. These observations are consistent with the notion that sexual creatures are inherently reluctant to mate with individuals whose appearance or behavior is different from the norm. The risk that such deviations are due to heritable maladaptations is very high. Thus, if a sexual creature, unable to predict natural selection's future direction is conditioned to produce the fittest offspring possible, it will avoid mates with unusual habits or features. Sexual creatures will then inevitably tend to group themselves into reproductively isolated species.

Artificially the speciation may be achieved by (i) Hybrid speciation and poplypoidy (ii) Gene transposition and (iii) Punctuated evolution. This will be discussed in the following paragraphs:

i) Hybrid speciation and Polyploidy

Occassionally, the hybridization between two different species leads to a distinct phenotype that may be fitter than the parental lineage so that natural selection may favor these individuals. Eventually, if reproductive isolation is achieved, it may lead to a separate species. Due to the fact that reproductive isolation between hybrids and their parents is particularly difficult to achieve, the hybrid speciation is considered an extremely rare event. Hybridization without change in chromosome number is called homoploid hybrid speciation. It occurs rarely but has been shown in *Heliconius* butterflies and sunflowers.

Hybridization plays an important role in the speciation of plants, since polyploidy is tolerated in plants more readily than in animals. Polyploidy plays an important role in the evolution of vascular plants. More than 47% of all species of Angiosperms exhibit polyploidy. Polyploidy is important in hybrids as it allows reproduction, with the two different sets of chromosomes, each being able to pair with an identical partner during meiosis. Polyploids also have more genetic diversity, which allows them to avoid inbreeding depression in small populations.

Polyploidy is a mechanism that has caused rapid speciation events in sympatry because offspring of tetraploid x diploid matings often result in triploid sterile progeny. However, not all polyploids are reproductively isolated from their parental plants, and gene flow may still occur for example through triploid hybrid x diploid matings that produce tetraploids, or matings between meiotically unreduced gametes from diploids and gametes from teraploids. It has been suggested that many of the existing plant and most animal species have undergone an event of polyploidization in their evolutionary history. Reproduction of successful polyploid species is sometimes asexual, by parthenogenesis or apomixes, as for unknown reasons many asexual organisms show polyploidy. Rare instances of polyploid mammals are known, but most often result in prenatal death.

ii) Gene Transposition

Dobzhansky studied fruit flies in 1930s and speculated that parts of chromosomes that switch from one location to another might cause a species to split into two different species. He mapped out how it might be possible for sections of chromosomes to relocate themselves in a genome. These mobile sections can cause sterility in inter-species hybrids, which can act as a speciation pressure. In theory, his idea was sound, but scientists long debated whether it actually happened in nature. Eventually a competing theory involving the gradual accumulation of mutations was shown to occur in nature so often that geneticists largely dismissed the moving gene hypothesis. However, in 2006 it was shown that jumping of a gene from one chromosome to another can contribute to the birth of new species. This validates the reproductive isolation mechanism, a key component of speciation.

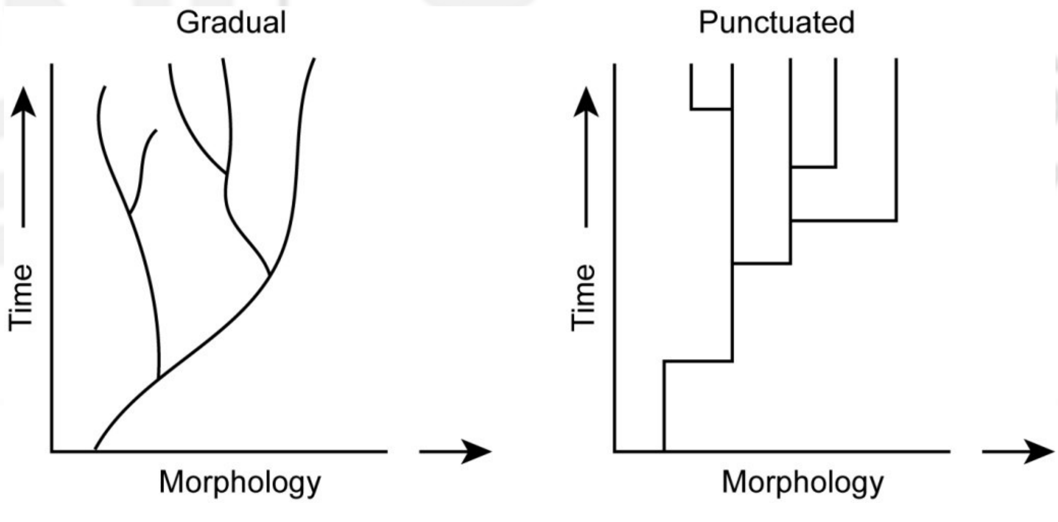


Fig. 14.3: Punctuated evolution.

Gradual evolution occurs where the increment of change is small compared to that of time. Punctuated evolution occurs where the increment of change is very large compared to that of time in discrete intervals, while most of the time there is virtually no change at all (Fig. 14.3).

Punctuated equilibrium is an important but often-misinterpreted model of evolutionary change. Punctuated equilibrium predicts that new species evolve when a large evolutionary change takes place in short periods of time. The model works as follow:

1. **Stasis:** A population of mollusks is experiencing stasis (a little or non-observable evolution takes place during a span of large period). They are living, dying, and getting fossilized every few hundred thousand years. Little observable evolution seems to be occurring judging from these fossils.

2. **Isolation:** A drop in sea level forms a lake and a small number of mollusks are isolated from the rest of the population.

3. **Strong selection and rapid change:** The small, isolated population experiences strong selection and rapid change because of the novel environment and small population size. The environment in the newly formed lake exerts new selection pressures on the isolated mollusks. Also, their small population size means that genetic drift influences their evolution. The isolated population undergoes rapid evolutionary change.

4. **No preservation:** No fossils representing transitional forms are preserved because of their relatively small population size, the rapid pace of change, and their isolated location.

5. **Reintroduction:** Sea levels rise, reuniting the isolated mollusks with their sister lineage.

6. **Expansion and stasis:** The isolated population expands into its original past range. Larger population size and a stable environment make evolutionary change less likely. The formerly isolated population of the mollusk may out-compete their ancestral population, causing it to go extinct.

7. **Preservation:** Larger population size and a larger range move us back to step 1: stasis with occasional fossils preservation.

14.4.2 Sympatric Speciation

Sympatric speciation is speciation that occurs when two or more populations of the same species live is the same geographic location, but evolve differently until they can no longer interbreed and considered as different species. It is different from allopatric speciation in which a new species is formed when a population splits into groups by a geographic barrier or migration. These species are called as Sympatric species which are closely related to one another and found together in restricted areas without any trace of physical barrier for dispersal (Fig. 14.4). Sympatric speciation can be seen in many different types of organism including bacteria, cichlid fish, and the apple maggot fly, but it can be difficult to tell when sympatric is occurring or has occurred in nature. There are a number of lakes around the world in which a large number of closely related fish species live together. Lake Malawi, Lake Tanganyika and Lake Victoria of Africa contain many species of cichlid fishes which are restricted only to these lakes and are not found anywhere else in the world. It is difficult to believe that these fishes could have originated somewhere else in the world. Their DNA, morphology and ecology is quite similar but they maintain the reproductive isolation between them. A hypothesis was proposed to explain the sympatric speciation in these fishes. Different populations of Cichlid fishes of these lakes were adapted for different food habits and feeding specialization while living in the same geographical area and achieved sufficient physical and adaptive separation to evolve reproductive barriers between them and evolved as different species. In parasitic insects different population shift to new host species, get separated from one another with gradual buildup of reproductive isolation and when this isolation is perfect these populations evolved as different species. Apple maggot flies used to lay their eggs only on the fruit of hawthorn trees, but less than 200 years ago, a subpopulation of these maggot flies started laying eggs on apples. Now there are two populations of maggot flies one laying eggs on hawthorn trees and other one apples with reproduction isolation between them and have evolved into two new species.

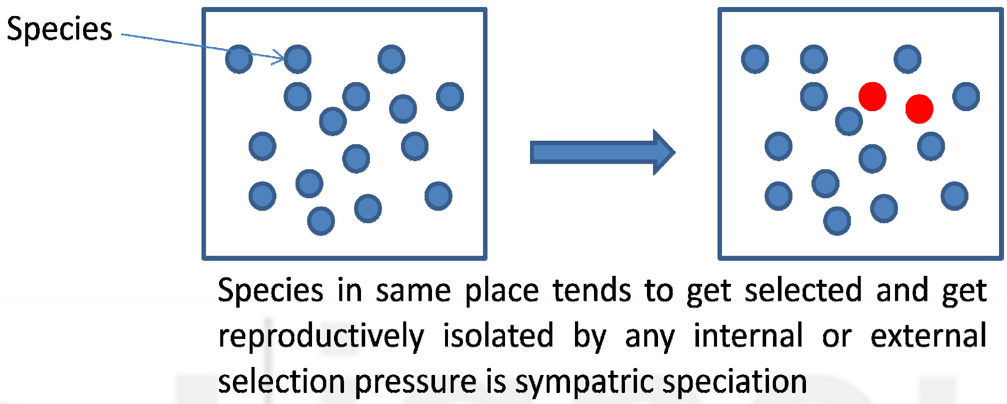


Fig. 14.4: Sympatric speciation.

Example of sympatric speciation are rare in nature. Sympatric speciation occurs more often in bacteria, because they are capable of exchanging genes with other individuals that are not parent and offspring in a process known as horizontal gene transfer. Sympatric speciation has been observed in *Bacillus* and *Synechococcus* species of bacteria and bacterioplankton *Vibrio splendidus*. Subgroups of species that are undergoing sympatric speciation will show few differences since they have been diverging for a relatively recent time on the slow timescale at which evolution takes place. It is proposed that one important factor in cases of sympatric speciation is adaptation to environmental conditions. If some members are specialized for living in a certain environment, that subgroup may go on to occupy a different environmental niche and eventually evolve into a new species over time.

14.4.3 Allopatric Speciation

Allopatric speciation is the evolution of species caused by the geographical isolation of two or more population of same species in isolated geographical area are called as allopatric species. Speciation is a gradual process by which isolated populations evolve into different species. A species is itself defined as population that can interbreed, so, during the speciation members of a population form two or more distinct populations that can no longer breed with each other. There are two types of allopatric speciations i.e. **Vicariance** and **Peripatric**. Vicariance is the splitting of one continuous population into two or more large groups that are geographically isolated from each other eg. Species distribution in Madagascar whereas **Peripatric** speciation is a mode of speciation in which a new species is formed from an isolated peripheral population eg Colonization of *Drosophilla* species in different Hawaiian archipelago island chain from the genus *Cyanea* (green) and species from the genus *Drosophila* (blue). Speciation arises peripatrically as they spatiotemporally colonize new islands along the chain.

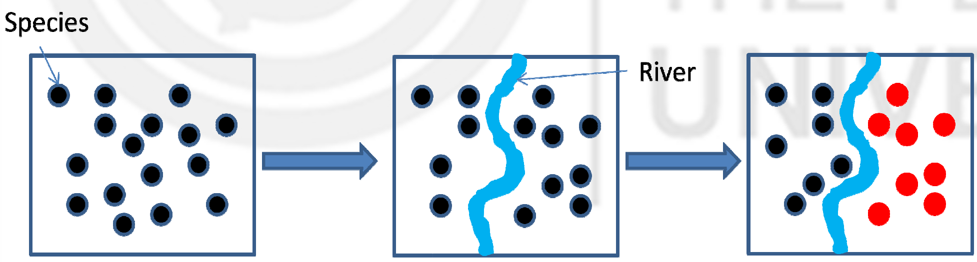
How Does Allopatric speciation occur?

Some time sudden natural geographical changes like earthquake, floods, geotechtonic shuffle or hit by extra terrestrial comets or asteroids to bring sudden geographical barrier or through human activities like constructions of **dams, canals, agriculture** which separates individuals of same species. This in the following years in long term or permanent isolation brings change in the species so that they cannot interbreed and sometime some members migrate to different location and never come back and evolve separately.

Another way is genetic mutations occur in different population over the period of time in different locations and build up in the different populations over the time. The different variations of genes may lead to different characteristics between the two populations (Fig. 14.5).

The populations become so different that members of the different populations can no longer breed with each other anymore if they were to be in the same habitat in the same time. If this is the case, allopatric speciation has occurred.

The following diagram represents an experiment on fruit flies where the population was forcibly separated and the two groups were fed a different diet. After many generations the flies looked different and preferred to mate with flies from their own group. If these two populations continued to diverge for a long time, they could become two different species through allopatric speciation.



Due to certain geographical barrier the same species tends to change and become get reproductively isolated from the initial population is Allopatric speciation

Fig. 14.5: Allopatric speciation.

A major example of allopatric speciation occurred in the Galapagos finches that Charles Darwin studied. There are about 15 different species of finches on the Galapagos islands, and each species look different and have specialized beaks for eating different types of foods, such as insects, seeds, and flowers. All of these finches came from a common ancestor species that must have emigrated to the different islands. Once populations were established on the islands, they became isolated from each other and different mutations arose. The mutations that caused the birds to be most successful in their respective environments became more and more prevalent, and many different species formed over the time. **When many new species emerge from one common ancestor in a relatively quickly geological timeframe, this is called adaptive radiation.**

When the Grand Canyon was formed, it created a natural barrier between the squirrels living in the area. About 10,000 years ago, the squirrel population was separated from each other by this geographical change and could no longer live in the same area. Over thousands of years, the divided squirrel populations became two different species. Kaibab squirrels live on the north rim of the canyon and have a small range, while Abert squirrels live on the south rim and live in a much larger range. Members of these two species have a similar size, shape, and diet, and with a slight colour differences, but they are no longer in contact with each other and have become so different during their separation that they are now separate species.

SAQ 2

Match column A with column B.

Column A	Column B
A) Sympatric speciation	i) Evolution of species by geographical isolation of two or more populations of species
B) Allopatric speciation	ii) Evolve from a single ancestral species

14.4.4 Isolating Mechanisms

If there is no external or internal governing forces there will not be any speciation. Isolating mechanisms are therefore important in the formation of species. Isolating mechanism is any process that reduces or prevent the gene flow between two populations. There are many types of isolating mechanisms.

Reinforcement (Wallace effect)

Reinforcement, sometimes referred to as the Wallace effect, is the process by which natural selection increases reproductive isolation. It may occur after two populations of the same species are separated and then come back into contact. If their reproductive isolation was complete, then they would have already developed into two separate incompatible species. If their reproductive isolation is incomplete, then further mating between the populations will produce hybrids, which may or may not be fertile. If the hybrids are infertile, or fertile but less fit than their ancestors, then there will be further reproductive isolation and speciation has essentially occurred (e.g., as in horses and donkeys) this type of separation which is not reproductively isolated may be called as subspecies or types. Reinforcement favoring reproductive isolation is required for both parapatric and sympatric speciation.

Ecological

Ecological Isolation occurs with interaction of individuals with their environment during resource acquisition. The natural selection governs through ecological factors where the populations in different environments, or populations exploiting different resources, experience contrasting natural selection pressures on the organisms to become reproductive isolated.

Sexual Isolation

Sexual selections can lead to speciation in many organisms it is seen independently of natural selection. It is also said as splitting of an existing species into two separate species, or the budding off of a new species from a parent species.

