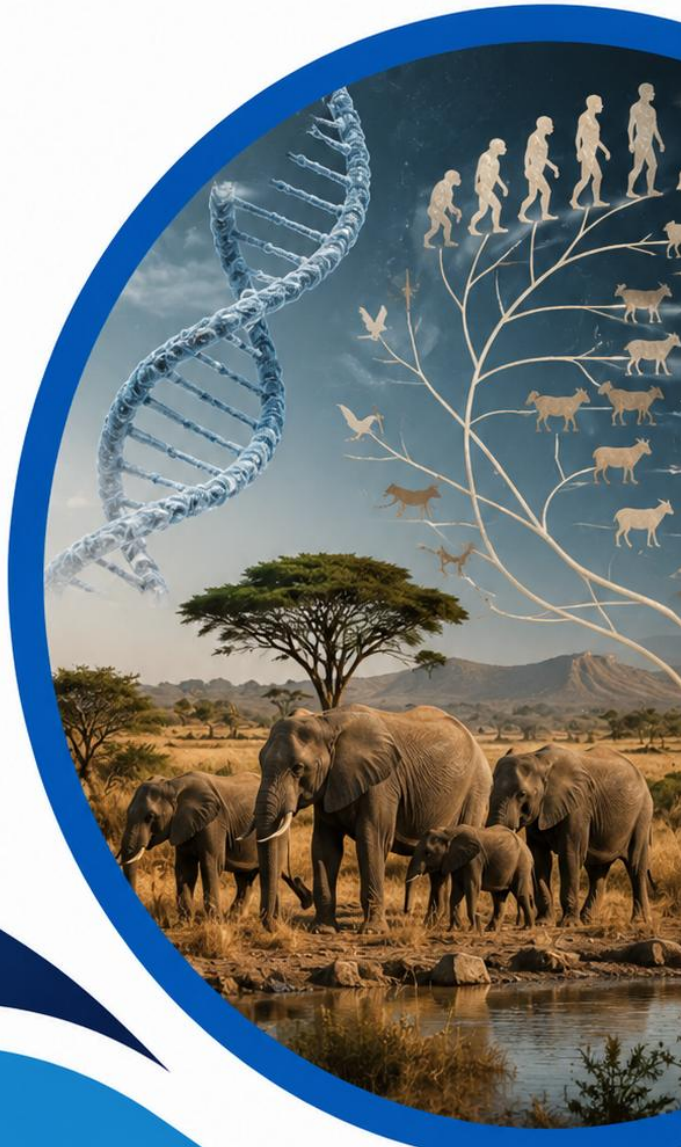




La-Net

# BIO 302

## POPULATION BIOLOGY AND EVOLUTION



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**Course code: BIO 302**

**Course title: Population Biology and Evolution**

**Course credit load: 2 Units**

## **Series 1: Biological Properties of Species**

- **Part 1.1: The Species Concept**

- Sub Part 1.1.1: Definitions and criteria for species
- Sub Part 1.1.2: The Biological Species Concept
- Sub Part 1.1.3: Alternative species concepts

- **Part 1.2: Morphological and Genetic Properties**

- Sub Part 1.2.1: Morphological characters and their variation
- Sub Part 1.2.2: Genetic structure of species
- Sub Part 1.2.3: Hardy-Weinberg equilibrium

- **Part 1.3: Ecological and Reproductive Properties**

- Sub Part 1.3.1: Ecological niche and habitat specificity
- Sub Part 1.3.2: Reproductive strategies and mating systems
- Sub Part 1.3.3: Life history traits

- **Part 1.4: Taxonomy and Nomenclature**

- Sub Part 1.4.1: Principles of biological classification
- Sub Part 1.4.2: Binomial nomenclature and taxonomic hierarchy
- Sub Part 1.4.3: Modern phylogenetic approaches



## Introduction

A species is the fundamental unit of biological classification and the basic unit on which natural selection acts. Defining what constitutes a species, describing its morphological and genetic properties, understanding its ecological and reproductive characteristics, and placing it correctly in a taxonomic framework are the foundational skills of population biology and evolutionary biology.

This Series introduces the major species concepts, the morphological and genetic properties used to characterise species, Hardy-Weinberg equilibrium as the null model of population genetics, the ecological and reproductive properties of species, and the principles of taxonomy and phylogenetics. These concepts underpin all subsequent Series in this course.

## Series Learning Outcomes

Upon completing this Series, you should be able to:

- **SLO 1.1** define a species and compare the major species concepts (Linked to Part 1.1),
- **SLO 1.2** describe the morphological and genetic properties used to characterise species (Linked to Part 1.2),
- **SLO 1.3** state the Hardy-Weinberg principle, apply it to calculate allele and genotype frequencies, and list the conditions required for equilibrium (Linked to Part 1.2),
- **SLO 1.4** describe the ecological and reproductive properties of species (Linked to Part 1.3),
- **SLO 1.5** describe the major life history strategies (Linked to Part 1.3), and
- **SLO 1.6** explain the principles of biological classification, binomial nomenclature, and modern phylogenetics (Linked to Part 1.4).



## 1.1 The Species Concept

### 1.1.1 Definitions and criteria for species

A species is a group of organisms that share common characteristics distinguishing them from all other groups. The species is the lowest universally recognised taxonomic rank. Defining a species is not straightforward: over 25 species concepts have been proposed. Each concept emphasises different criteria: morphological similarity, reproductive compatibility, ecological distinctness, or evolutionary history.

Practical criteria used to recognise species: morphological distinctness (differences in size, shape, colour, or anatomy visible to an observer); reproductive isolation (inability to interbreed freely and produce fertile offspring with members of other groups); ecological distinctness (occupation of a distinct ecological niche); and genetic distinctness (degree of DNA sequence divergence). No single criterion works for all groups; palaeontologists rely on morphology; microbiologists rely on DNA divergence.

Fill in the blank: The \_\_\_\_\_ is the lowest universally recognised taxonomic rank; over 25 species concepts have been proposed, each emphasising different criteria such as morphology, reproductive compatibility, or evolutionary history.

### 1.1.2 The Biological Species Concept

The Biological Species Concept (BSC), proposed by Ernst Mayr in 1942, defines a species as a group of actually or potentially interbreeding natural populations that are reproductively isolated from other such groups. It emphasises reproductive compatibility as the defining criterion. The BSC is the most widely used concept in animal biology and has driven much of the theory of speciation.

Strengths of the BSC: it provides a clear, testable criterion (can two populations interbreed and produce fertile offspring?); it explains the discreteness of species in nature. Limitations: it cannot be applied to asexual organisms (bacteria, many protists), fossils, or purely allopatric populations that never meet; hybridisation between recognised species is common in plants, challenging the



strict isolation criterion. Despite limitations, the BSC remains the dominant conceptual framework for animal speciation.

Fill in the blank: Ernst Mayr's Biological Species Concept defines a species as a group of interbreeding natural populations that are reproductively \_\_\_\_\_ from other such groups; it is the most widely used concept in animal biology.

### 1.1.3 Alternative species concepts

Morphological (typological) Species Concept: species defined by diagnostic morphological characters; practical and applicable to fossils and asexual organisms; but subjective (experts disagree on which characters are diagnostic) and ignores cryptic species (morphologically identical but genetically and reproductively distinct). Phylogenetic Species Concept (PSC): the smallest monophyletic group of organisms diagnosable by unique shared derived characters (synapomorphies); widely used in modern systematics.

Ecological Species Concept: a species is a lineage that occupies an adaptive zone different from related lineages; emphasises ecological roles. Cohesion Species Concept: a species is the most inclusive population sharing genetic and demographic cohesion. Recognition Species Concept: species defined by shared fertilisation systems (specific mate recognition system). In practice, most biologists apply a pluralistic approach, using whichever concept best fits the organism and question being addressed.

Fill in the blank: The \_\_\_\_\_ Species Concept defines a species as the smallest monophyletic group diagnosable by unique shared derived characters; it is widely used in modern phylogenetics and molecular systematics.



# COMPARING KEY SPECIES CONCEPTS

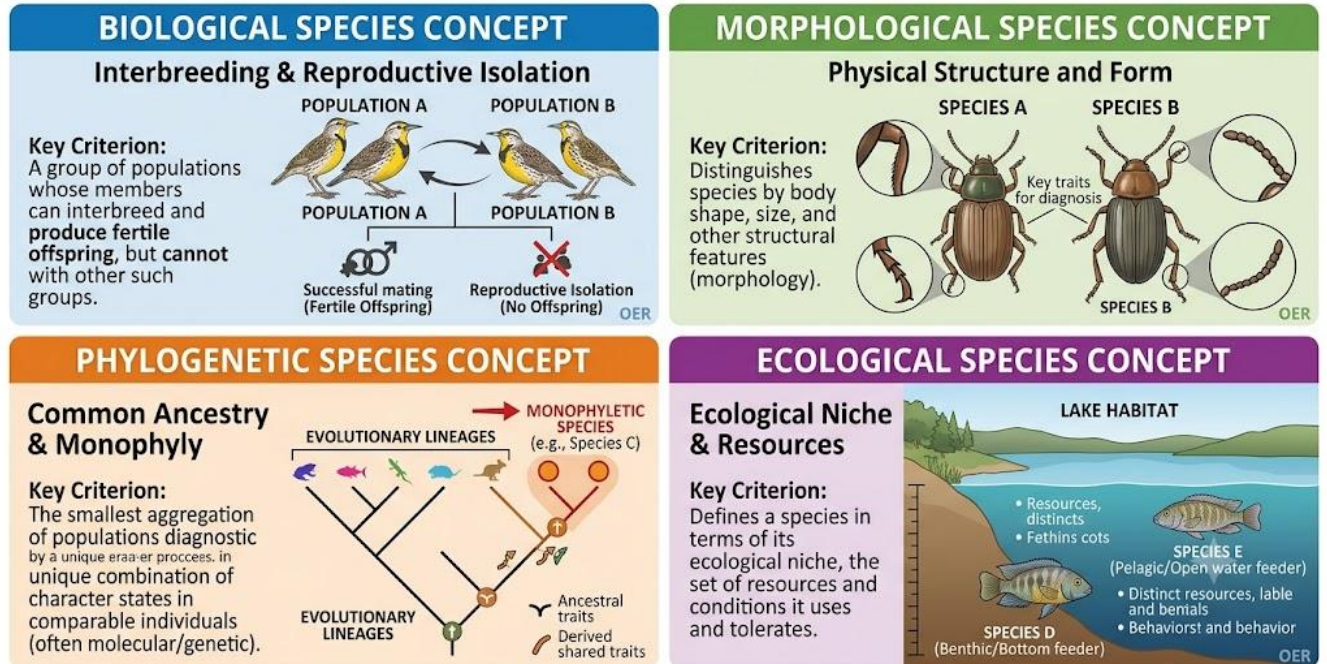


Figure 1.1: Diagram comparing four major species concepts

## Pilot questions 1.1

1. Define a species and state four criteria used to recognise species.
2. State the Biological Species Concept and give two strengths and two limitations.
3. Distinguish between the Morphological and Phylogenetic Species Concepts.
4. Explain why no single species concept is universally applicable.
5. Explain what a cryptic species is and why it challenges the Morphological Species Concept.

## 1.2 Morphological and Genetic Properties

### 1.2.1 Morphological characters and their variation

Morphological characters are the observable physical features of an organism: external (size, shape, colour, pattern, external anatomy) and internal (skeletal structure, organ morphology, cell ultrastructure). Morphological variation within a species is normal; it results from genetic variation, developmental plasticity, and environmental effects. Continuous variation (e.g. height,



body mass) is controlled by many genes; discontinuous variation (e.g. blood groups, flower colour) is controlled by one or few genes.

Polymorphism is the existence of two or more genetically distinct forms (morphs) within a population, each at a frequency too high to be maintained solely by mutation. Classic examples: ABO blood groups in humans; sickle-cell trait in malaria-endemic populations; colour morphs in the African swallowtail butterfly (*Papilio dardanus*). Morphological characters used in systematics must be heritable, discrete, and informative about evolutionary relationships rather than simply reflecting convergent adaptation to similar environments.

Fill in the blank: \_\_\_\_\_ is the existence of two or more genetically distinct forms within a population, each at a frequency too high to be maintained by mutation alone; ABO blood groups and sickle-cell trait are classic examples.

### 1.2.2 Genetic structure of species

The genetic structure of a species describes how genetic variation is distributed within and among populations. Allele frequencies measure the proportion of each allelic variant at a locus in the population. Heterozygosity ( $H$ ) measures the probability that two randomly drawn alleles at a locus are different; it is a standard measure of genetic diversity. A genetically diverse species has higher evolutionary potential to respond to selection and environmental change.

Gene flow: the movement of alleles between populations through migration; it homogenises allele frequencies and reduces genetic differentiation. Genetic drift: random changes in allele frequencies, more pronounced in small populations; it reduces heterozygosity over time.

Inbreeding: mating between close relatives; increases homozygosity and can expose recessive deleterious alleles.  $F_{ST}$  (fixation index) measures the degree of genetic differentiation among subpopulations:  $F_{ST} = 0$  means no differentiation;  $F_{ST} = 1$  means complete differentiation.

Fill in the blank: \_\_\_\_\_ ( $F_{ST}$ ) measures genetic differentiation among subpopulations; a value of 0 means all populations share identical allele frequencies; a value of 1 means populations are completely differentiated.



### 1.2.3 Hardy-Weinberg equilibrium

The Hardy-Weinberg principle states that in a large, randomly mating population free from mutation, migration, and selection, allele and genotype frequencies remain constant from generation to generation. For a locus with two alleles A (frequency  $p$ ) and a (frequency  $q$ ), where  $p + q = 1$ : genotype frequencies are  $AA = p^2$ ,  $Aa = 2pq$ ,  $aa = q^2$ , and  $p^2 + 2pq + q^2 = 1$ . This is the null model of population genetics: departures from equilibrium indicate evolutionary forces at work.

Five conditions required for Hardy-Weinberg equilibrium: (1) large population size (no genetic drift); (2) random mating; (3) no mutation; (4) no migration (no gene flow); (5) no natural selection. In practice, no real population meets all conditions; the Hardy-Weinberg model is used as a reference to detect which forces are acting. Application: if a recessive disorder has frequency  $q^2 = 0.0001$ , then  $q = 0.01$ ,  $p = 0.99$ , and carrier frequency  $2pq = 0.0198$  (approximately 2%).

Fill in the blank: The Hardy-Weinberg equation states that for a two-allele locus with allele frequencies  $p$  and  $q$ :  $p^2 + \underline{\hspace{1cm}} + q^2 = 1$ ; departures from these expected genotype frequencies indicate that one or more evolutionary forces are acting on the population.



# THE HARDY-WEINBERG EQUILIBRIUM MODEL: CONDITIONS & EVOLUTIONARY FACTORS

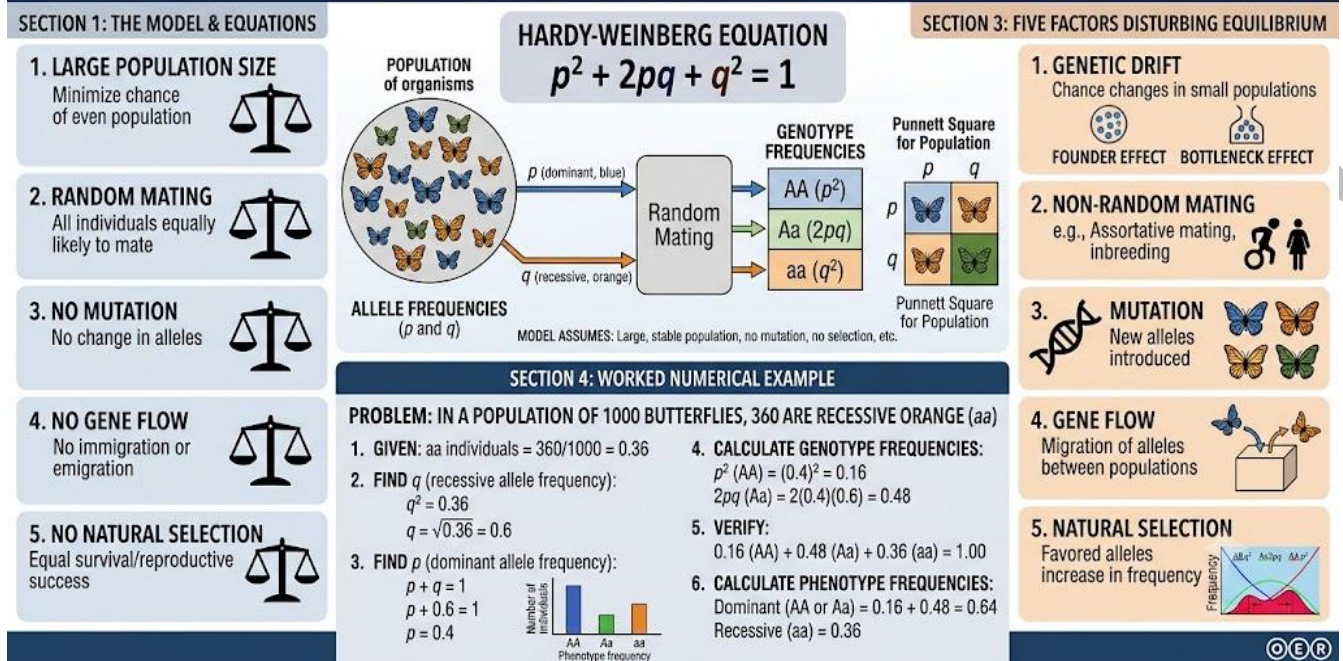


Figure 1.2: Diagram illustrating Hardy-Weinberg equilibrium and factors that disturb it

## Pilot questions 1.2

1. Distinguish between continuous and discontinuous variation with one example each.
2. Define polymorphism and give two examples in West African organisms.
3. Define gene flow and explain how it affects the genetic structure of populations.
4. State the five conditions required for Hardy-Weinberg equilibrium.
5. In a population, the frequency of the recessive allele (a) is 0.3. Calculate the expected frequencies of AA, Aa, and aa genotypes under Hardy-Weinberg equilibrium.

## 1.3 Ecological and Reproductive Properties

### 1.3.1 Ecological niche and habitat specificity

The ecological niche of a species encompasses all the resources, conditions, and biotic interactions it requires and tolerates. The fundamental niche is the full range of conditions the species can potentially occupy; the realised niche is the narrower range actually occupied due to



interspecific competition. Niche breadth varies: specialists occupy narrow niches (e.g. koala eating only Eucalyptus); generalists occupy broad niches (e.g. rats eating almost anything).

Habitat specificity refers to the degree to which a species is restricted to a particular habitat type. Stenotopic species are highly habitat-specific (e.g. mangrove specialists in the Niger Delta such as the mangrove kingfisher); eurytopic species tolerate a wide range of habitats (e.g. the pied crow *Corvus albus*, found from forest to desert in Nigeria). Habitat specificity reflects evolutionary history and physiological tolerance ranges; it determines a species' vulnerability to habitat loss and fragmentation.

Fill in the blank: The \_\_\_\_\_ niche is the full range of conditions a species could potentially occupy; the realised niche is the narrower range actually occupied due to competition from other species.