Reproductive Barriers

There are mainly two reproductive barriers i.e. Pre-zygote and Post-zygote reproductive barriers which help in speciation. These are critical evolutionary mechanisms due to which divergence in species occurs and a germline of species is also protected through cross species genetic contamination. These barriers maintain the integrity of a species by reducing gene flow between related species. Ernst Mayer has classified the reproductive isolation in number of ways majorly falling in categories: **Pre mating** and **Post mating isolations**.

Pre-mating Isolation

Pre-zygotic isolation mechanisms are the most economic in terms of the natural selection of a population, as resources are not wasted on the production of a descendant that is weak, non-viable or sterile. These mechanisms include physiological or systemic barriers to fertilization.

Behavioral Isolation

Different types of behavioral isolations have been noticed like courtship dances among various bird and animal species, sometimes proximity to each other is a isolation. Some animals tend to live in isolated male bands and search for females during mating season and only that way their behavior becomes a limitation due to non proximity with females in different seasons.

The songs of birds, insects and many other animals attract potential partners of their own species. The song presents specific patterns recognizable only by members of the same species, and therefore represents a mechanism of reproductive isolation. Specific lights, songs, noise, pheromones are released for specific species

Small morphological differences between species, differences in behavior can be enough to prevent mating. For example, *Drosophila melanogaster* and *D. simulans* which are considered twin species due to their morphological similarity, do not mate even if they are kept together in a laboratory. Studies of their sexual behavior show that the males court the females of both species but the females show a marked preference for mating with males of their own species. A different regulator region has been found on Chromosome II of both species that affects the selection behavior of the females. Pheromones also play an important role in the sexual isolation of insect species. These compounds serve to identify individuals of the same species and of the same or different sex.

Mechanical Isolation

The flowers of many species of Angiosperms have evolved to attract and reward a single or a few pollinator species (insects, birds, mammals). Their wide diversity of form, colour, fragrance and presence of nectar is, in many cases, the result of co-evolution (evolved together) with the pollinator species. This dependency on its pollinator species also acts as a reproductive isolation barrier.

Gametic Isolation

The synchronous spawning of many species of coral in marine reefs means that inter-species hybridization can take place as the gametes of hundreds of individuals of tens of species are liberated into the same water at the same time. There are chances of cross fertilization of several species but compatibility of gametes is important to fertilize. It has been observed that if in case fertilization occurs they are unable to produce hybrid offspring, despite the fact that the gametes are found at the same time and in the same place, is due to a phenomenon known as gamete incompatibility, which is often found between marine invertebrates.

Post-zygotic Isolation

If in case copulation occurs in different species then another mechanism is also there for preventing cross breeding and initiation of new linage. A number of mechanisms which act after fertilization preventing successful inter-population crossing are discussed below.

I Intrinsic Factors

- **Zygote mortality and non-viability of hybrids**

  A type of incompatibility that is found as often in plants as in animals occurs when the egg or ovule is fertilized but the zygote does not develop into organism or if develops it has reduced viability. Similar results are observed in mosquitoes of the *Culex* genus, the effect occurs in the interaction between the genes of the cell nucleus (inherited from both parents) as occurs in the genes of the cytoplasmic organelles which are inherited solely from the female progenitor through the cytoplasm of the ovule.

- **Incompatibility caused by microorganisms**

  In addition to the genetic causes of reproductive isolation between species there is another factor that can cause post zygotic isolation: the presence of microorganisms in the cytoplasm of certain species. The presence of these organisms in a species and their absence in another causes the non-viability of the corresponding hybrid for example

Wolbachia infection in mosquitoes, *Wolbachia* is a gram negative bacteria which is found is about 75% of insects naturally. If *Wolbachia* infected male copulates the non infected females there occurs cytoplasmic incompatibility due to which there is no production of F1 generation. This modification is brought up by *Wolbachia* in the organism and isolates post mating whereas when these infected mosquitoes are females they can have progeny. This is a example of cytoplasmic incompatibility.

- **Hybrid sterility**

  A hybrid has normal viability but is deficient in terms of reproduction or is sterile. This is demonstrated by the mule (A cross between a horse and a donkey or between a mare and a donkey, respectively) and in many other well known hybrids. In all of these cases sterility is due to the interaction between the genes of the two species involved; to chromosomal imbalances due to the different number of chromosomes in the parent species

II Extrinsic Factors

The conditions which are not internal like physiological; cytoplasmic or through genetic intrinsic factor of organism are categorized in extrinsic factors. Extrinsic factors are barriers of environment, temperature, altitudes, salinity, placements etc.

- **Multiple mechanisms**

  In general, the barriers that separate species do not consist of just one mechanism. The twin species of *Drosophila, D. pseudoobscura* and *D. persimilis*, are isolated from each other by habitat (*D. persimilis* generally lives in colder regions at higher altitudes), by the timing of the mating season (*D. persimilis* is generally more active in the morning and *D. pseuoobscura* at night) and by behavior during mating (the females of both species prefer the males of their respective species). In this way, although the distribution of these species overlaps in wide areas these isolation mechanisms are sufficient to keep the species separated. However, when hybrids are produced between both species, the gene flow between the two will continue to be impeded as the hybrid males are sterile.

- **Post-copulation or fertilization mechanisms in animals**

  Reproductive isolation between species appears, in certain cases, a long time after fertilization and the formation of the zygote, as happens – for example – in the twin species *Drosophila pavani* and *D. gaucha*. The hybrids between both species are not sterile, in the sense that they produce viable gametes, ovules and spermatozoa. However, they cannot produce offspring as the sperms of the hybrid male do not survive in the semen receptors of the females. In the same way, the sperm of the males of the two parent species do not survive in the reproductive tract of the hybrid female. This type of post-copulatory isolation appears as the most efficient system for maintaining reproductive isolation in many species.

The development of a zygote into an adult is a complex and delicate process of interactions between genes and the environment that must be carried out precisely, and if there is any alteration in the usual process, caused by the absence of a necessary gene or the presence of a different one, it can arrest the normal development causing the non-viability of the hybrid or its sterility. It should be borne in mind that half of the chromosomes and genes of a hybrid are from one species and the other half come from the other. If the two species are genetically different, there is little possibility that the genes from both will act harmoniously in the hybrid. From this perspective, only a few genes would be required in order to bring about post copulatory isolation.

SAQ 3

Fill in the blank with appropriate alternative given in the parentheses.

i) The ecosystem tends to remove (overlapping/distancing) species to avoid competition between them.

ii) The prezygotic isolation mechanisms are most economic in terms of (artificial/natural) selection of a population.

iii) A hybrid has (normal/abnormal) viability.

14.5 SUMMARY

In this unit you have learnt:

- The concept of species and the definition that the species are a group of interbreeding natural populations that are reproductively isolated from other such groups. The biological species concept is more realistic than the typological or nominalistic species concept. It explains species as a distinct unit of time, with a capacity to change continuously over long periods of time. In short, species has an evolutionary capacity.

- The different modes of speciation. (a) The sympatric speciation refers to speciation among populations living together. (b) Allopatric speciation refers to speciation in populations separated by space.

- Concept of ring species in which a population becomes isolated, changes gradually, pass the test of sympatry and become a distinct species.

- You have also learnt the concept of speciation i.e. Biological, Morphological, Ecological, Recognition and Evolutionary species concepts with the different types of isolating mechanisms: the geographical, ecological, mechanical, ethological and reproductive (both pre-mating and post-mating) all of which promote the formation and distinctness of species.

14.6 TERMINAL QUESTIONS

1. Match the following:

(A)	Separation of single population by any means so that they are not in contact with the original population	i)	Prezygotic and Postzygotic
(B)	A species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent.	ii)	Typological
(C)	Species are defined based on careful morphological attributes.	iii)	Polyphenism
(D)	Multiple distinct phenotypes that arise from a given genotype	iv)	Phylogenetic
(E)	Reproductive isolating barriers	v)	Isolation

2. What are postmating and prezygotic reproductive isolating barriers?
3. How does speciation occur under the biological species concept?
4. What are two types of allopatric speciation?
5. What is ecological speciation?
6. What are concepts of Speciation?
7. What is Isolation and what are its types?

14.7 ANSWERS

Self Assessment Questions

1. a) Species ere interbreeding groups of natural population which are reproductively isolated from other such groups.

   b) Think give your own answer.

   c) Species are real units in nature.

   d) i) Ecological, ii) *Ensantina,* iii) Mayr, iv) Interbreeding.

2. A) 2 B) 1

3. i) Overlapping, ii) Natural, iii) Normal.

Terminal Questions

1. A) Isolation, B) Phylogenetic, C) Typological, D) Polyphensim, E) Prezygotic and Postzygotic.

2. Refer to Subsection 14.3.2.
3. Refer to Subsection 14.3.1.
4. Refer to Subsection 14.2.2.
5. Refer to Subsection 14.3.3.
6. Refer to Section 14.3.
7. Refer to Subsection 14.3.4.

UNIT 15

EVOLUTIONARY CHANGE, SPECIES CONCEPT AND SPECIATION-II

Structure

15.1 INTRODUCTION

You have read about process of natural selection which is one of the major events of evolutionary change forming a part of the Unit 13. Apart from natural selection, isolation and genetic drift, gene flow and mutation also play vital role in the evolution of species. Mainly microevolution (*evolution on a small-scale*) refers to the changes in allele frequencies within a single population. Allele frequencies in a population may change due to four fundamental forces of evolution: *Natural Selection, Genetic Drift, Mutations and Gene Flow*. **Mutations are the ultimate source of new alleles in a gene pool.**

Two of the most relevant mechanisms of evolutionary change are: **Natural Selection** and **Genetic Drift**. One of the main controversial issues in population genetics is concerned with the relative importance of both mechanisms in determining evolutionary changes. Natural selection usually predominates in large populations whereas genetic drift does so in smaller population. Migration of some individuals from a population and merging into different population of same genus also initiate change in the species at the gene level, and thereby gene drift comes into operation. We will discuss these mechanisms of evolutionary changes in this unit.

Objectives

After studying this unit you should be able to:

- ❖ explain the concept of genetic repatterning during isolation process,
- ❖ classify different types of isolating mechanisms,
- ❖ discuss large scale change in genetic frequencies in small population- the genetic drift phenomenon, and
- ❖ explain population bottleneck and founder effect in relation to genetic drift.

15.2 GENETIC RE-PATTERNING DURING ISOLATION

Three important factors governing evolution are **Isolation, Adaptation** and **Variation**. Isolation is a kind of physical or environmental barrier that prevents **promiscuous breeding**. It may be called as **a phenomenon due to which a single population of a species gets divided into two or more subpopulations or groups without interbreeding between them through some internal or external factors**. So, isolation is simply the prevention of gene flow and is a major cause of speciation.

Isolation is a major cause of speciation. When a population is isolated by any means and colonization initiates with initial few organisms of the species, genetic repatterning is observed in such conditions as for example in an island during initial colonization by just a few individuals, or just a pair: or even a single gravid female. When a new population develops from these early colonisers of the island, they undergo drastic genetic repatterning. This is described as a genetic revolution. The founder being small in number, the first major change in the colonisers is a drastic reduction in the variability. Inbreeding further reduces variability. **Inbreeding eliminates recessives as homozygotes and consequently the genetic load is reduced.**

The introduction of species to a non colonized area where other components of mixing of population are absent tends to make a population as even population and more tolerant to the environment than the original individuals (homogyous) who colonized the place initially. The newer community becomes more stable in terms of gene dominance and tends to become hetrozygote with all the dominant expressions (Fig. 15.1).

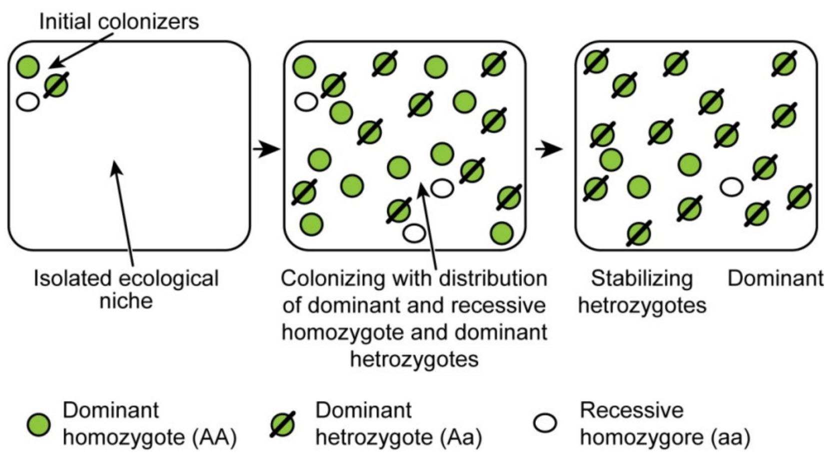


Fig. 15.1: Showing genetic repatterning in newly isolated ecological niche.

The decisive change is from a large open population to a small closed population. In the closed population, overdominance, that is the superior fitness of the heterozygote (say, Aa) over the other two homozygotes (AA and aa), increases. Non-allelic epistatic interaction of genes greatly alters the functioning of the gene complexes. As a result the genetic cohesiveness is broken and the founder population becomes plastic and pliable enough to be moulded into a newer one with better adaptations.

When a new population develops from these early colonisers of the island, they undergo drastic genetic repatterning. This is sometimes described as a genetic revolution. The founder being small in number, the first major change in the colonisers is a drastic reduction in the variability (Observe transition from A to B in Fig. 15.2 A to B). **Inbreeding further reduces variability (Observe C in Fig. 15.2). Inbreeding eliminates recessives as homozygotes and the genetic load is reduced**. The decisive change is from a large open population to a small closed population. In the closed population, overdominance, that is the superior fitness of the heterozygote (say, Aa) over the other two homozygotes (AA and aa), increases. Non-allelic epistatic interactions of genes greatly alter the functioning of the gene complexes. As a result the genetic cohesiveness is broken and the founder population becomes plastic and pliable enough to be moulded into a newer one with better adaptations. This, in essence, is the genetic repatterning or the genetic revolution.

The founder population, the peripheral isolate, usually becomes extinct due to the greatly reduced variability (C in Fig. 15.2) However, if it survives the genetic revolution, the population builds up to greater variability and better adaptedness (D in Fig. 15.2). It may even acquire greater variability than the original parental population and stabilise at a higher level of genetic cohesion as a new species (E in Fig. 15.2). This status of a new species, distinct from the parental species is made possible by the development of isolating mechanisms during the genetic revolution.

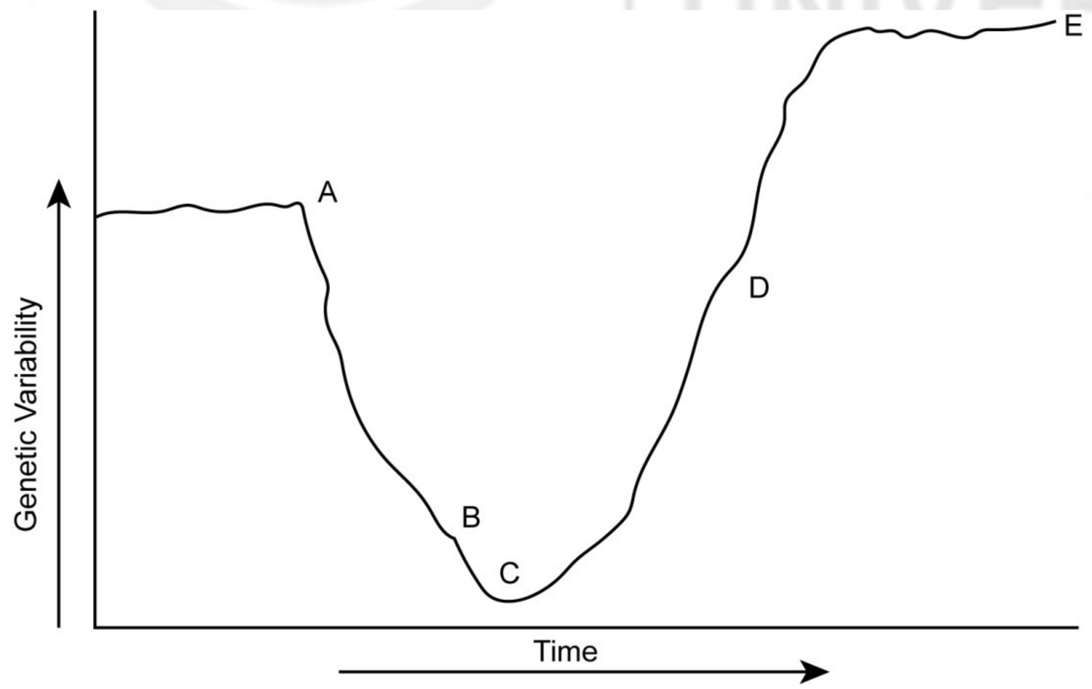


Fig. 15.2: Genetic revolution.

SAQ 1

Explain the concept of genetic repatterning during isolation.

15.3 ISOLATING MECHANISMS

As you are aware that if a species is divided in groups and isolated or separated from each other in such a way that they are unable to mate they might get developed into other species which may not mate again. The reproductive characteristics prevent species from fusing. Isolating mechanisms are particularly important in the *biological species concept*, in which species of sexual organisms are defined by *reproductive isolation*, it may be due to lack of gene mixture (Fig. 15.3).

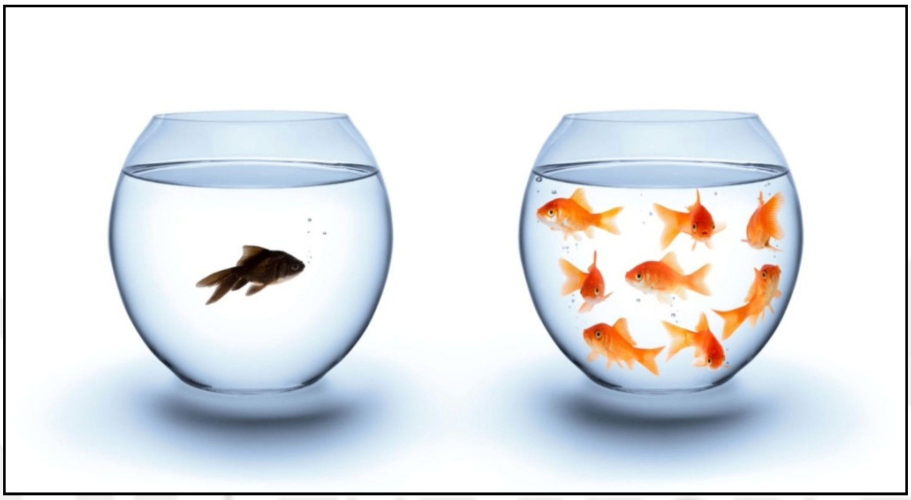


Fig. 15.3: Isolation of fishes in two jars as physical isolation.

In this Section we are to discuss the means by which populations get separated or isolated from each other, first gain the status of sub-species and finally evolve mechanisms which prevent them from mating with local populations to be called as a distinct species. In short, we are to discuss the mechanisms that are responsible for keeping populations from the access to each other that in turn leads to, origin of new species. You are aware that local populations generally interbreed among themselves with only rare cases of outbreeding. Therefore, the genotypes of different populations of a single species may show differences in some or many loci. The resulting phenotypes could be classified into sub-species based on the differences in parts. These subspecies because of their proximity to other populations tend to meet the other members with and consequently a single intermediate and variable population is formed. This would result in the loss of the status of subspecies for the population. However, if a sub-species is isolated over a long period of time and the breeding with its relations is prevented, then by continuing to accumulate the genetic differences it may lose its ability to interbreed with the parental species. Under such circumstances, the sub-species gets elevated to the status of a species, satisfying Mayr's definition of a species. **When two groups are geographically separated from each other, it is often difficult to determine whether they do interbreed any more.** In other words, could they be referred to as allopatric species? Once they move into the same territory, fail to interbreed and form intermediates, they may say to have passed the test of sympatry or they could be regarded as sympatric species. In many cases it has been noticed that once the species status has been established, selection tends to promote those characters which act as a deterrent for the formation of hybrids, since usually hybrid progeny have a reduced fitness.

George Romanes, an American neurologist who evinced a very keen interest in evolutionary problems once wrote, "without isolation or the prevention of interbreeding, organic evolution is in no case possible". Many recent studies on origin of new species have proved that Romanes was largely true in his assessment of the problem. Let us now look into the details of mechanisms of isolation.

Ernst Mayr (1970) classified isolating mechanisms into two major types. The *pre-mating isolating mechanisms* and *the post-mating ones.* The difference between the two types of mechanisms is as follows. **Pre-mating isolating mechanisms prevent the occurrence of mating and the post-mating ones ensure failure of such matings once they occur.** In the discussion on pre-mating isolating mechanisms, besides the biological barriers evolved by the organisms which prevent effectively mating between the individuals, isolation by space will also be included. We shall also examine how the ecology, seasons and even the behaviour of individuals could be instrumental in bringing about the isolation of populations leading to species formation. We shall also look into the details of post-mating isolating mechanisms which prevent the formation of successful hybrids, thereby ensuring the distinctness and identity of a species.

15.4 PRE-MATING ISOLATING MECHANISMS

We have mentioned earlier that pre-mating mechanisms are concerned with the prevention of occurrence of interspecific crosses. In such cases,

a) the potential mates do not meet in which case the isolation is due to either geographical, seasonal or habitat reasons.

b) the potential mates do meet but fail to mate in which case the isolation is due to ethological reasons.

c) the potential mates meet and mate but no transfer of sperm takes place in which case the isolation is due to mechanical reasons.

Let us have each one of these mechanisms examined in detail.

15.4.1 Geographical Isolation

Many species of organisms are restricted in their distribution even as they may be found over a vast geographical regions. Studies using distribution maps of organisms have shown that although species may be continuously found over vast areas, a close scrutiny would reveal that the distribution is rather restricted to those regions with suitable ecological features. For instance, the American plane tree, *Platanus occidentalis* although distributed over more than half the United States, the natural groves of the plants are confined to bottom lands and stream banks. This is true of several species of organisms whose populations are separated by barriers of territory which they cannot use for ecological reasons. For instance, take the case of amphibians. A small body of salt water could be a barrier for their dispersal. Oceanic islands are not inhabited by amphibians except as in the case of Hawaii where they are introduced by man. Salt water is also a barrier for fresh water fishes. Pacific ocean receives many parallel streams of fresh water, each of which had its own sub-species or species of fishes. Only the flooding during the rainy season joins the streams and the fish may be found together.

Similarly populations of land birds are separated by large bodies of water. Normally species and sub-species of birds living on opposite banks of rivers are different. Mayr observed that different sub-species of birds occupy different tropical islands despite that distances among these islands are not very far. Darwin reported that 21 of the 26 species of land birds and only 2 of the 11 species of marine birds are endemic to Galapagos islands. This is a significant finding in that the land birds could not migrate to either direction because of the water barrier and were confined to their territories. More than the birds, it is the mammals which are often stopped by water barriers. Rodents living in opposite banks of rivers usually belong to different sub-species. Mountains often separate organisms occupying low lands. Studies on the distribution of different species of rabbits showed their restricted distribution to specific geographical regions. *Sylvilagus floridanus* confines itself to planes while its cousin the jack rabbit *Lepus americanus* is found only in mountains in United States. Similarly the white footed mouse *Peromyscus leucopus* is found in priaries and its close relative *P. maniculatus* has invaded the mountains. Thus every natural feature could be a barrier to either a plant or an animal paving the way for sub-speciation and ultimately the speciation process.

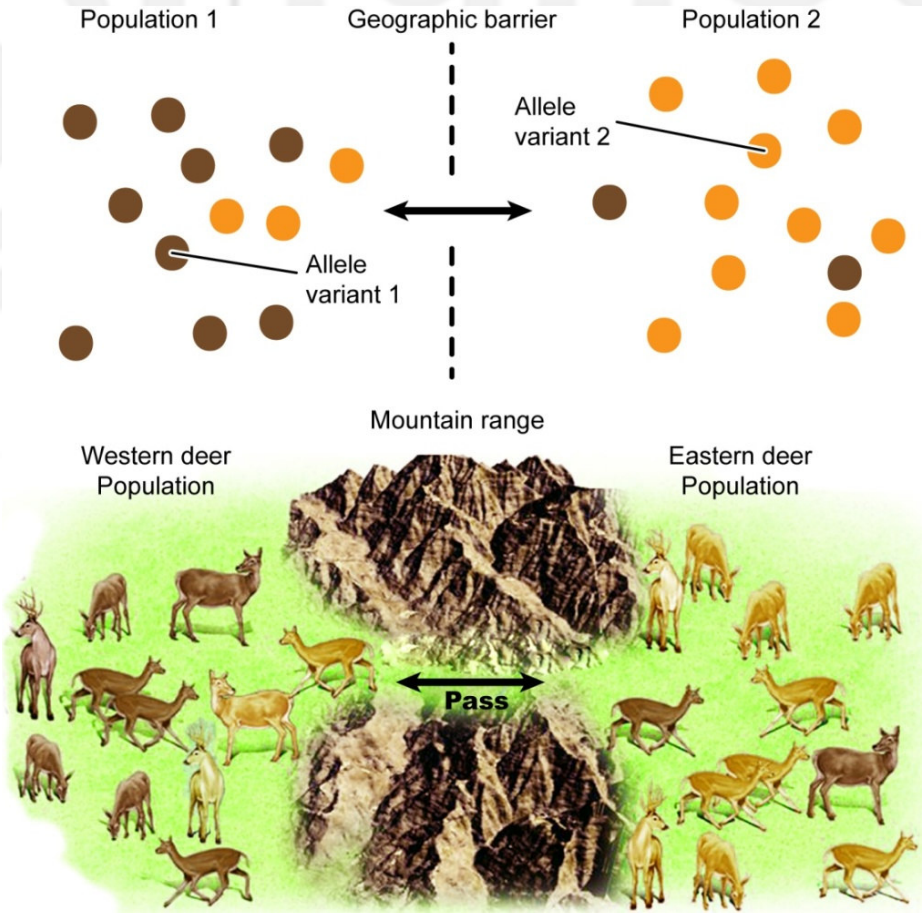


Fig. 15.4: Geographical Isolation in deer population due to mountain range barrier.

15.4.2 Ecological Isolation

Ecological isolation is based on the fact that population shows preference to one habitat over the other. These extensive forests become barriers to the dispersal of organims living in grasslands. The reverse that priaries being barriers to forest organisms is also true. The red tree mouse *Phenocomys longicaudus* lives on fir needle trees and feeds on fir needle. It is understandable that for these mice not only priaries but the non-fir forests will also be a barrier for dispersal.

You may recall MacArthur's study of five species of Warbler birds living in spruce trees. Five species of *Dendroica* are effectively isolated by ecological factors although they have a similar distribution. As a matter of fact, the ecological and food preference of the different species of warblers are very similar. Under such circumstances one would have expected a severe competition among them. But each species has carved a well defined niche and forages at a particular level in the trees. Differences in breeding dates and occupation of different habitats outside the breeding season are the contributing factors for the minimum competition and niche overlap among the species. There are other instances where potential mates keep away from each other because of their habitat preferences. In these cases there might even be a broad niche overlap and the individuals may exist in the same general area, but the distinctness of sub-species and species is maintained. Dice cited an example from United States where the two sub-species of mice *Peromyscus maniculatus* have overlapping niches and do not interbreed in nature, although there is interbreeding in the laboratory. Similarly another study showed that the fresh water and salt water races of the water snake *Natrix sipedon* may come close together but may not interbreed because of their habitat preferences.

An interesting study was reported by A. Pictet in Swiss moths *Nemeophila plantaginis.* Two races of the moth are known, one living at an altitude of above 2700 meters and the other below 1700 meters, The two races differ by a single gene. Midway at an altitude of 2200 meters a hybrid population of the two races is found and all the moths living here are heterozygous. When the two races are brought to the laboratory and bred, the offsprings exhibit typical Mendelian inheritance, namely that the F_2 consisted of both homozygotes and the heterozygote. The fact that at 2200 meters only heterozygous genotypes are found showed that there is a severe selection pressure against the homozygotes at this altitude and they are all eliminated. You may observe here that differences in habitat requirements act as barriers to random mating.

Breeding between populations or races or sub-species may be effectively prevented if the seasons in which they breed are to be different. This phenomenon appears to be quite common among plants. A good example comes from the study of five species of cypress trees belonging to the genes *Cupressus.* The five species of trees have distributed themselves as ten groups each one of which could be called a sub-species. Each group has a limited distribution and may be represented by a few trees. Very rarely hybrids are formed between any two groups despite the closeness of their existence. The reason appears to be that the groups shed their pollen at different times or seasons preventing the occurrence of cross pollination. The rare occurrence of hybrids is explained by the fact that some trees shed their pollen earlier than or later than the usual time.

Seasonal isolation is very effective among the animal groups which have a highly restricted breeding seasons. This is true of all poikilothermic vertebrates and invertebrates. A revealing example comes from the study of three species of frogs living and breeding in the same pond in north eastern United States. The three species *Rana clamitans, Rana pipiens* and *Rana sylvatica* have staggered breeding seasons. *R. sylvatica* completes breeding before others arrive at the pond and *R. clamitans* begins breeding only when all others have completed. The breeding time of each species appears to be determined by the temperature of the waters of the pond which they occupy. Table 15.1 gives you temperature of the water at which the frogs begin their breeding.

Table 15.1: Water temperature requirement for breeding of different spices of Rana.

Species of frog	Water temperature at which breeding commences
Rana sylvatica	44°F
R. pipiens	55°F
R. clamitans	>60°F

Further each species has developed specific and elaborate mating call and this again prevents breeding between sympatric forms. Finally even if mating takes place between species, the development fails beyond the embryonic stage. Thus the seasonal isolation has led to sterility barrier and the three species have no chance of forming hybrids.

15.4.3 Ethological Isolation

Members belonging to different species refrain from mating because of the behavioural differences between them. Such behavioural differences usually centre around specific courtship patterns which the species have evolved. The behavior patterns are more conspicuous in animals rather than in plants. The courtship behaviour is more pronounced among terrestrial and fresh water organisms than in marine forms. Mayr points out that in those forms where there is an elaborate courtship behaviour the interspecific hybrids are rare. Closely related species that do not have pair-binding courtship rituals do commonly give rise to hybrids. Mayr is of the opinion that in species where there is a courtship behavior pattern, the “engagement” may be broken if the pairs do not belong to the same species.