### 1.3.2 Reproductive strategies and mating systems

Reproductive strategy describes how a species allocates resources between reproduction and survival. r-selected species: reproduce early and rapidly, produce many small offspring with little parental care (e.g. annual weeds, locusts); adapted to unstable environments. K-selected species: reproduce later, produce few large offspring with extensive parental care (e.g. African elephants, great apes); adapted to stable environments near carrying capacity K.

Mating systems describe the pattern of mate choice and pair bonding. Monogamy: one male, one female (common in birds: approximately 90% of bird species). Polygyny: one male, multiple females (most Nigerian mammals: cattle, goats, most primates). Polyandry: one female, multiple males (rare; e.g. some shorebirds). Promiscuity: multiple mates for both sexes (e.g. chimpanzees). Sexual selection drives the evolution of secondary sexual characters (peacock tail, red deer antlers) through mate choice (female choice) and male-male competition.

Fill in the blank: \_\_\_\_\_ is the most common mating system in mammals; it occurs when one male mates with multiple females; it is associated with sexual dimorphism and competition among males for access to females.



### 1.3.3 Life history traits

Life history traits describe the key events and timings in an organism's life cycle: age at first reproduction; number of reproductive events (semelparity: one reproductive event then death, e.g. annual plants, Pacific salmon; iteroparity: repeated reproduction over a lifetime, e.g. perennial trees, mammals); clutch or litter size; offspring size and quality; and lifespan. These traits represent trade-offs: resources invested in reproduction now reduce survival and future reproduction.

The trade-off between current reproduction and survival is called the cost of reproduction. Key life history trade-offs: offspring number versus offspring size (many small or few large); early versus late reproduction; reproduction versus survival. Life history theory predicts that natural selection shapes these trade-offs differently depending on environmental conditions: high mortality environments favour early reproduction and many small offspring; low mortality, stable environments favour late reproduction and few, well-provisioned offspring.

Fill in the blank: \_\_\_\_\_ describes an organism that reproduces only once then dies (e.g. annual plants, Pacific salmon); \_\_\_\_\_ describes an organism that reproduces repeatedly over its lifetime (e.g. perennial trees, large mammals).



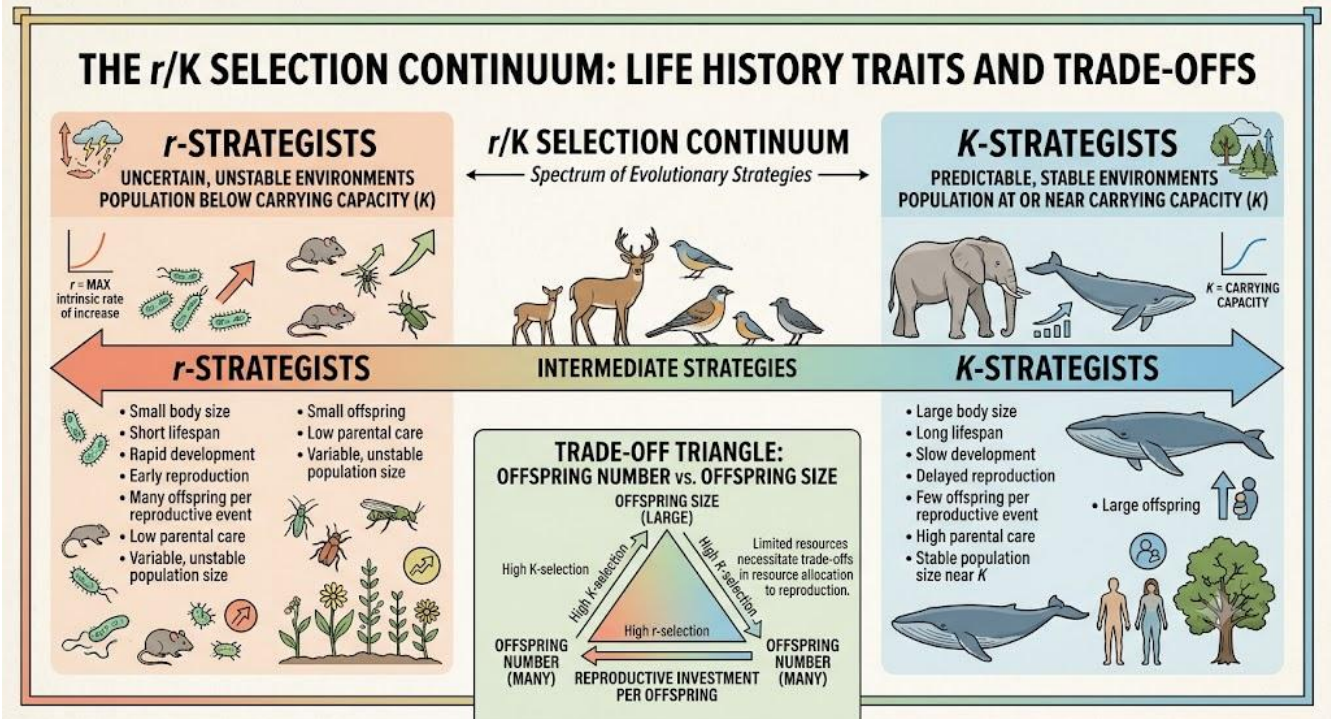


Figure 1.3: Diagram of life history trade-offs and  $r/K$  selection continuum

### Pilot questions 1.3

1. Distinguish between fundamental and realised niche with an example.
2. Distinguish between stenotopic and eurytopic species with a Nigerian example of each.
3. Distinguish between  $r$ -selected and  $K$ -selected reproductive strategies.
4. Distinguish between semelparity and iteroparity with one example of each.
5. Explain the cost of reproduction and describe one life history trade-off.

## 1.4 Taxonomy and Nomenclature

### 1.4.1 Principles of biological classification

Taxonomy is the science of naming, describing, and classifying organisms. Classification serves to organise the diversity of life, reveal evolutionary relationships, and provide a universal communication system for biologists. The hierarchical taxonomic system organises organisms



into progressively broader groups: Species, Genus, Family, Order, Class, Phylum (or Division in plants), Kingdom, and Domain.

Two main approaches to classification: phenetics (numerical taxonomy) groups organisms by overall similarity across many characters without regard to evolutionary history; cladistics (phylogenetic systematics, developed by Willi Hennig) groups organisms strictly by shared derived characters (synapomorphies) reflecting common ancestry. Modern taxonomy uses cladistics as its theoretical foundation. The five-kingdom system (Whittaker, 1969) is still taught widely; the three-domain system (Woese, 1977) based on ribosomal RNA is the accepted modern framework.

Fill in the blank: \_\_\_\_\_ groups organisms strictly by shared derived characters (synapomorphies) reflecting common ancestry; it is the theoretical foundation of modern taxonomy and molecular phylogenetics.

#### 1.4.2 Binomial nomenclature and taxonomic hierarchy

Binomial nomenclature, developed by Carl Linnaeus in the 18th century, gives every species a unique two-part Latin name: the Genus (capitalised) followed by the species epithet (lower case), both in italics (or underlined in handwriting). Examples: *Homo sapiens* (human); *Panthera leo* (lion); *Vigna unguiculata* (cowpea); *Oryza sativa* (rice). The system ensures universal, unambiguous names regardless of language or country.

The taxonomic hierarchy for the human (*Homo sapiens*) as example: Domain Eukarya; Kingdom Animalia; Phylum Chordata; Class Mammalia; Order Primates; Family Hominidae; Genus *Homo*; Species *Homo sapiens*. Higher taxa (above species) are defined by shared derived characters. Subspecies (trinomial nomenclature) are sometimes recognised for geographically distinct populations within a species; e.g. the Nigeria-Cameroon chimpanzee *Pan troglodytes ellioti*.

Fill in the blank: In binomial nomenclature, the scientific name of an organism consists of the \_\_\_\_\_ name (capitalised) followed by the species epithet (lower case), both written in italics.



### 1.4.3 Modern phylogenetic approaches

A phylogeny is a diagram (cladogram or phylogenetic tree) showing the inferred evolutionary relationships among taxa based on shared characters. Molecular phylogenetics uses DNA or protein sequence data to infer relationships; it has revolutionised our understanding of the tree of life, revealing that traditional morphological classifications were often misleading. Maximum parsimony, maximum likelihood, and Bayesian inference are the main tree-building methods.

Key phylogenetic concepts: monophyletic group (clade): a group comprising an ancestor and all its descendants; the only valid grouping in cladistics. Paraphyletic group: includes an ancestor but not all its descendants (e.g. "reptiles" excluding birds; invalid in cladistics). Polyphyletic group: members share a character not inherited from a common ancestor (convergent evolution; invalid in cladistics). Molecular clock: the approximately constant rate of DNA change over time, used to estimate divergence dates.

Fill in the blank: A \_\_\_\_\_ group (clade) includes an ancestor and all of its descendants; it is the only valid type of grouping in cladistic classification; paraphyletic and polyphyletic groups are not accepted.