A detailed study of the courtship behaviour of six species of *Drosophila* showed that courtship and mating could be divided into six phases. If there is incompatibility at any one of these six phases, the potential mates break off and the courtship is discontinued. Under laboratory conditions, the interspecific crosses have not been successful and the courtship was terminated even in the first stage. What is more interesting here is that even to a trained observer differences in courtship behavior exhibited by different species may appear to be trivial and insignificant. But the species recognise the specific signals and respond suitably. In certain other forms differences in courtship behaviour between species could be very pronounced, the courtship dances of the different species of *Uca* (shore crab) could be recognised from a distance. This is also true of mating dances of salamanders, turtles and birds.

Earlier it appeared that *Rana pipiens* consisted of a single species. This assumption was based on morphological considerations. But today researches have shown that there are a number of species and the frogs have no difficulty in recognizing their own species. Researchers could distinguish on the basis characteristic mating song of each species. Some species of birds which show only minor morphological differences can be easily differentiated by their songs.

Apart from the species specific dances and songs evolved by organisms to attract their mates. Bird songs, frog calls and the love songs by crickets and cicadas seen to identify the members of same species and prevent the mating between two different species. A study on frogs revealed that a few species can cross breed under laboratory conditions but not in the wild. Specific scents or pheromones are produced by certain organisms for purposes of species recognition. These pheromones have been proved to elicit selective response from males when left with females of two closely related species in the same area. A study by B. Patterson in Scandinavian valley has shown that nearly thirty seven species of moths belonging to a single genus live together without any interbreeding among them. The author concluded that despite all minor morphological differences among the species, conspecific matings are assured because of the specific pheromones produced by each species. Visual recognition is important in many birds. For example, Galapagos finches recognize each other by beak. A male finch may recognize and pursue a finch of different species due to fact that anatomically their beaks are not much different from one another and mistake may happen due to distance, but as soon as it is realized by male that it is the female of different species, he will withdraw. The male never involve itself with the female of other species. The beak is very conspicuous in courtship during which the male transfer the food to the beak of conspecific female. The fireflies send their sexual signals which are only responded by conspecific mate. Each species has its own flashing pattern and interval between the responded by female returning the same signal to attract the male for mating. In Angiosperms, if a pollen is transferred to stigma of another species, the germination will fail. In case the germination takes place with the formation of a pollen tube, the pollen tube will fail to reach the ovule. More or less, there is also a physiological incompatibility between the pistil and pollen. Essentially the above account tells you that specific behavioural patterns play a vital role in species recognition and serve as a powerful isolating mechanism.

15.4.4 Mechanical Isolation

In certain instances, differences in the morphology of genitalia between species make it impossible for normal mating to occur, and sympatric species tend to remain isolated. When there is no correspondence between the male and female external genitalia for copulation to occur, the members belonging to different species are reproductively isolated. When interspecific crosses occur between individuals having no exact correspondence in their genitalia, it resulted in the death of copulating pairs. Snails are usually quoted as examples of such fatal matings which occur due to mechanical differences in their genitalia. Similarly, inter-specific crosses in *Drosophila* may lead to an injury or death of either sex. The same is true for *Glossina*. In a fish, *Anableps* the male genital orifice is prolonged in the form of a tube whereas in the female a special scale which is free only on one side covers the genital aperture. This aperture is either on the right or left side. In the male also the intromittent organ is either on the right or left side, so the copulation take place side by side. So, a male with its intromittent organ on the right side copulate with female having its genital aperture on the left side or *vice versa*. The morphological specificity in animals is complex and controlled by Pleiotropic genes and any change in this gene shall alter the morphological specificity of the genital organ making the intercourse difficult or fetal. It must also be stated that differences in copulatory organs, in many instances, have not proved to be a barrier for interbreeding. Breeding between dogs belonging to different races is an often cited example.

Mechanical isolation appears to play a more important role in the speciation of plants. Since many plants are aided by insects and birds in cross pollination, a morphological compatibility is required between the plants and the pollinating agents. You may recall the example in which the flowers of different species of *Pedicularis* plant are pollinated differently by bumble bees. Further, queen bees with their long mouth parts pollinate the nectar producing species of *Pedicularis* and the other species of the plants are pollinated sternotribically or nototribically. The bees may pick up pollen of one species on a particular part of their body and this area many not come into contact with receptive structure of flower of another species, as a result the Pollen is not transferred thereby decreasing the frequency of hybridization.

15.5 POST-MATING ISOLATING MECHANISMS

The second category of isolating mechanism that may permit interspecific mating but ensures reduced viability is called post-mating isolating mechanism. This category could be subdivided into two types.

- **Interspecific sterility:** Organisms belonging to different species may mate, but may not produce any offspring.
- **Hybrid sterility:** Here the interspecific cross may result in an F_1 offspring but the offspring is invariably sterile.

We shall now briefly look into each one of these sterility mechanisms with plant and animal examples.

15.5.1 Interspecific Sterility

In interspecific sterility, the failure in mating occurs because of inability of the sperm to reach the egg in animals and the pollen to reach ovules in plants. In plants interspecific crosses usually result in the non-growing of the pollen tubes or the slowing down of the growth. If pollen from another species is transferred to a plant along with the pollen from conspecific individuals, the growth of the pollen tube of the latter is much faster than the former and the fertilisation is conspecific.

In certain cases of interspecific crosses the pollen tube begins to grow but then bursts ensuring that no fertilisation occurs. Such an event occurs when the chromosome number of the male parent is higher than female parent. For instance, three species: of tobacco plants are known to occur: *Nicotiana tabacum, N, sylvestris* and *N. tomentosa. N, tabacum* has 48 chromosomes and the other two species have 24 each. Probably *N. tabacum* is a tetraploid produced by a cross between the other two species. A cross between either of the two species and *N. tabacum* is successful only if the latter is used as a female parent. In such a cross the style tissues have 48 chromosomes and the pollen tube has only 12 chromosomes, giving a ratio of 4:1. When the cross is between *N. sylvestris* and *N. tomentosa,* the style tissue of both the species has 24 chromosomes and the pollen tube has 12 chromosomes giving a 2:1 ratio. But if *N. tabacum* were to be a male parent, and the either of the other two species a female, then the style tissue has 24 chromosomes and the pollen tube has 24 chromosomes giving 1:1 ratio. It is only under these circumstances, that is when the ratio is close to 1:1, the bursting of pollen tube occurs. It is assumed that a high osmotic pressure in the pollen tube causes it to burst and that this trait is controlled by a gene. Essentially a genetically coupled physiological mechanism prevents interspecific crosses in the tobacco plant.

There are other instances where a zygote may be formed but its further development may not occur beyond a stage. In interspecific crosses of jimson weed plant, the embryo dies around the eight cell stage. In the case of hybrid plants, it is believed that there is an inadequate nutritional relationship between the developing embryos and the endosperm resulting in the death of the embryos.

Other causes for developmental arrest or mortality of zygote may be genetical, cytological, biochemical, embryological or physiological. For eg., *Rana pipiens* and *Rana sylvatica* hybridize under laboratory condition but the embryonic development of zygote is arrested after early gastrulation. In *Ambystoma,* the zygotic mortality is due to lack of nucleolus. Gametic mortality has been reported frequently after mating of individuals from two different species. The gametes remain viable for a long time in the genital tract of conspecific individuals. The male gamete can tolerate only a narrow range of pH, temperature and humidity and due to this reason they die once outside the genital tract. When mating takes place between the individuals of different species, the sperms experience a different or changed physiological condition in the genital tract of the female and its viability is decreased to a large extent without reaching or fertilizing the ovum. Mating between different species of *Drosophila* may lead to insemination reaction where there is enormous swelling in the wall of vagina and subsequent killing of sperms. In such cases where fertilization take place between individuals of two distinct species, resulting hybrids are non-viable and die before development is complete. In many cases embryo undergo a few take place during embryogenesis as a result embryo fail to survive. Even if the embryo completes its development, its survival in nature will not be possible. *Ranunculus millani* is found in wet habitat and *R. dissoctifolius* in dry habitat. Their hybrids fail to compete with either parents in respective habitat, either fail to survive or fail to reproduce because they are sterile and have inappropriate mating behavior.

The genetic basis of interspecific sterility is not clearly understood in many cases. Yet, one good example comes from studies on the tropical fish of the genus *Xiphophorus. X. maculatus* (moon fish) carries a dominant gene (Sd) responsible for a dark spot on its dorsal fin. The gene produces macromelanophores which are potential tumours. In a closely related species X. *helleri* (swordtail), the gene occurs in recesive form (sd). A cross between the two species produced fertile F_1 offspring. The hybrid offspring has the heterozygous genotype (Sdsd) and in such a condition the fins are more heavily pigmented than the homozygous (SdSd) genotype. The Sdsd progeny always has lethal tumours. A backcross of Sdsd fish with the recessive genotype (sdsd) has shown that half the progeny have lethal genotype (Sdsd). Thus in *Xiphophorus* interspecific sterility manifests in the form of production of offsprings with lethal genes in them.

15.5.2 Hybrid Sterility

Hybrid sterility is defined as the inhibition of the reproductive capacity of F1 or later generation hybrids between genetically different populations belonging to different species. In hybrid sterility the F1 hybrid zygote is either fully viable but partially or completely sterile or a deficient F2 is produced. The hybrid sterility may have a chromosomal or genic basis. Difference between the structure of chromosome like multiple translocations are responsible for sterility because most of the gametes remain deficient for a whole chromosome (Aneuploid) or for certain portion of chromosome. A diploid hybrid between *Perimula verlicillaria* and *P. floribunda* is sterile and found in nature. They can also produce a tetraploid hybrid artificially and these hybrids are fully fertile. The diploid hybrids are sterile due to unpaired chromosomes whereas tetraploids are fertile due to paired chromosomes. This explains that sterility is caused by incompatibility in chromosome structure rather than genes. One the other hand, during the hybridization between *Drosophila pseudoubscura* and *D. persimilis,* the chromosomes pair normally but males are sterile and show aneuploidy. This is called the genic sterility. Similarly hybridization between horse and donkey produce mule which is sterile. Both horse and donkey have 33 chromosomes which do not pair and cause sterility in mule. Further, the hybrids in general are found to have grossly abnormal reproductive system. If normal reproductive system is preset, then meiosis is abnormal and nonviable gametes are produced. So, various types of reproductive isolating mechanisms operate in different groups of animals to maintain the distinctness and uniqueness of species.

SAQ 2

i) Match the following :

Column I	Column II
a) Non-meeting of the potential mates	i) Ethological isolation
b) Potential mates do meet but fail to mate	ii) Mechanical isolation
c) Potential mates meet and mate but no transfer of sperms	iii) Geographical, seasonal or habitat isolation

ii) Answer in about 50 words each.

a) Explain the concept of geographical isolation with suitable examples.

b) How does habitat preference of organisms promote speciation process?

c) Cite an example to show that highly restricted breeding seasons of populations contribute to isolation process.

d) Discuss the role played by courtship behavior and scents in the isolation process.

e) Distinguish the terms interspecifc sterility and hybrid sterility.

15.6 GENETIC DRIFT

In this section we shall be discussing a phenomenon associated with small populations. You may recall from your studies in Genetics that in large populations the frequencies of alleles tend to remain constant generation after generation provided the populations do not experience any mutation, genetic recombination, gene migration and selection. You may further recall that this phenomenon is known as Hardy-Weinburg equilibrium. But evolution essentially depends on changing gene frequencies. You may find illustrations of how gene frequencies are altered in natural populations by factors such as mutations and natural selection. Such factors although they affect gene frequencies, do it in a small way. But genetic drift is a phenomenon that causes a large change or a drift in the frequencies of genes in small populations. The phenomenon was first investigated by the American population geneticist Sewall Wright and therefore is also known as Sewall Wright effect.

It is generally believed that genetic drift occurs as a result of sampling error. As we have said earlier it occurs in small populations such as peripheral isolates. We may demonstrate genetic drift by a small experiment. Take beads of same size but different colours, say blue, red, green and yellow. Take a thousand of each colour and mix them well in a bag or mug. 4000 beads now constitute a population. Now put your hand in without looking, pick up just four beads with your finger tips. Let us say that you get two blues, one red and one green. This will mean that the blues have increased from 25% to 50% but the yellows are reduced to zero. You could see that the random drifting or large scale changes in the frequencies of coloured beads is a result of sampling error. Just as the frequencies of coloured beads drift randomly in the experiment, in small populations or peripheral isolates gene frequencies may drift due to sampling error. Hence the phenomenon is known as genetic drift.

Can such drift be observed in natural populations? The answer appears to be yes. Let us take a small population of mice living in the rice barn of a farmer as four or five extended families. The farmer tries a variety of methods like setting up of traps, use of a shot gun, surprise visits, cats etc, to eradicate them. Such acts of the farmer exert a severe selection pressure on the mice. Under such circumstances the trails that would be selected are the swiftness, short tail, hearing acuity, and cautiousness. Naturally the frequencies of the alleles that control these traits would tend to be high in the population as only those mice which possess such traits can survive in an hostile environment. After a couple of months, let us say there is an environmental change and a severe winter sets in. The farmer confines himself to a fire place and as a result the selection pressure on those traits we mentioned earlier is now lifted. And in order to survive in a changed environment, the mice need to possess totally a different set of traits and essentially mice with such traits would be selected for. Thus swiftness and visual acuity are no more the traits that would be selected for, but the mice with a thick fur on them and similar such traits which would protect them from the severity of the winter would be selected. The net result is that the frequencies of the alleles that controlled the traits in the earlier environment undergo a drift i.e., their frequencies become significantly low in the new environment. It should be emphasised that such a drift is characteristic of only small populations.

Sewall Wright suggested that genetic drift may have important consequences for evolution. At one time he even seemed to have suggested that, in special circumstances, genetic drift may override Darwinian natural selection. This view was criticised by the Oxford biologists R.A. Fisher and E.B. Ford who showed that natural selection is the chief agent of evolutionary change not only in large and medium populations, but also in very small populations. E.B. Ford demonstrated the occurrence of wingspot polymorphism in small populations of Meadow Brown butterflies in the Isles of Scylly, at the South Western tip of England. For, where the polymorphism occurs, it is the surest indication that natural selection is operating at its highest potential. Sewall Wright also found such arguments to be true and has now modified his genetic drift theory into a more acceptable shifting balance theory.

Genetic drift can easily be confused with natural selection. The difference is whether or not the allele is actively participating in the change in allele frequencies. If the allele affects an organism in a way that causes more reproduction of the DNA, the allele will increase in frequency. If it causes harm, it will decrease. This is caused by the allele's direct effects on the organism and the environment. This is natural selection. When the allele is increased or decreased simply because it was present in the organisms that survived, this is genetic drift. There are two types of genetic drift (Fig. 15.5).

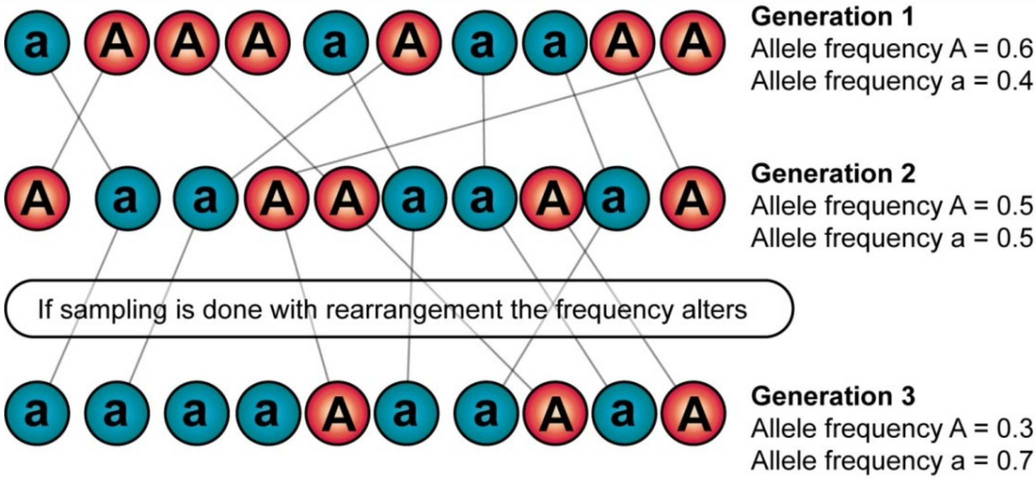


Fig. 15.5: Genetic drift can be seen if there is rearrangement and selection.

15.6.1 Population Bottleneck

A population bottleneck or genetic bottleneck is a sharp reduction in the size of a population due to large scale environmental events like earthquakes, floods, fires, disease, or droughts, anthropogenic activities and large scale insecticide use which can reduce the variation in the gene pool of a population. Thereafter, a smaller population, with a correspondingly smaller genetic diversity, remains to pass on genes to future generations of offspring through sexual reproduction. Genetic diversity remains lower, increasing only when gene flow with another population occurs or very slowly increasing with time as random mutations occur. As a consequence of such population size reductions and the loss of genetic variation, the robustness of the population is reduced and its ability to adapt to and survive selecting environmental changes, like climate change or a shift in available resources, is reduced. Alternatively, if survivors of the bottleneck are the individuals with the greatest genetic fitness, the frequency of the fitter genes within the gene pool is increased, while the pool itself is reduced. The genetic drift caused by a population bottleneck can change the proportional distribution of alleles by chance and even lead to fixation or loss of alleles. Due to the smaller population size after a bottleneck event, the chances of inbreeding and genetic homogeneity increase, leading to the potential for inbreeding depression to occur. Smaller population size can also cause deleterious mutations to accumulate (Fig. 15.6).

A slightly different form of a bottleneck can occur if a small group becomes reproductively (e.g. geographically) separated from the main population, such as through a founder event where for example a few members of a species successfully colonize a new isolated island, or from small captive breeding programmes such as animals at a zoo. Alternatively, invasive species can undergo population bottlenecks through founder events when introduced into their invaded range.

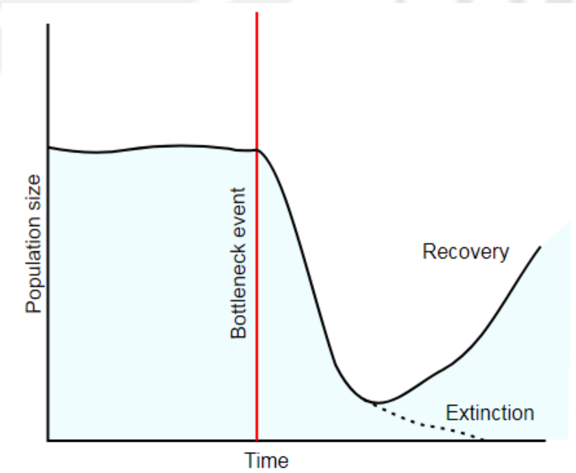


Fig.15.6: Bottle neck effect showing reduction of population.

Population bottlenecks play an important role in conservation biology (see minimum viable population size) and in the context of agriculture (biological and pest control). During 1980, elephant seal was hunted to a large extent and by 1890 only 20 of them were left. These seal breed in harem style where a single male mates with a group of females. It is quite possible that due to this type of mating all the offsprings at this extreme bottleneck point must have the common father. Since 1890 the population of elephant seals increase upto 30,000. Biochemical analysis revealed that all these seal were genetically almost identical. Other species of seals that maintained their population high exhibit a high genetic variability. The rescue of elephant seal from their extinction was possible due to their conservation. This seal has a very low potential for evolution in response to environmental changes. It does not matter that that they have very low population but example proves that such other species which are on the verge of extinction due to population bottleneck may be considered for protection through conservation. Chettah is another species that exhibit almost no genetic variation, however, the reason for this bottleneck is not known. It is believed that (i) they were killed in large numbers by cattle farmers to protect their live stocks, (ii) were hunted in large numbers as a game and (iii) were captured by Egyptians as pets. At present they are suffering from high infertility due to intense breeding that took place after bottleneck. Antibiotics kill harmful bacteria in your system, regardless of what alleles they have. The populations of harmful bacteria that cause symptoms are severely reduced until they no longer cause symptoms. If someone quits his/her antibiotic regiment before all the bacteria are killed, a small population is left. This much smaller population could have allele frequencies that are very different from the original population of bacteria. These changes do not reflect the success or failure of the different alleles, but rather the effects of random selection of bacteria. The new alleles will dominate the population until selection or more genetic drift cause the allele frequencies to change (Fig. 15.7).

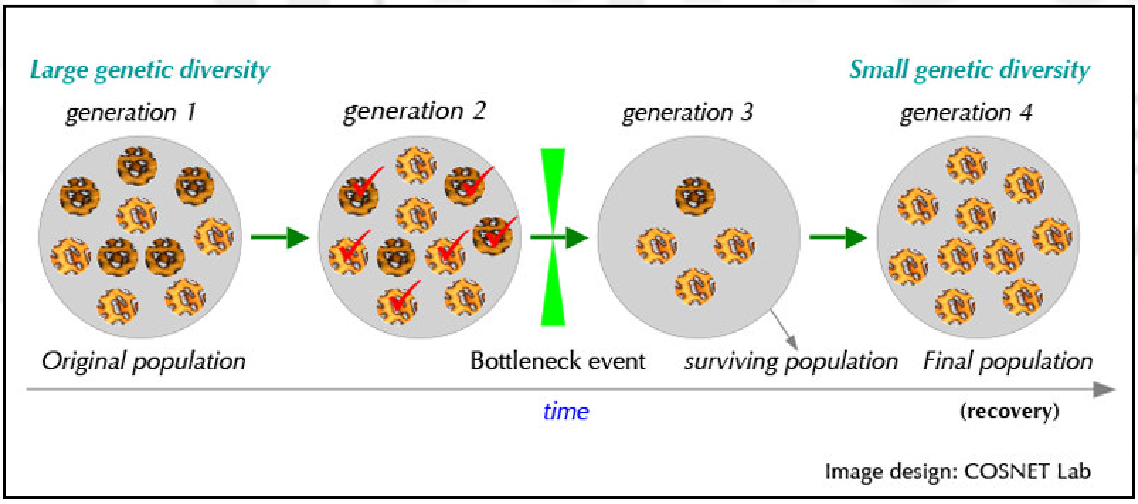


Fig.15.7: Showing Population bottleneck.

15.6.2 Founder Effect

In another type of genetic drift known as the founder effect, a new population is formed, or founded, in a new location. If this new population does not interact and reproduce with the main population, the allele frequencies in this population will be much different from that of the parent population. Many islands, contain species that only exist on a single island because of the founder effect. For instance, if only two birds of a species land on an island, their alleles alone will account for the diversity. While these alleles will dominate at first, mutations will arise in the population that will lead to new adaptations. Because the two populations of birds are separated, they cannot share this new adaptation. With enough time, the two populations can diverge to a point which they can no longer interbreed. This is one way that separate species are created (Fig. 15.8).

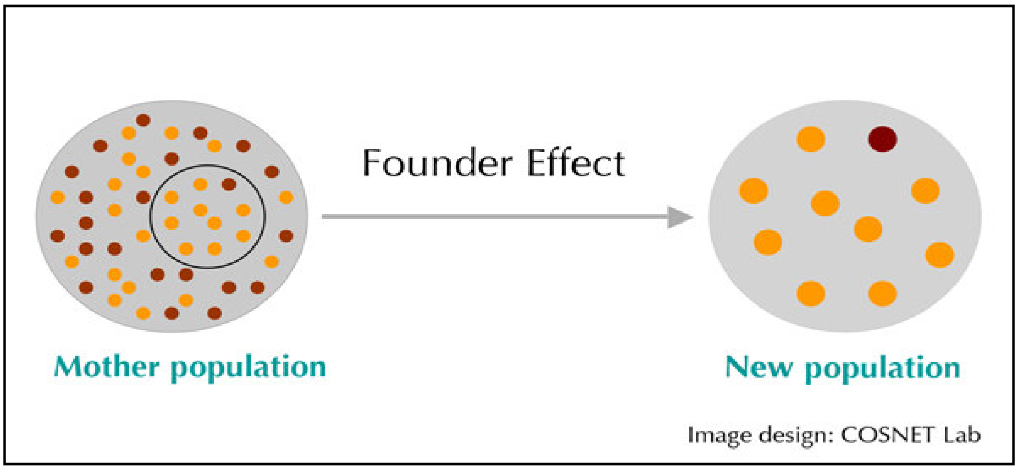


Fig. 15.8: Founder effect shown in mother population.

In a hypothetical population situation suppose a population of rabbits lives in the woods. The rabbits have many different coat colours: black, brown, tan, white, grey, and even red. In the population, the different alleles that create coat colour are equally distributed. A disease comes into the rabbit population and kills 90% of the rabbits. The only rabbits that are left are red and grey rabbits, simply by chance. The genes have thus "drifted" from 6 alleles to only 2. This is an example of a bottleneck effect. Whereas in real life genetic drift happens all the time in populations, although it is not easily seen. Often, mutations arise that have little effect on the organism. These mutations get passed on if the organism reproduces, and do not get passed on if the organism does not survive. Although genetic drift used to be thought of in only small populations, however, even large populations experience genetic drift of certain alleles, because a small number of individuals carry the alleles. Whether or not these alleles are duplicated is not a function of natural selection, but of chance. Many alleles come or go in populations without affecting great change.

SAQ 3

Fill in the blanks:

i) Genetic ……………… can easily be confused with ……………… selection.

ii) ……………… kill harmful bacteria in your system regardless of what ……………… they have.

iii) In a type of genetic drift known as ………………, a new population is formed.

iv) In real life ……………… ……………… happens all the time in population.

15.7 SUMMARY

Let us summarise what you have studied so far:

- Evolutionary changes occur due to many progressive events including natural selection, isolation, genetic drift, gene flow and mutations. These changes also play vital role in evolution of species.
- The concept of genetic repatterning in which a new population develops from the early colonisers of the island by a process of genetic revolution is explained. Reduction in variability, elimination of homozygote recessives by inbreeding process, overdominance resulting in heterozygote superiority and non-allelic epistatic interactions are some of the genetic events that break the genetic cohesiveness of populations. Such events render the founder population more plastic and pliable and move it into a new species with better adaptations.
- Genetic repatterning is one of such event which is seen from the initial colonization of species in a deserted or non habited area which tends to eliminate the recessive gene from the population as they grow.
- Reproductive Isolation is a mechanism by which individuals are able to maintain the species content. The reproductive characteristics prevent species from fusing.
- The different types of isolating mechanisms–the geographical, ecological, mechanical, ethological and reproductive (both pre-mating and post-mating) promote the formation and distinctness of species.
- Isolating mechanisms are particularly important in the *biological species concept*, in which species of sexual organisms are defined by reproductive isolation. There are two broad kinds of isolating mechanisms that are pre mating Isolating mechanism and post-mating isolating mechanism.
- Genetic drift is a process that may operate in small populations bringing about large scale changes in gene frequencies. This is also known as Sewall Wright effect, in small populations in which the drift is due to sampling error.
- Along with natural selection, mutation, and migration; genetic drift is also a basic mechanisms of evolution.
- It is the change in the frequency of an existing gene variant (allele) in a population due to random sampling of organisms as there are mainly two types of genetic drift i.e., Population Bottleneck and Founder Effect.

15.8 TERMINAL QUESTIONS

1. To what type of isolation the following barriers contribute to?

   a) Oceanic islands inhabited by amphibians ……………….. .

   b) Salt water as a barrier for fresh water organisms ……………….. .

c) Large bodies of water as barrier for land birds ……………….. .

d) Priaries as barrier for forest organisms ……………….. .

e) Mountains as barriers for low land organisms ……………….. .

f) Restricted breeding seasons ……………….. .

g) Courtship patterns ……………….. .

h) Specific mating calls ……………….. .

i) Distinct morphology of genitalia ……………….. .

j) Hybrid sterility ……………….. .

k) Higher chromosome number of male parent ……………….. .

2. "In small populations the gene frequencies often tend to drift". Justify the logic of the statement with a suitable example.

15.9 ANSWERS

Self Assessment Questions

1. When a new population develops from early colonisers of the islands they undergo a variety of genetic changes by way of reduced variability, elimination of recessive homozygotes, reduction in genetic load, superior fitness of heterozygotes and non-allelic epistatic interactions, all of which result in a genetic revolution or more precisely the genetic repattering.

2. i) a) iii), b) i), c) ii).

   ii) a) The concept of geographical isolation refers to the restriction of organisms to certain specific geographical regions with suitable ecological features. For instance oceanic islands are not inhabited by amphibians. Pacific ocean receives many parallel streams of fresh water each of which has its own species or sub-species of fishes which live isolated.

   b) Habitat preference do promote speciation process. In Swiss moth, *Nemeophila plantagenis* the habitat preference of the two races appears to contribute to the speciation process. One race of the moth lives at an altitude of about 2700 meters and the other race below 1700 meters. Although the two races breed in the laboratory the hybrid population is confined at an altitude of 2200 meters.

   c) The five species of Cyprus trees of the genus *Cupressus* are divided into 10 groups. Each one of these could be called as sub-species. Very rarely hybrids are formed between two groups although the groups live close enough. The reason appears to be that the groups shed their pollens at different times or season, preventing the occurrence of cross pollination.

d) Courtship behaviour patterns which are very specific for each species act as a deterrent for the members belonging to different species. Mayr opines that where there is courtship behaviour pattern the engagement may be broken if the pairs do not belong to the same species. Similarly specific scents produced by certain organisms to attract their mates help in the process of species recognition.

e) In Interspecific sterility organisms belonging to two different species may mate but may not produce any offspring. In Hybrid sterility the interspecific cross may result in a sterile F_1 offspring.

3. i) drift

ii) Antibiotics, alleles

iii) Founder effect

iv) Genetic drift

Terminal Questions

1. a) Geographic isolation

b) Geographic isolation

c) Geographic isolation

d) Ecological isolation

e) Ecological isolation

f) Ecological isolation

g) Ethological isolation

h) Ethological isolation

i) Ethological isolation

j) Mechanical isolation

k) Reproductive isolation

l) Reproductive isolation

2) In small populations genetic drift occurs due to sampling error. It refers to accidental but pronounced fluctuations in the frequency of a particular allele. In a population consisting of 100 individuals, assuming an allele is present only in one individual, the chances are that either the allele is irrevocably eliminated from the population in one or two generations or the frequency of allele may increase by 10%. In other words, due to genetic drift, the genes may be consequently lost or completely fixed in small populations. For an example refer to Section 15.6.2.