## 'CLADOGRAM: UNDERSTANDING MONOPHYLETIC, PARAPHYLETIC, & POLYPHYLETIC GROUPINGS

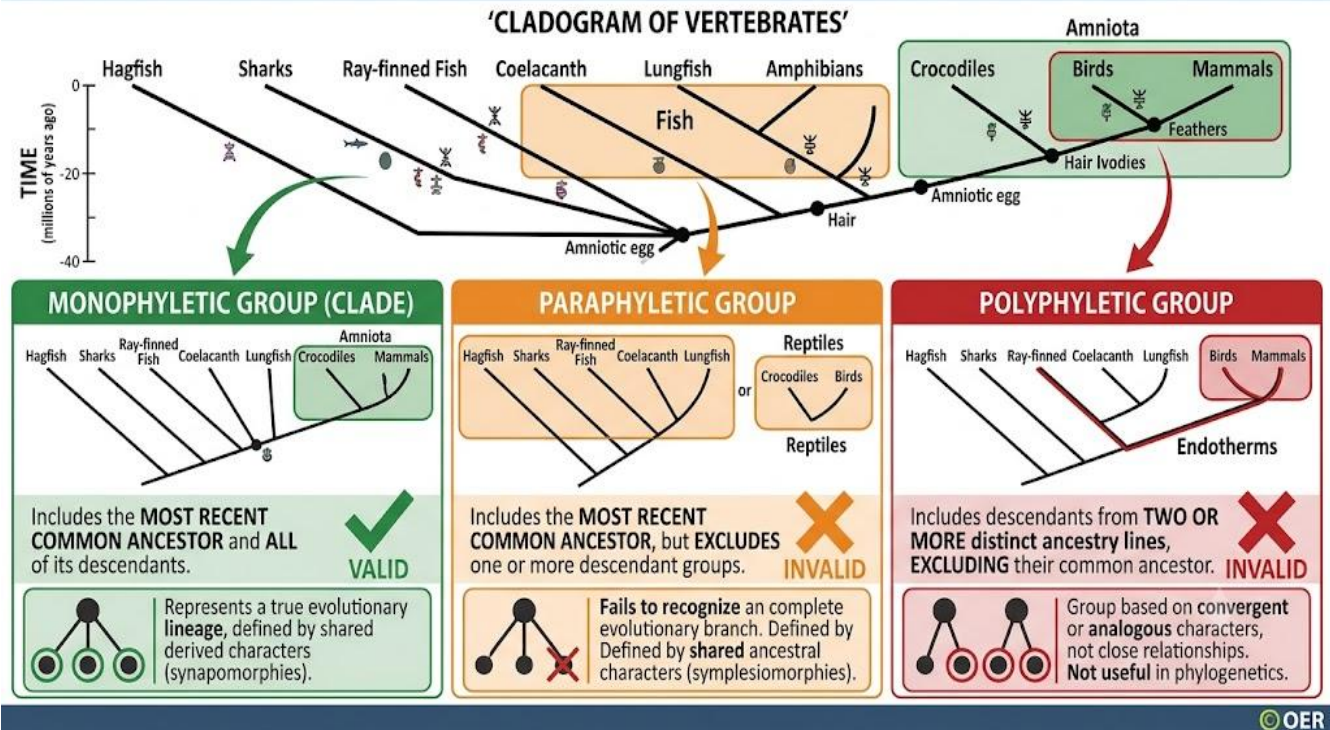


Figure 1.4: Cladogram illustrating monophyletic, paraphyletic, and polyphyletic groups

### Pilot questions 1.4

1. Distinguish between phenetics and cladistics as approaches to classification.
2. Write the binomial names of four organisms and state the rules of binomial nomenclature.
3. Give the complete taxonomic classification of the cowpea (*Vigna unguiculata*).
4. Distinguish between monophyletic, paraphyletic, and polyphyletic groups.
5. Explain what the molecular clock is and how it is used in phylogenetics.



## Series Summary

This Series examined what defines a species and how species are characterised biologically, genetically, and ecologically. Four major species concepts were discussed: the Biological Species Concept defines a species as a group of organisms that can interbreed and are reproductively isolated from others; the Morphological concept relies on diagnostic physical characters; the Phylogenetic concept defines a species as the smallest monophyletic group sharing derived characters; and the Ecological concept defines a species by the unique adaptive zone it occupies. Genetically, species show both continuous variation (traits influenced by many genes and the environment) and discontinuous variation (distinct categories such as blood groups); population genetic measures such as allele frequencies, heterozygosity, gene flow, genetic drift, and the  $F_{ST}$  statistic describe how genetic diversity is distributed within and between populations. The Hardy-Weinberg equilibrium provides a mathematical null model against which evolutionary change can be detected: when a population meets five conditions (large size, random mating, no mutation, no migration, and no selection), allele and genotype frequencies remain stable across generations.

Ecologically, a species occupies a fundamental niche defined by all conditions it can tolerate, but competition and other interactions restrict it to a smaller realised niche in practice. Species are described as stenotopic if they tolerate a narrow range of environmental conditions or eurytopic if they tolerate a wide range. Reproductive strategies range from r-selection (many small offspring produced rapidly in unstable habitats) to K-selection (few large offspring with high parental investment in stable habitats), and mating systems vary from monogamy to polygyny, polyandry, and promiscuity, with sexual selection shaping many of these patterns. Life history strategies are either semelparous (reproducing once then dying) or iteroparous (reproducing repeatedly), and there is always a trade-off between the number and size of offspring a parent can produce. Finally, the Series covered taxonomy: the binomial nomenclature system introduced by Linnaeus, the hierarchical classification from Domain to Species, the distinction between phenetic and cladistic approaches to classification, the three-domain and five-kingdom systems, and the use of molecular phylogenetics to reconstruct evolutionary relationships.



## Glossary of Terms

- **Allele frequency:** the proportion of a particular allelic variant at a given locus in the population gene pool.
- **Binomial nomenclature:** the system of naming organisms with a two-part Latin name: Genus (capitalised) and species epithet (lower case), both in italics; introduced by Linnaeus.
- **Biological Species Concept (BSC):** Mayr's definition: a species is a group of interbreeding natural populations that are reproductively isolated from other such groups.
- **Clade:** a monophyletic group comprising an ancestor and all its descendants; the fundamental unit of cladistic classification.
- **Cladistics:** the classification method that groups organisms strictly by shared derived characters (synapomorphies) reflecting common ancestry; the basis of modern taxonomy.
- **Cost of reproduction:** the reduction in survival or future reproductive success caused by current reproductive investment; the basis of life history trade-offs.
- **Cryptic species:** two or more morphologically identical but genetically and reproductively distinct species; they challenge the Morphological Species Concept.
- **Ecological niche:** the sum of all biotic and abiotic conditions a species requires; encompasses resources, tolerances, and interactions with other species.
- **Eurytopic species:** a species with broad habitat tolerance, capable of surviving in a wide range of environmental conditions.
- **FST (fixation index):** a measure of genetic differentiation among subpopulations;  $FST = 0$  means no differentiation;  $FST = 1$  means complete differentiation.
- **Fundamental niche:** the full range of biotic and abiotic conditions in which a species could potentially survive and reproduce in the absence of competitors.
- **Gene flow:** the transfer of alleles between populations through migration; homogenises allele frequencies and reduces genetic differentiation among populations.
- **Genetic drift:** random fluctuations in allele frequencies in a population; more pronounced in small populations; reduces genetic diversity over time.



- **Hardy-Weinberg equilibrium:** the state in which allele and genotype frequencies in a population remain constant across generations in the absence of evolutionary forces.
- **Heterozygosity (H):** the probability that two randomly chosen alleles at a locus are different; a standard measure of genetic diversity.
- **Iteroparity:** a life history strategy in which an organism reproduces repeatedly over multiple breeding seasons; e.g. perennial plants, most mammals.
- **K-selected species:** a species with low intrinsic growth rate; produces few large offspring with extensive parental care; adapted to stable environments near carrying capacity.
- **Monophyletic group:** a group comprising an ancestor and all of its descendants; the only valid grouping in cladistic classification.
- **Molecular clock:** the approximately constant rate of nucleotide substitution over time; used to estimate divergence dates between lineages.
- **Paraphyletic group:** a group that includes an ancestor but excludes some of its descendants; not accepted as valid in cladistic classification.
- **Phylogenetic Species Concept (PSC):** defines a species as the smallest monophyletic group diagnosable by unique shared derived characters (synapomorphies).
- **Polygyny:** a mating system in which one male mates with multiple females; the most common mammalian mating system.
- **Polymorphism:** the existence of two or more genetically distinct forms within a population, each at a frequency too high to be maintained by mutation alone.
- **Polyphyletic group:** a group whose members share a character not inherited from their most recent common ancestor (convergent evolution); not valid in cladistics.
- **Realised niche:** the subset of the fundamental niche actually occupied by a species in the presence of competitors and predators.
- **r-selected species:** a species with high intrinsic growth rate; produces many small offspring with little parental care; adapted to unstable or disturbed environments.
- **Semelparity:** a life history strategy in which an organism reproduces only once then dies; e.g. annual plants, Pacific salmon.



- **Sexual selection:** a form of natural selection in which traits that increase mating success are favoured, even if they reduce survival; produces secondary sexual characters.
- **Stenotopic species:** a species with narrow habitat tolerance, restricted to a specific type of environment.
- **Synapomorphy:** a shared derived character inherited from a common ancestor; the key evidence used to delimit clades in cladistic classification.
- **Taxonomy:** the science of naming, describing, and classifying organisms; includes both nomenclature and the construction of classification systems.