UNIT 16

SPECIES EXTINCTION

Structure

16.1 INTRODUCTION

In the unit 16 you have studied about macro-evolution and its mechanism and pattern. In the present unit you will learn regarding species extinction. As you know, there has been a continuous increase in the biodiversity on the earth ever since first life originated about 3.5 billion years ago. However, this increase has not been steady and characterized by the fast pace of speciation being followed by periods of negligible change and then episodes of mass extinction. Extinction is actually a very common feature of life on the earth when viewed over long (e.g. geological) timescales. More than 99% of the species that have ever lived have gone extinct. The concept of extinction was first proposed by the scientists in the late 18th century. Georges Cuvier, a naturalist studied the fossils of an animal now known as the American mastodon, or *Mammutamericanum*, and arrived at the conclusion that all such creatures must have died out in the distant past. Cuvier is now being praised for being ahead of his time but in his own lifetime, many of his ideas about extinction were harshly criticized.

Extinction is one of the most common of all ecological/evolutionary processes and information on extinction comes from many sources, including laboratory experiments, field studies and the fossil record. **In simple words extinction means death of a taxon.** But in a broad sense extinction also includes the effects of its disappearance from the environment with which it has interacted. Short term extinction involving few species and causes of their extinction can be well understood whereas the causes of long term extinction is still a topic of debate. We will discuss these aspects of extinction in this unit.

Objectives

After studying this unit, you should be able to:

- define various terms related to extinction,
- explain the relationship between extinction and speciation,
- distinguish among different types of extinction,
- analyse the causes and influence of big five mass extinctions, and
- explain the phenomenon of sixth extinction.

16.2 THE MEANING OF EXTINCT

A species is said to be extinct when the last individual of that species disappears. The extinction of the genus is followed by the death of last individual of the last species of that genus and so on. In historical times, the death of the last individual of small number of species followed by its extinction has been observed in reality. For example, the last Tasmanian tiger (*Thylacinus cyanocephalus*), a wolf-like marsupial mammal, died in Hobart Zoo on 7 September 1936. however, unconfirmed sightings of Tasmanian tigers in the wild are still occasionally reported, illustrating that even for such a large and distinctive contemporary animal it is very difficult to verify its extinction.

A species is **extinct** when no member of the species exists anywhere on the earth.

A species is **extinct in the wild** if it exists only alive in captivity.

A species is **locally extinct** if it is no longer alive in its habitat but is still found in other areas.

A species is **ecologically extinct** if it persists in very few numbers so that its effects on other species are negligible and unimportant.

16.2.1 Pseudoextinction

There are two reasons for the species (or higher taxa) extinction. Real extinction is when the lineage has died out and left no successors. This is clearly defined for modern species, but for fossils, real extinction has to be distinguished from pseudoextinction. **Pseudoextinction of a species occurs when all the members of the species are extinct but members of daughter species are alive.** This may be an error or artefact in the evidence, and not because the underlying lineage really ceased to exist.

There are three types of pseudoextinction, the first two of which are due to taxonomic artefacts described as under:

1) Species may sometimes evolve into a new form and may change its taxonomic name. Due to continuous evolution, later forms may look sufficiently different from earlier ones. The ancestor species cease to exist even though there is a continuous breeding lineage and the relationship between the ancestor and the descendant still exists.

2) A higher taxon may cease to have any members if it is defined phenetically and only some divergent lineages persist. A higher taxon, such as a family, can undergo pseudoextinction if the taxon is defined phenetically.

3) Some lineages, called Lazarus taxa, apparently disappeared entirely for short or extended periods by pseudotermination but later it reappears. The first disappearance is a pseudoextinction, and may be misrecorded as a real extinction if the later reappearance is overlooked for some reason.

16.2.2 Vulnerability to Extinction

When environments are damaged by human activity, the ranges and population sizes of many species will be reduced, and some species will go extinct. Rare species must be carefully monitored and managed in the efforts of conservation. Ecologists have observed that particular categories of species are most vulnerable to extinction. The five categories most frequently used in conservation planning are as follows:

- Species with a narrow geographical range
- Species with a single or a few populations
- Species with small population sizes
- Species in which population size is declining
- Species that is hunted or harvested by people

The following categories of species have also been lined up to extinction, though they are not considered as all-encompassing as the previous five categories:

- Species that need a large home range
- Animal species with a large body size
- Species that are not effective dispersers
- Seasonal migrants
- Species with little genetic variability
- Species with specialized niche requirements
- Species that are found in undisturbed and unspoilt environments
- Species that forms permanent or temporary aggregations
- Species that have not had prior contact with people
- Species that have recently become extinct or threatened with extinction of closely related species

Before proceeding further, try to answer the following SAQ:

SAQ 1

Give ansers for each of the following:

i) When all the members of the species are extinct but members of daughter species are alive.

ii) The concept of extinction was first proposed in the late 18th century by the scientists.

16.3 NATURAL CAUSES OF EXTINCTION

Extinction is a unavoidable consequence of natural selection. The discovery that species go extinct was made relatively recently in human history: it dates from the late eighteenth and early nineteenth centuries. As the global flora and fauna became better and better known through the eighteenth century, it became increasingly likely that some fossil forms were no longer alive. Extinction is a normal process but human-mediated extinctions rates have soared over the past few hundred years (Fig. 16.1). Devastating growth in human population over more than 50,000 years has given quantitative negative footprints to the biodiversity. This has led directly or indirectly in the 100- to 10,000-fold increase in the ‘‘natural’’ or ‘‘background’’ extinction rate that normally occurs as a consequence of gradual environmental change, newly established competitive interactions (by evolution or invasion), and occasional chance calamities such as fire, storms, or disease. Estimation of present and future extinction rate is done using variety of measures such as species–area models and changes in the World Conservation Union’s (IUCN) threat categories over time. Based on the global assessment of all known species, some 31, 12, and 20% of known amphibian, bird, and mammal species, respectively (by far the best-studied of all animal groups), are currently listed by the **International Union for Conservation of Nature and Natural Resources (IUCN)** as under threat.

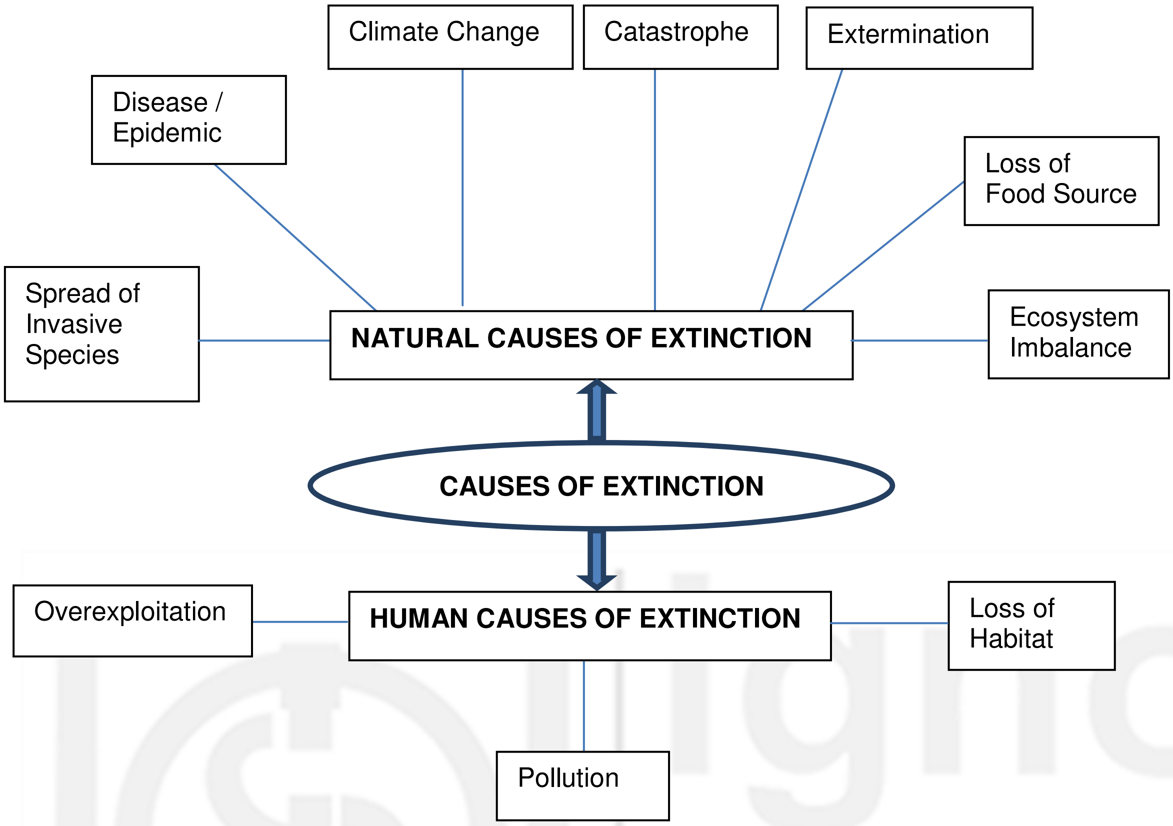


Fig. 16.1: Causes of Extinction.

Let us now discuss about various natural causes of extinction in the following subsection.

16.3.1 Climate Change

Climate Change is caused by a number of things and its effect on the extinction is very big. Sometimes periodic natural climate changes that occurred too rapidly resulted in the death of certain organisms that have not been able to move or adapt. Huge species extinction occurred in the last ice age and also the extreme warming made the environment intolerable to the cold adapted creatures. Atmospheric change like the rapid evolution of plants and hence increase in oxygen led to the extinction of approximately all other life forms. As for those oxygen was toxic. Great lives were lost in the deep past as a result of sudden increase in methane. And today, we are in the midst of another great extinction, this one is due in part to the sudden increase in CO_2 and in part to toxins introduced by human industry. The changes in sea levels and currents are a result, in part, of the melting freshwater. The currents on which the marine life depends was formed when the denser, saltier water sinks. Small rise in the ocean floor can displace a lot of water onto the already occupied land. Therefore, spreading and rising of ocean floor also affects sea level. The gases from the volcanic activity absorbed by the water can change the chemical composition hence making it unsuitable for some life forms.

16.3.2 Catastrophe

All sorts of catastrophic events can cause extinctions. In the Earth's history, at times, the atmosphere has been made so toxic and hot due to massive volcanic eruptions that many organisms were not able to survive. The great meteor that struck Earth 65 million years ago destroyed the impact site completely at that time. It is well known that a meteor impact on the Yucatan peninsula in Mexico caused the disappearance of the dinosaurs 65 million years ago. Hypothesis says that too much exposure to cosmic radiations. Can cause gene mutation. But, it is extremely difficult to avoid these radiations as they are sourced from space and the sun. Supernova remnants are one source of cosmic radiation.

16.3.3 Loss of Food Source

Massive disasters like fire and floods may lead to food starvation of organisms. Organisms that are incapable of moving or changing their food habits or lack adequate nourishment are supposed to become extinct. Mass starvation is the quick, one-way, sure-fire route to extinction—specially since hunger-weakened populations are much more prone to disease and predation—and the effect on the food chain can be disastrous.

16.3.4 Disease/Epidemic

Due to climate change, certain species become more susceptible to disease and epidemics which can lead to their eventual extinction. Many types of diseases –from fungi, viruses, bacteria—spread and kill faster than the antibodies and other defences can adapt. For example: a fungus is spreading rapidly in the isolated population of Tasmanian wolf and the future prospects of their survival is negligible. Amphibian chytridiomycosis (a fungal infection that ravages the skin of frogs, toads, and salamanders and causes death within a few weeks) and Tasmanian devil facial tumour disease (DFTD) currently are the two very infectious diseases, threatening to cause extinctions in Australia. Anthropogenic changes are most probably going to enhance emerging disease threat to biodiversity and it is critical to further develop strategies to manage these threats. Anthropogenic changes include movement of diseases and hosts, habitat destruction and fragmentation and climate change.

16.3.5 Spread of Invasive Species

Invasive species spread foreign territory and utilize the resources of the other species. Once competition increases, as a result of the survival of the fittest plan, usually the natural species will die off. Invasive species may be the prime cause of extinction in island ecosystems. The prime cause for the global extinction of local flora and fauna continues to be introduction of predators, parasites and pests by human beings, especially to islands. For Example, introduction of European red foxes had negative influence on many species, and were responsible for the extinction of the desert rat kangaroo and feral cats. That would have resulted in the extinction of several ground-dwelling birds.

According to National Geographic, examples of some of the species that became extinct because of invasions include:

- In 1979, the Yunnan lake newt in part of China went extinct after the introduction of exotic frogs and fish in their habitat.
- In 1985, invasive predators made the Hawaiian thrush extinct in part.
- In 1983, the extinction of the Guam broadbill, a bird was marked as the result of introduction of the brown tree snake to its habitat.

16.3.6 Extermination

In case of accidental transplant of a plant or animal of one ecosystem into another (usually by an unwitting human or an animal host), it can reproduce wildly, resulting in the extermination of the native population. Some massive animals like mastodons of North America were possibly eliminated by Stone Age humans. Past two centuries have witnessed deliberate eliminations as well as exterminations of many species of mammals, birds, fish and plants by hunting done by humans.

16.3.7 Ecosystem Imbalance

All organisms live within a system of interdependent relationships with other species.

Elimination or extinction of any one key species within the system is capable of bringing an unfortunate elimination of several others. For example, elimination of top predators such as sharks (killed for their fins) can cause disturbance in the ecological balance and leading to the loss of one or more species within their specific ecosystem.

16.4 HUMAN CAUSES OF EXTINCTION

Extinctions caused by humans are not necessarily new phenomena according to the studies done by **IUCN** but today it is becoming much more rapid. Some experts estimate the present rapid loss of species to be between 100 and 1,000 times higher than the natural extinction rate, unlike other's estimated rates as high as 1,000-11,000 times higher. In comparison to other large bodied animal small bodied species are more likely to suffer from the changes that happened to the planet due to indulgence by humans.

Extinctions can disrupt our ecological processes like pollination and seed distribution and a collapse of the food chain which can cause more extinction. Regardless of the state their presence (alone or in combination), these stressors result in small, fragmented populations of wild flora and fauna that get highly influenced to inbreeding, and to the risks of small abundance that is also known as demographic instability. Stressed population usually decline further when not interfered with and become endangered.

16.4.1 Overexploitation

Overexploitation or unsustainable hunting and harvesting causes mortality at high rates and the population becomes severely reduced in numbers. In fact their populations can drop to an extent from which they cannot recover. The pattern of overexploitation of plants and animals in many cases are very similar. Several examples like the ivory of the elephants, the fur and organs of the tiger, the deliciousness of tuna and the supposedly medicinal effect of shark's fin, clearly tell why we have hunted animals to the point of extinction. Also, the dodo, passenger pigeon, great auk, and Steller's sea cow were hunted to extinction. Then there are thousands of rare species worldwide which are harvested and sold for the various purposes like pets, houseplants, wood, or herbal medicine. According to the report of The World Wide Fund (WWF), 23% of extinctions are solely caused by overhunting. Over-consumption and killing of many animals by humans for economic gains is a reason of their forced extinction. In early times overhunting has caused extinctions of giant lemurs and elephant birds in Madagascar, Miss Waldron's red colobus monkey in Ghana, moas in New Zealand, Alagoascurrasow in northeastern Brazil and giant kangaroos in Australia.