## Concept Check Questions [Series 1]

### Objective Questions

1. Ernst Mayr's Biological Species Concept defines a species as a group of interbreeding natural populations that are reproductively \_\_\_\_\_ from other such groups. (Linked to SLO 1.1)
2. The Hardy-Weinberg equation for a two-allele locus states that  $p^2 + \text{_____} + q^2 = 1$ , where  $p$  and  $q$  are allele frequencies. (Linked to SLO 1.3)
3. \_\_\_\_\_ (FST) measures genetic differentiation among subpopulations; a value of 0 means no differentiation; a value of 1 means complete differentiation. (Linked to SLO 1.2)
4. \_\_\_\_\_ describes an organism that reproduces only once then dies; \_\_\_\_\_ describes repeated reproduction over a lifetime. (Linked to SLO 1.5)
5. In binomial nomenclature, the scientific name consists of the \_\_\_\_\_ (capitalised) followed by the species epithet (lower case), both in italics. (Linked to SLO 1.6)

### Short-Answer Questions

6. State the Biological Species Concept and give two limitations. (Linked to SLO 1.1)
7. State the five conditions required for Hardy-Weinberg equilibrium. (Linked to SLO 1.3)
8. Distinguish between fundamental and realised niche. (Linked to SLO 1.4)



9. Distinguish between r-selected and K-selected species with one example each. (Linked to SLO 1.5)
10. Distinguish between monophyletic, paraphyletic, and polyphyletic groups. (Linked to SLO 1.6)

#### Long-Answer Questions

11. Describe the major species concepts, compare their strengths and limitations, and explain the morphological and genetic properties used to characterise species. (Linked to SLOs 1.1, 1.2)
12. State the Hardy-Weinberg principle; list its five conditions; calculate genotype frequencies given allele frequencies; and explain how departures from equilibrium indicate evolutionary forces. (Linked to SLO 1.3)
13. Describe the ecological and reproductive properties of species; explain life history strategies; and outline the principles of taxonomy, binomial nomenclature, and modern phylogenetics. (Linked to SLOs 1.4, 1.5, 1.6)

### Answers to Concept Check Questions [Series 1]

#### Objective Questions

1. Isolated.
2.  $2pq$ .
3.  $F_{ST}$  (fixation index).
4. Semelparity; iteroparity.
5. Genus.

#### Short-Answer Questions

6. BSC: a species is a group of interbreeding natural populations reproductively isolated from other such groups. Two limitations: cannot apply to asexual organisms (bacteria, many protists) or



fossils; hybridisation between recognised species is common in plants, blurring reproductive boundaries.

7. Large population size (no genetic drift); random mating; no mutation; no migration (no gene flow); no natural selection.
8. Fundamental niche: the full range of conditions a species could potentially occupy in the absence of competitors. Realised niche: the narrower range actually occupied due to competition; always a subset of the fundamental niche.
9. r-selected: many small offspring; little parental care; early reproduction; unstable habitats; e.g. desert locust. K-selected: few large offspring; extensive parental care; late reproduction; stable habitats near K; e.g. African elephant.
10. Monophyletic: ancestor plus all descendants (valid clade; e.g. Mammalia). Paraphyletic: ancestor plus some but not all descendants (invalid; e.g. "Reptilia" excluding birds). Polyphyletic: members share a convergent character not from most recent common ancestor (invalid; e.g. "flying vertebrates").

#### Long-Answer Questions

11. Species concepts: BSC (Mayr 1942: interbreeding populations reproductively isolated; strengths: clear criterion, explains species discreteness; limitations: not applicable to asexuals, fossils, or allopatric populations; hybridisation in plants is common); Morphological (diagnostic characters; practical for fossils and asexuals; but subjective; misses cryptic species); Phylogenetic (smallest monophyletic group with synapomorphies; widely used in molecular systematics; but can inflate species numbers by splitting polymorphic taxa); Ecological (distinct adaptive zone; emphasises function; useful in ecology). Morphological properties: continuous variation (many genes; e.g. height) vs discontinuous (few genes; e.g. blood groups); polymorphism (two or more forms; ABO blood groups; sickle-cell trait; Papilio dardanus colour morphs). Genetic properties: allele frequencies; heterozygosity ( $H$  = measure of genetic diversity);  $F_{ST}$  (genetic differentiation among populations); gene flow (homogenises allele frequencies); genetic drift (random change; more pronounced in small populations); inbreeding (increases homozygosity).
12. Hardy-Weinberg principle: in a large, randomly mating population free from mutation, migration, and selection, allele and genotype frequencies remain constant across generations. For two alleles  $A$  ( $p$ ) and  $a$  ( $q$ ):  $p + q = 1$ ; genotype frequencies:  $p^2$  ( $AA$ ) +  $2pq$  ( $Aa$ ) +  $q^2$  ( $aa$ ) = 1. Five conditions: large population (no drift); random mating; no mutation; no migration; no selection.



Worked example: if  $q = 0.3$ , then  $p = 0.7$ ;  $AA = 0.49$ ;  $Aa = 0.42$ ;  $aa = 0.09$ . Departures from expected genotype frequencies indicate evolutionary forces: excess homozygosity = inbreeding or drift; deficiency of heterozygotes = assortative mating or selection against heterozygotes; allele frequency change between generations = selection or drift or migration.

13. Ecological properties: fundamental niche (all conditions species could potentially occupy) vs realised niche (actual, narrower range due to competition); niche breadth (specialists: stenotopic e.g. mangrove kingfisher; generalists: eurytopic e.g. pied crow). Reproductive strategies: r-selected (high  $r$ ; many small offspring; short lifespan; unstable habitats e.g. locusts; annual weeds); K-selected (low  $r$ ; few large offspring; long lifespan; stable habitats e.g. African elephant, chimpanzee). Mating systems: monogamy (90% birds); polygyny (most mammals); polyandry (rare, some shorebirds); promiscuity (chimpanzees). Sexual selection: mate choice and male competition produce secondary sexual characters. Life history: semelparity (reproduce once; annual plants, Pacific salmon) vs iteroparity (repeat breeding; perennial trees, mammals); cost of reproduction; offspring number-size trade-off. Taxonomy: phenetics (overall similarity) vs cladistics (synapomorphies; common ancestry); three-domain system (Bacteria, Archaea, Eukarya) from rRNA data; binomial nomenclature (Linnaeus; Genus epithet, italics); hierarchy (Domain-Kingdom-Phylum-Class-Order-Family-Genus-Species); monophyletic group (ancestor + all descendants = valid clade); paraphyletic (excludes some descendants; invalid); polyphyletic (convergent character; invalid); molecular phylogenetics (DNA sequences; maximum likelihood; Bayesian inference); molecular clock (constant substitution rate; estimates divergence dates).

## Answers to Pilot Questions [Series 1]

### Part 1.1

1. A species is a group of organisms sharing common characteristics distinguishing them from all other groups; it is the lowest universally recognised taxonomic rank. Four criteria: morphological distinctness; reproductive isolation; ecological distinctness (distinct niche); genetic distinctness (DNA sequence divergence).
2. BSC: a species is a group of actually or potentially interbreeding natural populations reproductively isolated from other such groups (Mayr, 1942). Two strengths: provides a clear, testable criterion; explains why species appear discrete in nature. Two limitations: inapplicable to



asexual organisms and fossils; plant hybridisation is widespread, making reproductive isolation criterion difficult to apply.

3. Morphological Species Concept: species defined by diagnostic observable physical characters; practical for fossils and asexuals; but subjective and misses cryptic species. Phylogenetic Species Concept: species defined as the smallest monophyletic group diagnosable by unique shared derived characters (synapomorphies); more objective; based on evolutionary history; widely used in molecular systematics.
4. No single concept is universally applicable because different groups of organisms present different challenges: asexual organisms (bacteria, many protists) cannot be defined by reproductive isolation; fossils lack reproductive information; allopatric populations that never meet cannot be tested for interbreeding; hybridisation between plant species is common; morphologically identical cryptic species require genetic data to resolve. Each concept works best for a particular type of organism and question.
5. A cryptic species is a species that is morphologically indistinguishable from one or more other species but is genetically and reproductively distinct. Examples include many mosquito species (*Anopheles gambiae* complex in Nigeria, which contains at least seven sibling species that are indistinguishable by morphology but differ in malaria vector competence). Cryptic species challenge the Morphological Species Concept because they show that morphological similarity does not guarantee conspecificity.

## Part 1.2

1. Continuous variation: a trait that varies along a continuous range, controlled by many genes and influenced by the environment; e.g. human height or body mass. Discontinuous variation: a trait that falls into distinct, non-overlapping categories, controlled by one or few genes; e.g. ABO blood group (A, B, AB, O) or sickle-cell genotype (HbA/HbA, HbA/HbS, HbS/HbS).
2. Polymorphism: the existence of two or more genetically distinct forms within a population, each at a frequency too high to be maintained by mutation alone. Two West African examples: (1) sickle-cell polymorphism in human populations across malaria-endemic Nigeria (HbA and HbS alleles maintained by balancing selection: heterozygote HbA/HbS has higher malaria survival than HbA/HbA); (2) wing colour polymorphism in the African swallowtail butterfly *Papilio dardanus* (females are mimetic polymorphs resembling different distasteful butterfly species).



3. Gene flow is the transfer of alleles from one population to another through the movement and successful reproduction of individuals (immigration and emigration). Effects on genetic structure: gene flow homogenises allele frequencies among populations, reducing genetic differentiation ( $F_{ST}$  approaches 0 with high gene flow); it counteracts the diversifying effects of genetic drift and local natural selection; high gene flow prevents local populations from diverging into separate species; low gene flow allows populations to differentiate and eventually speciate.
4. Five conditions required for Hardy-Weinberg equilibrium: (1) very large (effectively infinite) population size, so that random sampling error (genetic drift) is negligible; (2) random mating (panmixia): every individual has an equal probability of mating with every other individual regardless of genotype; (3) no mutation: no new alleles are introduced and existing alleles are not converted to new forms; (4) no migration (no gene flow): no individuals enter or leave the population carrying alleles from other populations; (5) no natural selection: all genotypes at the locus have equal fitness (equal survival and reproductive rates).
5. Given  $q = 0.3$  and  $p = 1 \text{ minus } 0.3 = 0.7$ .  $AA = p^2 = (0.7)^2 = 0.49$  (49%).  $Aa = 2pq = 2 \times 0.7 \times 0.3 = 0.42$  (42%).  $aa = q^2 = (0.3)^2 = 0.09$  (9%). Check:  $0.49 + 0.42 + 0.09 = 1.00$ .

### Part 1.3

1. Fundamental niche: the full range of abiotic and biotic conditions in which a species could potentially survive, grow, and reproduce if all resources were available and no competitors or predators were present. Realised niche: the subset of the fundamental niche that a species actually occupies in the presence of competitors, predators, and other biotic interactions; it is always equal to or narrower than the fundamental niche. Example: a grass species may be able to grow in both wet and dry soil (fundamental niche) but is excluded from wet soil by a competitive sedge species, so it only grows in dry soil (realised niche).
2. Stenotopic species: restricted to a narrow, specific habitat type; shows high habitat specialisation; example: the mangrove kingfisher (*Ispidina picta*) in Nigeria, found exclusively in mangrove forest and adjacent coastal freshwater habitats in the Niger Delta; it cannot survive in the forest interior or savanna. Eurytopic species: tolerates a wide range of habitat types and environmental conditions; shows low habitat specialisation; example: the pied crow (*Corvus albus*), which is found across the full range of Nigerian habitats from rainforest edges and urban areas in Lagos to savanna farmland and semi-arid environments in Kano State.



3. r-selected strategy: high intrinsic rate of increase ( $r$ ); many small offspring per reproductive event; minimal parental investment per offspring; early age at first reproduction; short lifespan; populations fluctuate widely and are well below carrying capacity in unpredictable or disturbed environments; examples: locusts, annual weeds, rats, mosquitoes. K-selected strategy: low intrinsic rate of increase; few large offspring per reproductive event; high parental investment per offspring; late age at first reproduction; long lifespan; populations are regulated near carrying capacity in stable, competitive environments; examples: African forest elephant, chimpanzee, large trees.
4. Semelparity: an organism reproduces in a single reproductive event during its lifetime, then dies; all reproductive effort is concentrated into one occasion; this maximises reproductive output in unpredictable environments where survival to a second reproduction is uncertain; examples: annual plants (cowpea, maize), Pacific salmon, mayflies. Iteroparity: an organism reproduces repeatedly over multiple seasons or years throughout its lifetime; reproductive effort is spread across many events; this is favoured when adult survival is high and each offspring has a reasonable probability of surviving; examples: perennial trees (shea butter tree), mammals (elephant, human), and most birds.
5. The cost of reproduction is the reduction in future survival or reproductive performance caused by current reproductive investment; investing resources in current offspring reduces the resources available for maintaining the parent's own body and producing future offspring. Life history trade-off: offspring number versus offspring size. A female has a fixed amount of energy available for reproduction; she can either produce many small offspring (each with lower individual survival probability) or fewer large, well-provisioned offspring (each with higher survival probability). Natural selection shapes where a species sits on this trade-off depending on environmental conditions: high-mortality, food-unpredictable environments favour many small offspring; low-mortality, competitive environments favour fewer large offspring.

#### Part 1.4

1. Phenetics (numerical taxonomy): classifies organisms by overall similarity across as many characters as possible, without regard to whether characters are ancestral or derived or whether similarity reflects common ancestry or convergent evolution; it produces phenograms; it is objective in character use but can group distantly related look-alikes together. Cladistics (phylogenetic systematics): classifies organisms strictly by shared derived characters



(synapomorphies) inherited from a common ancestor; it produces cladograms; it explicitly reflects evolutionary history; paraphyletic and polyphyletic groups are rejected; it is the theoretical basis of modern taxonomy.

2. Four binomial names: *Homo sapiens* (human); *Panthera leo* (lion); *Vigna unguiculata* (cowpea); *Oryza sativa* (rice). Rules of binomial nomenclature: (1) the first part is the Genus name, always written with a capital letter; (2) the second part is the species epithet, always written in lower case; (3) both parts are written in italics when typeset or underlined when handwritten; (4) the name is in Latin or latinised Greek, ensuring international neutrality; (5) each species has only one valid scientific name (the earliest validly published name under the International Codes of Nomenclature).
3. Cowpea (*Vigna unguiculata*): Domain Eukarya; Kingdom Plantae; Division (Phylum) Magnoliophyta (flowering plants); Class Magnoliopsida (dicotyledons); Order Fabales; Family Fabaceae (legumes); Genus *Vigna*; Species *Vigna unguiculata*.
4. Monophyletic group (clade): includes an ancestor and all of its descendants; all members share a synapomorphy inherited from their common ancestor; the only valid grouping in cladistics; e.g. Class Mammalia (all mammals and only mammals descended from the mammalian ancestor). Paraphyletic group: includes an ancestor and some but not all of its descendants; one or more descendant lineages are excluded; invalid in cladistics; e.g. "Reptilia" as traditionally defined (includes lizards, snakes, crocodilians, turtles) excludes birds, which are also descendants of the reptilian ancestor. Polyphyletic group: members share a character that arose independently (convergent evolution) rather than being inherited from the group's most recent common ancestor; invalid in cladistics; e.g. "warm-blooded vertebrates" grouping birds and mammals, which evolved endothermy independently.
5. The molecular clock is the observation that DNA sequences (and amino acid sequences in proteins) accumulate mutations at an approximately constant rate over geological time. It is used in phylogenetics to estimate the time of divergence between lineages by comparing the degree of molecular difference between them: greater molecular divergence indicates an earlier divergence date. Calibration: the clock is calibrated using fossil dates for known divergence events; the calibrated rate is then applied to lineages without a fossil record. Limitations: substitution rates vary among genes, taxa, and time periods (rate heterogeneity); multiple substitutions at the same site can be undetected (saturation); relaxed molecular clock models accommodate rate variation.



## References and Attributions [Series 1]

### Textual References (Books and External Sources)

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- FAO (Food and Agriculture Organization of the United Nations). (2025). Guidelines for sustainable agriculture. FAO.

### Figures, Plates, Tables, and Boxes

- Figure 1.1: Comparison of four major species concepts Attribution: AI generated. Suggested OER search string: "species concepts comparison diagram biological morphological phylogenetic ecological OER".
- Figure 1.2: Hardy-Weinberg equilibrium diagram with conditions and disturbing factors Attribution: AI generated. Suggested OER search string: "Hardy-Weinberg equilibrium conditions factors allele frequency diagram OER".
- Figure 1.3: r/K selection continuum and life history trade-offs diagram Attribution: AI generated. Suggested OER search string: "r K selection life history trade-offs continuum diagram offspring number size OER".
- Figure 1.4: Cladogram showing monophyletic, paraphyletic, and polyphyletic groups Attribution: AI generated. Suggested OER search string: "cladogram monophyletic paraphyletic polyphyletic clade diagram phylogenetics OER".



Course code: BIO 302

Course title: Population Biology and Evolution

Course credit load: 2 Units

## Series 2: Natural Selection and Variations

- **Part 2.1: Darwin and the Theory of Natural Selection**
  - Sub Part 2.1.1: Historical background and Darwin's observations
  - Sub Part 2.1.2: The four postulates of natural selection
  - Sub Part 2.1.3: Evidence for natural selection
- **Part 2.2: Modes of Natural Selection**
  - Sub Part 2.2.1: Directional selection
  - Sub Part 2.2.2: Stabilising and disruptive selection
  - Sub Part 2.2.3: Balancing selection
- **Part 2.3: Sources and Types of Variation**
  - Sub Part 2.3.1: Mutation as the ultimate source of variation
  - Sub Part 2.3.2: Recombination and genetic variation
  - Sub Part 2.3.3: Phenotypic plasticity and norm of reaction
- **Part 2.4: The Modern Evolutionary Synthesis**
  - Sub Part 2.4.1: Integrating genetics and Darwinian evolution
  - Sub Part 2.4.2: Microevolution and macroevolution
  - Sub Part 2.4.3: Non-selective mechanisms of evolution



## Introduction

Natural selection is the central mechanism of evolution. It acts on heritable variation in fitness-related traits within populations, changing allele frequencies over generations. Understanding the sources and maintenance of variation is equally important: without variation, selection has no raw material. Together, natural selection and its interaction with variation, mutation, drift, and gene flow explain the diversity of life.

This Series covers Darwin's theory and its four postulates, direct evidence for natural selection, the three main modes of selection (directional, stabilising, disruptive), balancing selection, the sources of variation (mutation and recombination), phenotypic plasticity, and the Modern Evolutionary Synthesis that unified classical Darwinism with Mendelian genetics and population genetics.

## Series Learning Outcomes

Upon completing this Series, you should be able to:

- **SLO 2.1** describe the historical context of Darwin's theory and state the four postulates of natural selection (Linked to Part 2.1),
- **SLO 2.2** describe and give examples of the evidence for natural selection (Linked to Part 2.1),
- **SLO 2.3** distinguish between directional, stabilising, disruptive, and balancing selection and describe the population-level consequences of each (Linked to Part 2.2),
- **SLO 2.4** describe mutation and recombination as sources of variation and explain phenotypic plasticity (Linked to Part 2.3),
- **SLO 2.5** explain the Modern Evolutionary Synthesis (Linked to Part 2.4), and
- **SLO 2.6** distinguish between microevolution and macroevolution, and describe non-selective mechanisms of evolutionary change (Linked to Part 2.4).



## 2.1 Darwin and the Theory of Natural Selection

### 2.1.1 Historical background and Darwin's observations

Charles Darwin (1809-1882) developed the theory of evolution by natural selection based on observations made during his voyage on HMS Beagle (1831-1836). Key observations: the diversity of life forms in geographically isolated regions (especially the Galapagos Islands); the resemblance between fossil species and living species in the same region; and Malthus's essay on population (1798), which noted that populations tend to grow faster than food supply, implying a struggle for existence.

Darwin also drew on Thomas Malthus's observation that populations grow geometrically but resources grow arithmetically, producing inevitable competition. Alfred Russel Wallace independently arrived at the same theory in 1858; Darwin and Wallace jointly presented their ideas to the Linnean Society in 1858, and Darwin published *On the Origin of Species* in 1859. Before Darwin, the prevailing view was fixism (species are fixed and unchanging); Darwin's theory replaced this with the concept of gradual change through selection.