Commercial fishing and whaling demonstrate this pattern well, with the industry working one species after another to the point of diminishing returns, a process sometimes termed "fishing down the food chain". Since the eighteenth century, most of the world's baleen whale species, and several toothed whales are threatened with extinction due to commercial whaling for the purpose of meat and oil.

16.4.2 Pollution

Pollution is increasingly becoming an important factor in the detriment of wildlife and biodiversity. Pesticides, cleaning agents, drugs, carbon emissions, and other chemicals used by humans are making their way into the food webs of many ecosystems around the globe. When unnatural chemicals get introduced into air, soil and sea, contamination caused to these interferes with the metabolism of animals which is intolerable to them.

Carbon monoxide, sulphur dioxide and nitrogen oxides are air pollutants. Water and soil pollutants include heavy metals such as mercury, cadmium and lead – and pesticide and herbicide compounds.

All of these factors work in alliance with each other, causing the extinction at a very high pace. The bald eagle is a common example of a species that became endangered due to the use of a pesticide called DDT. This led to the discovery of bioaccumulation and biomagnification, which is the steady increase in concentration of a contaminant with increasing level in the food chain. DDT is not metabolized and does not break down in the body and since it is not excreted, the carnivore accumulates most of the DDT that was present in all of the prey organisms. DDT interferes with calcium deposition in eggshells, causing them to be thin, fragile, and often crushed by the parents in the nest.

Acid deposition is the falling of acids and acid-forming compounds from the atmosphere to Earth's surface. Acid deposition includes acid rain, acid snow, acid smog, and other acidic material. The burning of fossil fuels like nitrogen oxides and sulphur oxides are combined with air where they combine with water to form nitric acid and sulphuric acid which result in acid rain. Acid rain dissolves nutrients in the soil, including calcium and potassium, rendering them unavailable to plant life. It is lethal to microorganisms, hence preventing decomposition from returning nutrients to the soil. Acid deposition also reduces agricultural yields and corrodes marble, metal, and stonework, an effect that is noticeable in cities. Thus, the forests in these areas are dying and acidification of lakes directly kills algae, invertebrates, amphibians, and fish, ultimately increasing the rates of extinction.

16.4.3 Loss of Habitat

Climate change and natural disasters can destroy habitat. But the biggest cause of extinctions today is human population. The land use practices like deforestation, urban and suburban development, agricultural cultivation, and water management projects put tremendous pressure on organisms and/or destroy their natural habitat.

It is opined that we will lose all our rainforest in next coming 100 years if we are incapable of ceasing deforestation. Thirteen million hectares of forest have been either destroyed completely or converted. Our coral reefs are also under threat. These are home to around 25% of marine animals and unfortunately 27% of coral reefs have been destroyed till date. Where the large animals, including elephants, buffalo and the predator cats, cannot adapt to their shrinking territories, some species are able to move to new territories. But many are perishing.

SAQ 2

Give one/two words answer for each of the following:

i) The reason that caused the disappearance of the dinosaurs 65 million years ago-

ii) The phenomenon of the steady increase in concentration of a contaminant with increasing level in the food chain, is called as.

16.5 MASS EXTINCTION AND SPECIATION

Extinction is a natural process. Background extinction and Mass extinction are of two types of extinctions.

16.5.1 Background Extinction

Considering ecological factors such as climate change, competition between species, loss of habitat and available resources, the average rate of extinction across geological history has been about 10-25 species per year. This is known as background extinction and is a regular event in the process of evolution. It is **caused by the poor adaptation to the ongoing changes in the environment and** the rate of the background extinction is steady over geological time.

16.5.2 Mass Extinction

Mass extinction occurs due to rapid environmental changes and **exposure to harsh conditions during a short period of time** where species do not have sufficient time to adapt to the changes. Mass extinction has been periodical process throughout the existence of life on Earth. A mass extinction is a relatively sudden, global decrease in the diversity of life forms within a short period of geological time.

Occurrence of following is essential for a mass extinction:

- Extinctions occur all over the world.
- A great number of species go extinct.
- Different and many types of species go extinct.
- The extinctions are arrayed in a small periods of geological time (a few million years).

Similarities between Background Extinction and Mass Extinction

- Background extinction and mass extinction both are involved in the elimination of species from the earth.
- Background extinction and mass extinction both occur due to either continuous or fast environmental changes.

Difference between Background Extinction and Mass Extinction

- Ecological factors such as the climate change, loss of habitat, and competitive disadvantages related to other species cause the background extinction while mass extinctions are caused by the overly rapid, widespread environmental changes and catastrophic global events.
- Background extinction requires a long time but Mass extinction occurs within a short period of time.
- Background extinction is a continuous process, which is a result of the evolution. Mass extinction occurs due to rapid environmental changes.

16.5.3 Speciation

Speciation is the evolutionary process by which populations evolve to become distinct species. Destruction of biodiversity due to extinction is incomprehensible, but this destruction, however, is not the whole story. One method to acknowledge as to how extinction develops new niches is to review mass extinction events – geologically brief periods where great numbers of species go extinct simultaneously. During the period of extinction, the changes in the environment were very fast and most of the species were not able to keep evolutionary pace with the changing environment. As a result almost 90% species living in the world in that era went extinct. But extinction is a driving force for novelty and every mass extinction was followed by speciation.

In fact, this pattern is the rule and not an exception. For example, following the Permian mass extinction, we observe a constant increase in new species. But there are many species that were earlier not known in the fossil record. The Permian extinction caused the loss of so many species and changed the evolutionary landscape for the surviving species. This resulted in the explosion of speciation that appears very fast when viewed in geological time scale. The most famous Cretaceous – Paleogene (KPg) extinction event was similarly followed by outbreak of mammalian speciation, as small mammals that survived the extinction radiate and fill niches left open up by the dinosaurs. Without this event, the direction of evolution of mammals would certainly look very distinctive.

SAQ 3

Fill in the blanks:

i) A relatively sudden, global decrease in the diversity of life forms within a short period of geological time is …………….. .

ii) Every mass extinction is followed by ……………… .

16.6 BIG FIVE MASS EXTINCTIONS

Mass extinctions are very mysterious phenomena. According to the scientists, when a great number of species go extinct simultaneously, at the same time, something traumatic must have happened during the ancient past environment. Thus, they identify mass extinctions by tracking the life spans of species through the fossil record. Mass extinctions were not at all instantaneous but were really a combination of a number of large scale extinction events that would have occurred within a relatively short span of time (which in geologic past could mean a few hundred thousand years) leaving devastating effects.

There have been five episodes of natural mass extinction in the fossil record. During each of the five episodes of natural mass extinction a large percentage of species disappeared (Table 16.2). A sixth episode, beginning around 30,000 years ago up to the present time, incorporates the effects of hunting and habitat loss as human populations have spread across the continents (explained in Sixth Extinction).

Table 16.2: Periods of Extinction and their respective effects.

Period of Extinction	Millions of years ago (mya)	Losses	Type of Life Effected
Ordovician-Silurian	439	85% of all species	corals, trilobites, branchiopods, echinoderms and similar marine organisms

Devonian	360	75% of all species	corals, brachiopods, bryozoans, ammonoids fish, placoderms, acanthodians and agnathans
Permian-Triassic	251	96% of all species	trilobites, molluscs, brachiopods and many vertebrates
Triassic-Jurassic	205	95 percent of marine species and more than 70 percent of terrestrial ones	Molluscs, sponges, marine vertebrates, large amphibians
Cretaceous–Paleogene	65	75% of all species	Ammonites, marine reptiles, dinosaurs, microscopic marine planktons, bivalves and echinoderms

Many minor extinctions have occurred through the Earth's history.

16.6.1 The Ordovician-Silurian Extinction

The very first mass extinction in Earth's history was the Ordovician-Silurian Extinction about 439 million years ago(mya). In fact, the Ordovician-Silurian extinction was the second most devastating mass extinction in the eartht's history. This extinction event ocurred during the Hirnantian Age of Ordovician Period followed by Rhuddanian Age of the Silurian Period. The end-Ordovician extinction is generally characterized by two factors: the first phase of extinction is widely known to have occurred due to rapid cooling at the end of the Ordovician Period, and the second phase as caused by the sea-level fall associated with the glaciation. The drop in sea level would have caused the draining of the large epicontinental seas and subsequent reduction in the available habitat for organisms living in these areas. There are no records that would suggest a collision (meteorite or comet) impact like the one identified at the end of the Cretaceous Period as no concentration of iridium has been identified near the extinction. Considering that much of the flora and fauna of that time was adapted to shallow, warm waters, this was really devastating. These species were not able to tolerate the colder, deeper oceans and many were diminished. Almost 85% of the species on the earth went extinct such as corals, trilobites, and similar marine organisms. It was so bad that over 100 families went completely extinct, including about 1/3 of all families in the phylum *Brachiopoda* (animals that created many of the seashells of the ancient world).

Scientists earlier believed that the mass extinction was caused by an ice age which happened when one of the four supercontinents – Gondwana moved to the South Pole. While ice age is still one of the most popularly accepted theories for this mass extinction event, there are other theories also. According to one other theory, a sudden burst of gamma rays triggered the extinction.

There was a ten-second burst that left the earth's atmosphere bare of almost half of its ozone instantaneously, exposing most of the organisms to high levels of UV radiation. But volcanism and weathering were considered to be the final possible climatic causes that would have led for the extinction.

According to a new hypothesis, galactic Bow Shock (a bow shock forms when material in front of a moving object is compressed) event may also be a possible cause of the Ordovician-Silurian extinction. Our Milky Way galaxy moving at a rapid pace through space, may compress the intergalactic gas in front of it. Once the Solar System is out of the protective magnetic field of the galaxy, it becomes exposed to the cosmic rays that are caused by Bow Shock created by the Milky Way. Thus, it is possible that radiations from galactic Bow Shock could have caused the Ordovician mass extinction with deadly radiations causing DNA damage and genetic mutations that would have wiped out more than 60% of life forms on the earth.

16.6.2 The Devonian Extinction

The Late Devonian extinction that took place approximately 360 million years ago is a complex and poorly understood. Another global cooling trend and lowering sea levels led to the **Devonian extinction**, when about 75% of all species went extinct. The impact of an extraterrestrial body such as a comet has also been considered as one of the possible cause. Tropical species that lived in shallow seas were the most affected. Particularly most affected were bryozoans, ammonoids, corals, brachiopods and fish. Marine animals were hard hit though freshwater fish were barely affected. Placoderms, acanthodians and almost all agnathans were not able to survive and vanished once for all. The Late Devonian mass extinction is considered to be a prolonged marine biotic crisis extending for 20-25 million years (late Middle Devonian to the Devonian/Carboniferous boundary) and punctuated by 8-10 extinction events. The two most extensive extinction events are to be the Kellwasser Event (at the Frasnian-Famennian boundry) and the Hangeberg Event (at or near the Devonian-Carboniferous boundry). One of the most interesting theories of the Devonian extinction is the "Devonian Plant Hypothesis". The theory, first proposed by Thomas Algeo, Robert Berner, J. Barry Manard and Stephen Scheckler in 1995, acclaimed the spread of land plants as the eventual cause for mass extinctions in the tropical oceans.

16.6.3 The Permian-Triassic Extinction

The next mass extinction occurred 251 million years ago, right at the border between the Permian and Triassic periods when life nearly ended entirely. According to Douglas Erwin it is the "Mother of Mass Extinctions". About 150 years ago, John Phillips used this extinction to define the end of the Paleozoic Era and the beginning of the Mesozoic. The Permian-Triassic extinction is also known as the "Great Dying," because 96% of all species on the planet wiped out and over 50% of all families of living things. Every living thing that have existed in the last 250 million years evolved from the 4% of life that survived. This extinction hit plants, terrestrial animals, marine animals, and even bacteria so badly that it has rewritten earth's evolutionary history. This period led to the extinction of trilobites, molluscs, brachiopods and many vertebrates. The insects suffered the only mass extinction of their history.

The Permo-Triassic (PT) extinction is a major watershed in the history of life on the earth, especially for life in the ocean. The event was complex and spread over millions of years, with at least two separate phases of extinction. Various explanations have been put forth for this extinction event such as asteroid impact, flood basalt eruptions, methane release, decrease in oxygen levels, disturbances in sea level or a combination of some of the above activities. Current causes of Permian extinction events were aimed at the biological and physical causes of disturbing the biological nutrient cycles. The studies of oxygen isotopes and the proportions of calcium to magnesium in the fossil shell materials from Permian era were the basis of the hypothesis as regards temperature crisis in the shallow marine (surface) waters. According to several studies differences in the carbon isotope record may give an indication of a disturbed biological cycle.

While there are several hypotheses, the leading explanation is that a piece of the planet's core burnt its way to the surface and exploded into massive volcanic eruptions that lasted a million years. The outcome was disturbances in weather patterns, consequential global warming, acid rains etc that would have been really catastrophic for the living organisms having air, water, and sunlight requirements. A sudden increase in methane due to methane producing microbes in the atmosphere is thought to have resulted in warming temperatures, ocean acidification, and other changes to the carbon cycle. According to the other hypothesis, the warming and drying of the land environments during the Permian Period decreased the amount of organic matter buried in sediments as coal or petroleum, which disturbed the amount of organically fixed carbon dioxide recycling through the atmosphere.

16.6.4 The Triassic-Jurassic Extinction

The Triassic-Jurassic extinction, also known as **End-Triassic extinction** occurred 205 million years ago. Out of the five major extinctions, **End-Triassic extinction** ranks fourth in the severity. This mass extinction event spread over 18 million years and was a combination of smaller mass extinction periods (two or three phases of extinction). This mass extinction vacated terrestrial ecological niches, which allowed dinosaurs to become dominant. Thus, this period drove the evolution of dinosaurs.

There are several different hypotheses such as climate change, flood basalt eruptions and an asteroid impact as a reason for the loss of life during this extinction. It is quite likely that some massive disturbance, such as widespread volcanic eruptions (perhaps from the breakup of the supercontinent Pangaea), a collision with an asteroid, or both, would have caused the dramatic change in the Earth's climate that could have resulted in the end of so many species.

The exact number of species killed in this event is unknown, but very high. It eliminated more than 95 percent of marine species and more than 70 percent of terrestrial ones, it did result in drastic reductions of some living populations. Most of the dominant vertebrates were killed off in this era of rapid warming. The creatures left standing were the archosaurs, ancestors of the dinosaurs. Roughly half of all the species alive at the time such as molluscs, sponges, marine vertebrates, and large amphibians became extinct. Strangely, plants were not so badly affected.

16.6.5 Cretaceous–Paleogene Extinction

Cretaceous–Tertiary extinction (K–T extinction) is also known as **K–Pg extinction** or **Cretaceous–Paleogene extinction**. This extinction is responsible for knocking out approximately 80 percent of all species of animals. This occurred at or very close to the boundary between the Cretaceous and Paleogene periods, about 66 million years ago. This extinction is perhaps the most well-known of the big five mass extinctions as the end of the Cretaceous-Paleogene brought on the extinction of dinosaurs. Many other species of ammonites, marine reptiles, microscopic marine planktons, bivalves and echinoderms among other groups of animals, also went extinct. The absence of food and requirement of breathing oxygen affected mostly the largest animals, like the land dwelling dinosaurs. Smaller animals that require less oxygen and were able to store food survived the unfavourable conditions and then could flourish after the extreme conditions that had passed. This event effectively ended 75% of life on the earth but allowed for the evolution of mammals on the land and sharks in the sea.

A combination of volcanic activity, asteroid impact, and climate change are some of the causes of this extinction.The impacts of extremely large asteroids are considered to be the most important cause of the fifth mass extinction. High levels of iridium was found as an evidence in the layers of rock that is very commonly present in asteroids, comets, and meteors. This layer of rock is also called the **K-T boundary**. The K-T impact crater,one of the largest impact structures identified so far is a 180 km, roughly egg-shaped geological structure called Chicxulub that would have been deeply buried under the sediments of the Yucatán Peninsula of Mexico.

Try to attempt the following SAQ before proceeding further.

SAQ 4

i) Which mass extinction is known as “Mother of Mass Extinctions"/Great Dying?

ii) Which was the very first mass extinction in Earth's history about 439 million years ago (mya)?

16.7 SIXTH EXTINCTION

There are several records of extinctions that occurred in our geological past and most of them were caused by natural catastrophe such as volcanic activity and collision comets. But the Earth is in the middle of a sixth mass extinction today. The current fate of Bluefin Tuna, Rhinos, Tigers and Gorillas is not natural. Species are disappearing at an alarming rate. The sixth extinction is anticipated to be the most destructive extinction event ever since the occurring of asteroid impact that eliminated out the dinosaurs once forever. In the past, the rate of extinction and the rate of evolution of new life forms were completely balanced owing to the subsistence of the biological cycle and balance of the ecosystem. But this balance has been disturbed with the advent of the human race. The current rates of extinction are 1000 times faster than the natural rate and therefore, it has become difficult for the biological cycle to keep up with the pace.

The Sixth Extinction is also called the Anthropocene, or Age of Man extinction since it is being caused by the human race (Fig. 16.2). Loss of habitat, over-hunting, pollution,climate change and genetic mutations are being credited as the major causes of this mass extinction which has been named the Holocene Extinction. Human actions like increasing temperatures, introduction of exotic species and simplification of land forms are causing homogenization of global faunas which if left unchecked, could ultimately lead to the elimination of whole lines of phyla. Our current extinction crisis is exclusive in Earth's history according to geologists and biologists due to its some unique features:

1) Spread of non-native species all over the earth.

2) Single species (human beings) taking over an important proportion of the earth's primary production (25 to 40% of the planet's net primary production)

3) Evolution increasingly directed by human actions resulting in the growth of something called the technosphere.

4) Humans have become the top predator both on land as well as across the sea.

The impacts of a still-avoidable sixth mass extinction would be catastrophic, widespread and, of course, irreversible. The destruction of flora and fauna will have serious ecological, economic and social consequences. Scientists give an example of the lions that were once distributed over most of the Africa, southern Europe, and the Middle East, all the way to north-western India. The vast majority of lion populations have been wiped out today which is a matter of great concern for all of us. The new study that has generated so much conversation estimates that as many as three-quarters of animal species could be extinct within several human lifetimes (Fig. 16.2).

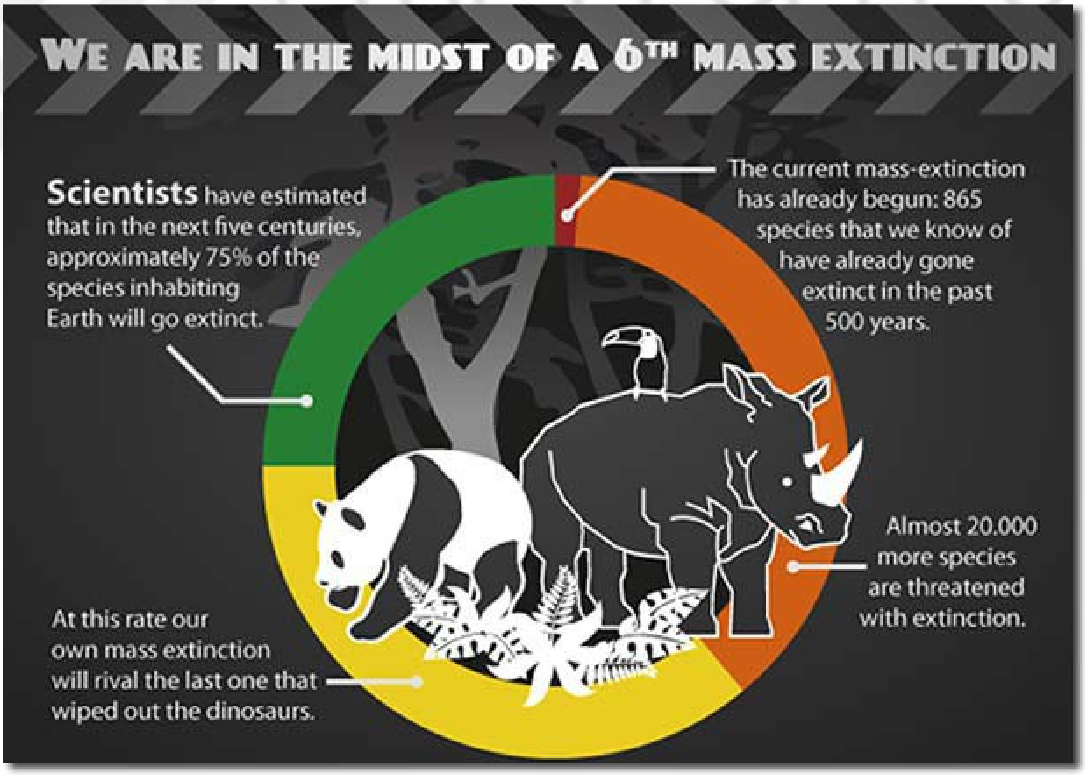


Fig. 16.2: Sixth Extinction.

16.8 ROLE OF EXTINCTION IN EVOLUTION

Evolution and extinction are mutually exclusive but go hand in hand with one another. The one, in a sense, "needs" the other. Extinction cannot occur unless evolution had already produced organisms that could meat of the ultimate fate. One can't understand evolution, really, without understanding extinction. And you can't understand extinction without first grasping ecology: the rules that govern how organisms of different species live in the same ecosystems, and control system determining the number of organisms, and number of different species living in any given specific habitat area.

Mass extinctions reduce drastically the diversity of the species by destroying the specific lineages and also their descendent species. But mass extinction can also play an imaginative role in evolution. On one hand it cuts the branches of a tree but on the other hand, it can also stimulate the growth of other branches. The elimination of plants and animals in a short span of time, occupying a particular habitat creates freedom, reduce competition for resources and increase new resources for remaining species. Over the period of natural selection, these lineages and their daughter lineages may evolve specializations and adapt themselves to the never opportunities taking the place of previous species in the ecosystem, or may evolve different, new ecological strategies. Thus, mass extinction allows lineages having minor roles earlier to spread and diversify to become more extensive. The surviving lineages are able to fill the vacant niches left behind by mass extinctions. For example, mammals occupied a small group of rodents-like organisms most of that time, even though they are present for more than 200 million years. In the end-Cretaceous mass extinction occurred, when dinosaurs went extinct 65 million years ago, mammals were able to get diversified and in less than 20 million years, they evolved into the great variety of mammals.

Our present understanding of the role of extinction in evolution is appallingly meagre. Extinction apparently comprises three main components:

(i) The species, geographically widespread can only go extinct when the stress is beyond the experience of the species, and thus outside the reach of natural selection.

(ii) The largest mass extinctions result in reconstitution of the environment wherein minor groups are allowed to expand and diversify, eliminating some of the successful groups.

(iii) It is unpredictable, in fact, that which species will be victimised due to an extinction event. Except for a few cases, there is very little evidence of extinction being selective in the positive.

Extinction was a crucial part of the theory given by Charles Darwin, the grand father of evolution, (1861) in *Origin of Species*. He wrote, "So profound is our ignorance, and so high our presumption, that we marvel when we hear of the extinction of an organic being; and as we do not see the cause we invent cataclysms to destroy the world, or invent laws on the duration of the forms of life!" Special importance was attached to extinction by Darwin keeping in view the same number of species getting extinctions in the history of life as the number of new species originate. An evolutionary biologist cannot ignore

extinction as the present day biodiversity is the result of cumulative accumulation of all those that originate. The same selective pressures that forces some species to go extinct, drives others to adapt and evolve.
The end-Permian event wiped out many of the dominating species and allowed new groups to evolve, including the earliest dinosaurs, crocodiles and relatives of mammals and lizards. Similarly, the end-Triassic event then again eliminated many prominent groups, and set the environment suitable for the dinosaurs to take over.

Extinction event (of a single species, or perhaps a few of species) cause changes in the ecosystem of the remaining species, sometimes influencing their reproduction ability also. The extinction of one species in competition might give an opportunity to the other species to increase in number. At the same time, there may be a decrease in the number of other species also owing extinction.

SAQ 5

i) What is the number one cause of Sixth Extinction?

ii) The extinction of species is not normally considered an important element of………………… theory, in contrast to the opposite phenomenon, speciation.

16.9 SUMMARY

In this unit we have learnt that:

- Extinction is a natural process. Extinction is quite simply the 'death' of a taxon. But it is not only the disappearance of single specie but it is also the effects of its disappearance to the environment that it interacts with.

- Pseudoextinction of a species occurs when all the members of the species are extinct but members of daughter species are alive. There are three types of pseudoextinction.

- Extinction is a normal process but human-mediated extinctions rates have soared over the past few hundred years. The climate change, disease, spread of invasive species; extermination, ecological imbalance etc. are the natural factors causing a species to become extinct. Overexploitation, pollution and loss of habitat are man-made causes of extinction.

- The two types of extinctions are background extinction and mass extinction. Background extinction is a natural regular event in the process of evolution. It is **caused by the poor adaptation to the ongoing changes in the environment and** the rate of the background extinction is steady over geological time. A mass extinction is a relatively sudden, global decrease in the diversity of life forms within a short period of geological time.

- Destruction of biodiversity due to extinction is incomprehensible, but this destruction, however, is not the whole story. Every mass extinction was followed by speciation.
- Mass extinctions are very mysterious phenomena. Mass extinctions were not at all instantaneous but really a combination of a number of large scale extinction events that occurred within a relatively short span of time (which in geologic time could mean a few hundred thousand years) leaving devastating effects.
- There have been five episodes of natural mass extinctions in the fossil record- Ordovician-Silurian, Devonian, Permian-Triassic, Triassic-Jurassic and Cretaceous–Paleogene extinction.
- The Sixth/Holocene Extinction is also called the Anthropocene, or Age of Man extinction since it is directly linked to human evolvement to the changes of the planet. Humans have become the top predator both on land and across the sea. The impacts of a still-avoidable sixth mass extinction would be catastrophic, widespread and, of course, irreversible.
- Evolution and extinction go hand in hand together. The one, in a sense, "needs" the other. Extinction cannot occur unless evolution had already produced organisms that could suffer that ultimate fate.

16.10 TERMINAL QUESTIONS

1. Explain the similarities and differences between background and mass extinction.
2. How did mammals survive the Triassic inspite of their smaller size?
3. Explain the phenomenon of Pseudo extinction along with its three types.
4. Discuss the role of human beings in Sixth Extinction?
5. Explain the role of extinction in evolution with examples?

16.11 ANSWERS

Self Assessment Questions

1. i) Pseudoextinction; ii) Georges Cuvier.
2. i) A meteor impact on the Yucatan peninsula in Mexico.

   ii) Biomagnification.
3. i) Mass Extinction, ii) Speciation.
4. i) The Permian-Triassic Extinction.

   ii) The Ordovician-Silurian Extinction.
5. i) Human Race, ii) Neodarwinian.

Terminal Questions

1. Refer to Sub Section 16.4.1.
2. Refer to Sub Section 16.5.4.
3. Refer to Sub Section 16.2.1
4. Refer to Section 16.6.
5. Refer to Section 16.7.

SUGGESTED READINGS

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7. Extinction: A Radical History by Ashley Dawson, OR Books, 2016

8. Fossils: The Evolution and Extinction of Species by Niles Eldredge, Stephen Jay Gould and Murray Alcosser published by Princeton University Press, 1997.

9. The Sixth Extinction: An Unnatural History by Elizabeth Kolbertpublished by Henry Holt & Company, 2015

10. Extinction and Evolution: What Fossils Reveal About the History of Life by Niles Eldredge (Author), Carl Zimmer (Introduction) Firefly Books; Annotated edition (September 11, 2014).

11. Mass Extinction by Ashraf M.T. Elewa, Springer Science & Business Media, 2007.

ONLINE TOOLS AND WEB RESOURCES

- https://www.coursera.org/learn/molecular-evolution.
- https://www.coursera.org/learn/genetics-evolution.
- https://swayam.gov.in/courses/4062-environmental-biology-genetics-and-evolution.

GLOSSARY

Adaptive radiation : The tendency of successful species to diversify into all types of ecological niches.

Allopatry : Organisms belonging to same species are separated by space and occupy different territories.

Carrying capacity : The capacity of the environment to sustain and optimal population size.

Coevolution : Simultaneous evolution of two or more ecologically related species.

Endemic : Refers to organisms which are narrowly restricted in their distribution.

Fossil : Petrified remains of the organisms of the past.

Genetic drift : Changes in gene frequency in small populations because of random processes.

Group selection : A selection which aims the extinction of certain populations so that other populations could be propagated. This concept of selection suggests that populations in the unit of selection and not the individual.

Huntington's chorea : A rare hereditary disease affecting brain resulting in choreiform (dance like) movement, intellectual deterioration and psychosis.

Hybrid sterility : The sterility of the offsprings of the interspecific crosses.

Interspecific sterility : Failure in mating because of the inability of the sperm of one species to reach the egg of another species in animals and that of pollen to reach the ovules in plants.

Kin selection : Selection favouring the altruistic behaviour of an individual towards its own relatives or individuals having some of its own gene.

Palaeontology : The study of the life of the past through fossil records.

Pangenesis : A theory of inheritance proposed by Darwin according to which all organs in the body produce pangenes, that is minute particles that are carried away by the blood stream and segregated out into gametes.

Peripatry : Populations living in isolation at the peripheral territory of a parent population.

Post-mating isolating mechanism	:	The isolating mechanism taking effect after mating.
Pre-mating isolating mechanism	:	The isolating mechanism taking effect before mating.
Radioactive dating	:	Determining the age of geological deposits and fossils based on the rate of decay of radioactive elements.
Rassenkreis	:	The mechanism by which a sub-species slowlv evolves and becomes a new species by geographical isolation.
Speciation	:	Formation of new species from parent population.
Stabilising selection	:	Natural selection which maintains a well-adapted condition by eliminating any marked deviations from it (it is also called normalising selection_.
Sympatry	:	Individuals belonging to a species living in the same area.
Ungulates	:	Hoofed mammals.