Fill in the blank: Darwin published \_\_\_\_\_ in 1859, proposing that species change over time through the action of natural selection on heritable variation; Alfred Russel Wallace independently arrived at the same theory in 1858.

### 2.1.2 The four postulates of natural selection

Darwin's theory of natural selection rests on four postulates. (1) Variation: individuals within a population differ from one another in their traits. (2) Heritability: at least some of the variation is heritable (passed from parent to offspring). (3) Differential survival and reproduction (fitness differences): individuals with certain trait variants survive and reproduce more successfully than others in a given environment.

(4) Selection: because of fitness differences and heritability, the traits of individuals that survive and reproduce more successfully will become more common in the population over successive generations. All four postulates must hold for natural selection to operate; if variation is not



heritable, it cannot respond to selection; if all variants have equal fitness, no selection occurs. These four postulates were later mathematised by population geneticists into the breeder's equation: response to selection (R) = heritability ( $h^2$ ) x selection differential (S).

Fill in the blank: The four postulates of natural selection are: (1) variation within populations; (2) \_\_\_\_\_ of variation; (3) differential survival and reproduction; and (4) change in trait frequency over generations.

### 2.1.3 Evidence for natural selection

Direct evidence: industrial melanism in the peppered moth (*Biston betularia*): before industrialisation, the pale form was camouflaged on lichen-covered bark; after industrial soot blackened bark, the melanic (dark) form increased in frequency because it was better camouflaged from predatory birds. After the Clean Air Acts reduced pollution, pale forms increased again. This remains one of the most cited examples of observed directional selection.

Additional evidence: antibiotic resistance in bacteria (selection for resistant strains by antibiotic use; a major public health crisis); pesticide resistance in insects (malaria mosquitoes *Anopheles gambiae* in Nigeria have evolved resistance to pyrethroids and DDT); beak size variation in Darwin's finches (*Geospiza*) correlated with seed availability; artificial selection in domesticated animals and plants demonstrating that selection changes heritable traits; the fossil record showing directional change over geological time.

Fill in the blank: Industrial \_\_\_\_\_ in the peppered moth (*Biston betularia*) is a classic example of directional natural selection; the dark melanic form increased in polluted industrial areas because it was better camouflaged from bird predators on soot-blackened bark.



## INDUSTRIAL MELANISM IN THE PEPPERED MOTH (*Biston betularia*) - A CASE OF DIRECTIONAL NATURAL SELECTION

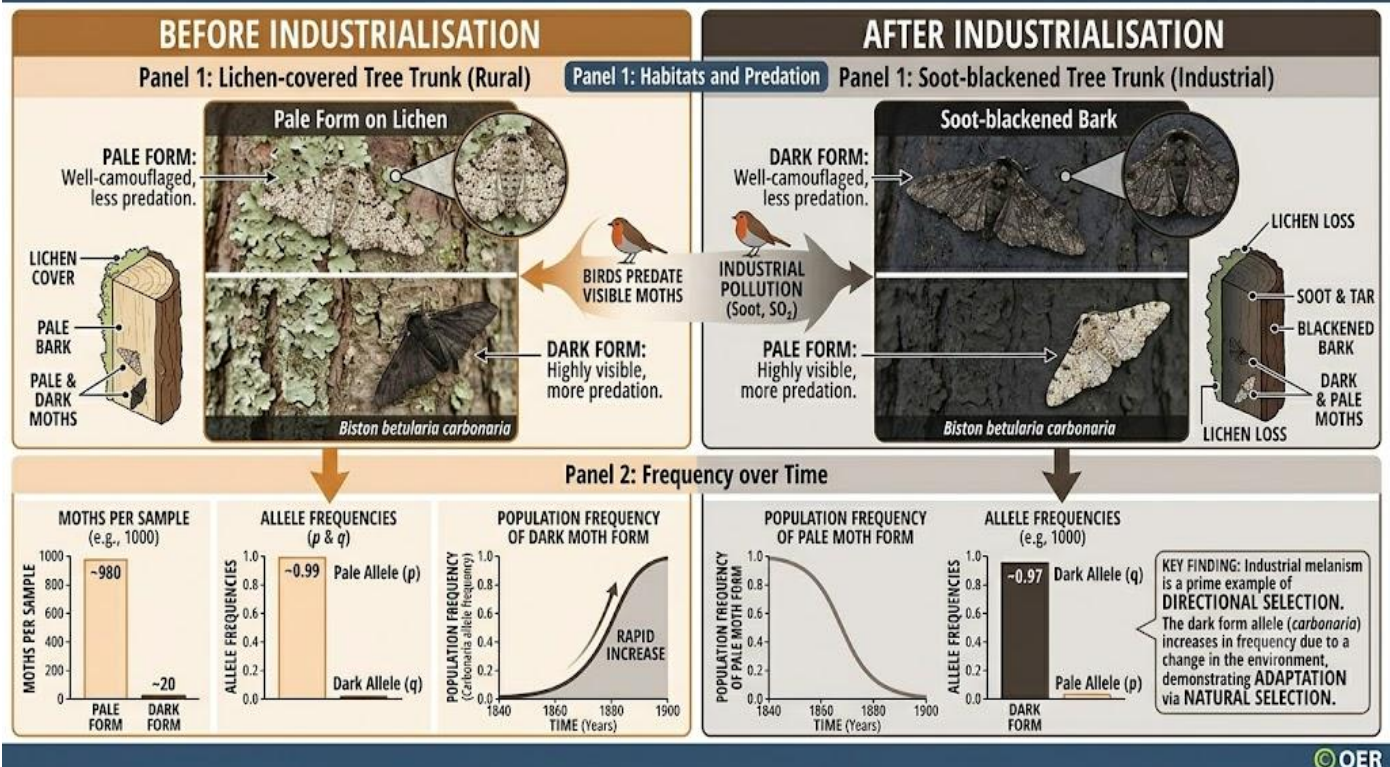


Figure 2.1: Diagram illustrating industrial melanism in the peppered moth

### Pilot questions 2.1

1. State the four postulates of natural selection.
2. Explain what observation by Malthus influenced Darwin's thinking.
3. Describe industrial melanism as evidence for natural selection.
4. Explain how antibiotic resistance provides evidence for natural selection.
5. Explain why all four postulates must hold for natural selection to operate.

## 2.2 Modes of Natural Selection

### 2.2.1 Directional selection

Directional selection favours individuals at one extreme of the phenotypic distribution, shifting the population mean toward that extreme over time. It reduces variation and moves the



population mean in one direction. Examples: the evolution of longer necks in giraffe ancestors (taller individuals had better access to leaves); antibiotic resistance in bacterial populations (selection consistently favours resistant genotypes); Biston betularia melanism (selection consistently favoured the dark form under industrial pollution).

Directional selection is most common when the environment is changing in one direction. In a graph of phenotypic distribution over time, the bell-shaped curve shifts left or right. Directional selection reduces genetic variation for the selected trait unless new mutations replenish it. Artificial selection (selective breeding of crops and livestock) is deliberately applied directional selection; Nigerian plant breeders use it to improve the yield of cowpea, maize, and cassava varieties at the National Cereals Research Institute (NCRI) and Institute of Agricultural Research and Training (IAR&T).

Fill in the blank: \_\_\_\_\_ selection favours individuals at one extreme of the phenotypic distribution and shifts the population mean in one direction over generations; it is the type of selection operating in antibiotic resistance and industrial melanism.

### **2.2.2 Stabilising and disruptive selection**

Stabilising selection favours intermediate phenotypes and acts against both extremes. It reduces phenotypic variance without shifting the mean. Classic example: human birth weight. Babies at both extremes (very low or very high birth weight) have higher mortality; intermediate birth weights (approximately 3 to 4 kg) have highest survival. Stabilising selection is the most common mode in stable environments; it maintains well-adapted intermediate phenotypes and reduces the frequency of extreme variants.

Disruptive (diversifying) selection favours both extremes and acts against intermediate phenotypes; it increases phenotypic variance and can split one population into two distinct groups. Example: beak size in the African seed-cracker finch (*Pyrenestes ostrinus*) in Cameroon; birds with very small or very large beaks are favoured for different seed sizes; intermediate beaks are less efficient at either. Disruptive selection can promote polymorphism within a population and, if combined with assortative mating, may initiate sympatric speciation.



Fill in the blank: \_\_\_\_\_ selection favours both extreme phenotypes and acts against intermediate individuals; it increases phenotypic variance in the population and can promote polymorphism or sympatric speciation if combined with assortative mating.

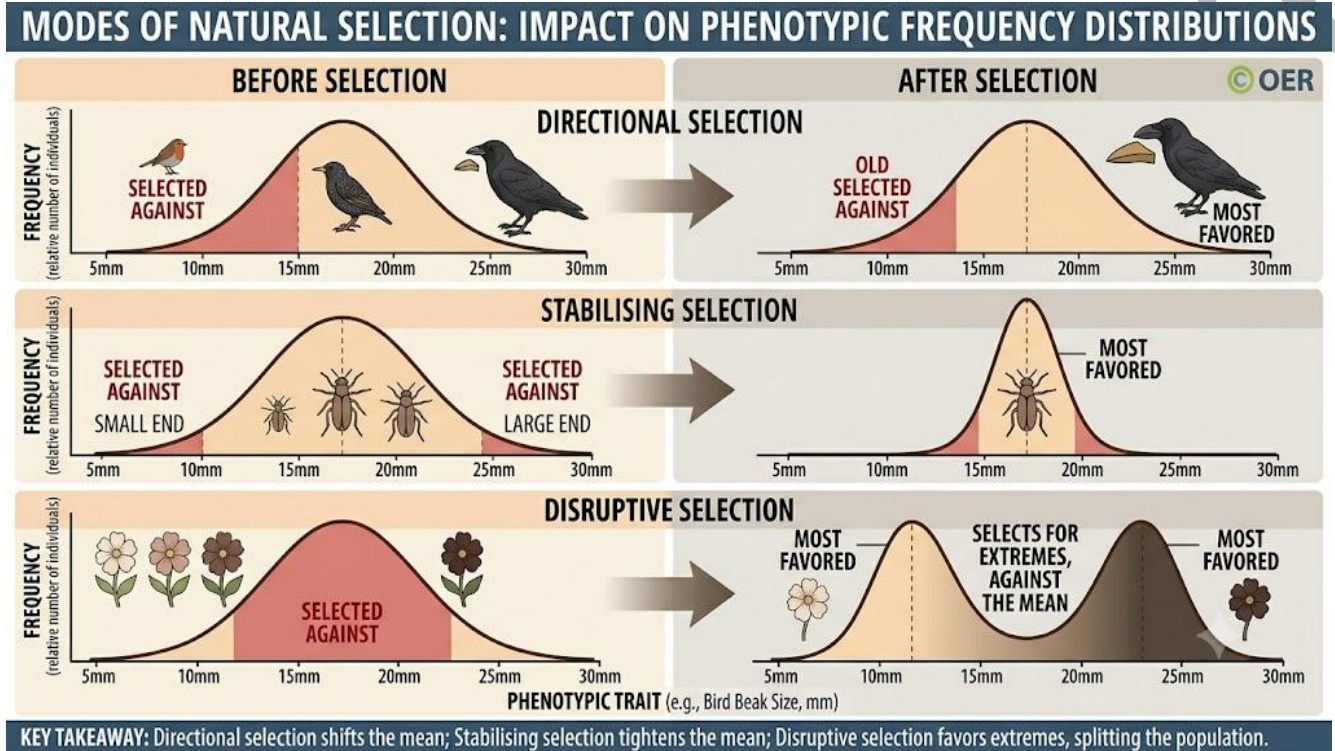


Figure 2.2: Diagrams of the three modes of natural selection

### 2.2.3 Balancing selection

Balancing selection maintains two or more alleles in a population at stable frequencies above those expected from mutation alone. It is a major mechanism maintaining genetic polymorphism. Two main forms: heterozygote advantage (overdominance): the heterozygote  $Aa$  has higher fitness than either homozygote  $AA$  or  $aa$ ; the classic example is sickle-cell trait in Nigeria ( $HbA/HbS$  heterozygotes have higher survival in malaria-endemic regions than  $HbA/HbA$  or  $HbS/HbS$  homozygotes).

Frequency-dependent selection: fitness of a genotype depends on its frequency; negative frequency-dependent selection favours rare morphs (the rarer a colour morph, the less recognised by predators; e.g. snail shell colour in *Cepaea*); this maintains polymorphism by giving an



advantage to whichever allele is rarer. Temporal and spatial variation in selection pressures: different environments at different times or in different patches within the species range can favour different alleles, maintaining diversity across the population as a whole.

Fill in the blank: \_\_\_\_\_ advantage (overdominance) maintains two alleles in a population by giving the heterozygote higher fitness than either homozygote; the sickle-cell polymorphism in malaria-endemic Nigeria is the most cited example.

### Pilot questions 2.2

1. Define directional selection and give two examples.
2. Explain stabilising selection with the example of human birth weight.
3. Explain disruptive selection and state one consequence it can have for a population.
4. Explain heterozygote advantage (overdominance) using the sickle-cell example.
5. Distinguish between directional and stabilising selection in terms of effect on mean and variance.

## 2.3 Sources and Types of Variation

### 2.3.1 Mutation as the ultimate source of variation

Mutation is the ultimate source of all new genetic variation; it is any heritable change in the DNA sequence. Types: point mutation (substitution, insertion, or deletion of one or a few bases); chromosomal mutation (deletion, duplication, inversion, or translocation of chromosomal segments); polyploidy (multiplication of entire chromosome sets; very common in plant evolution; most crop plants are polyploids). Mutations are random with respect to fitness: they are not directed toward improvement.

Most mutations are neutral or deleterious; beneficial mutations are rare but are the raw material on which selection acts. Mutation rates vary: approximately 1 per  $10^8$  base pairs per replication in bacteria; approximately 1 per  $10^9$  base pairs per generation in humans; but the large genome sizes and many cell divisions mean each human newborn carries approximately 60 to 100 new



point mutations. Mobile genetic elements (transposons) also generate genetic diversity by inserting into and disrupting genes or creating copy-number variation.

Fill in the blank: Mutation is the \_\_\_\_\_ source of all new genetic variation; most mutations are neutral or deleterious; the rare beneficial mutations are the raw material on which natural selection acts to drive evolutionary change.

### 2.3.2 Recombination and genetic variation

Sexual reproduction generates enormous genetic variation through two mechanisms. Independent assortment: at meiosis I, homologous chromosome pairs segregate independently; for  $n$  chromosome pairs,  $2^n$  combinations of paternal and maternal chromosomes are possible ( $2^{23}$  = approximately 8 million in humans). Crossing over (recombination): during prophase I, homologous chromosomes exchange segments at chiasmata, producing recombinant chromosomes with new allele combinations not present in either parent.

Recombination is the primary source of new combinations of existing alleles, producing more variation per generation than mutation alone and allowing favourable alleles to be combined on the same chromosome (breaking up unfavourable linkages). High recombination rates are favoured in variable environments because they generate diverse offspring. In asexual organisms, all offspring are genetically identical to the parent (clones), and the only new variation comes from mutation; this limits their ability to respond to changing environments.

Fill in the blank: \_\_\_\_\_ over during meiosis I exchanges segments between homologous chromosomes at chiasmata, producing recombinant chromosomes with new allele combinations that were not present in either parent.



## SOURCES OF GENETIC VARIATION DURING MEIOSIS: INDEPENDENT ASSORTMENT & CROSSING OVER

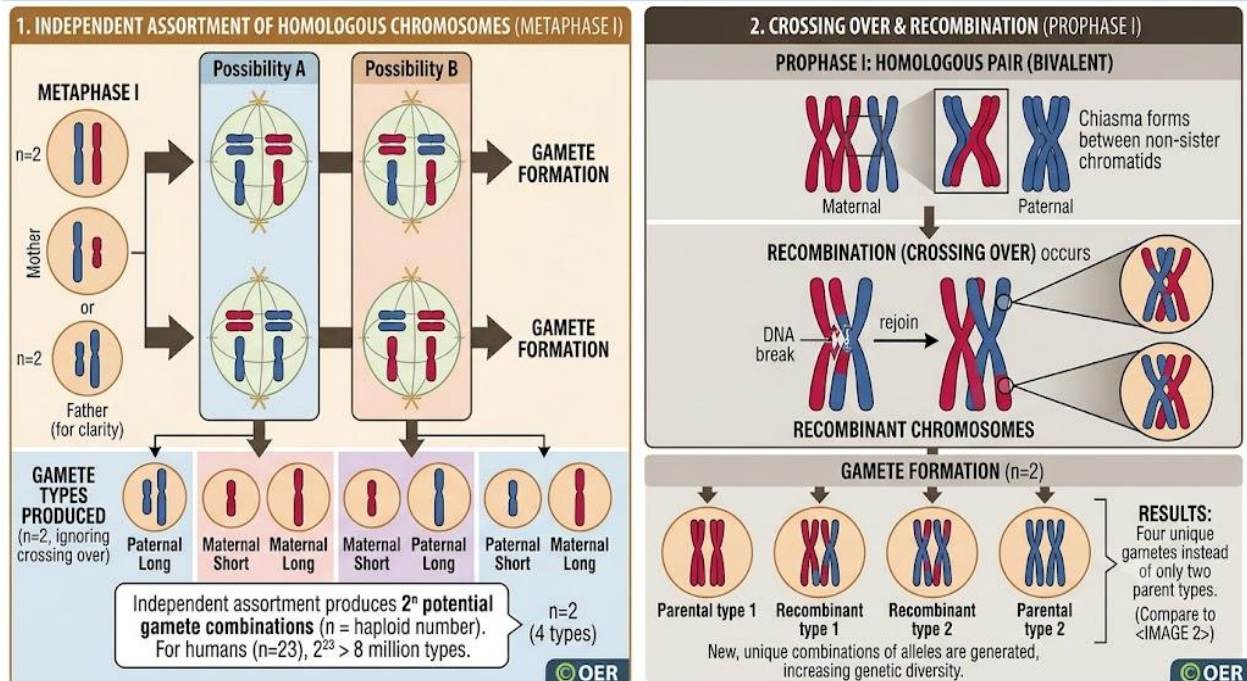


Figure 2.3: Diagram showing independent assortment and crossing over as sources of genetic variation

### 2.3.3 Phenotypic plasticity and norm of reaction

Phenotypic plasticity is the ability of a single genotype to produce different phenotypes in different environmental conditions. It allows organisms to adjust their morphology, physiology, or behaviour in response to environmental variation without genetic change. Examples: a tree growing in a windy exposed site develops a shorter, more wind-resistant form than the same genotype grown in a sheltered forest; tadpoles of some frog species develop larger tails when predators are present.

The norm of reaction is a graph describing how the phenotype of a specific genotype changes across a range of environmental conditions (e.g. body size plotted against temperature). Different genotypes can have different norms of reaction (crossing reaction norms produce genotype-by-environment interaction, or G x E). Phenotypic plasticity is itself a heritable trait subject to selection. High plasticity is favoured in variable environments; canalization (low plasticity,



consistent phenotype across environments) is favoured when one phenotype is consistently optimal.

Fill in the blank: The norm of \_\_\_\_\_ describes how the phenotype of a specific genotype changes across a range of environmental conditions; crossing norms of reaction between genotypes indicate genotype-by-environment interaction.

### Pilot questions 2.3

1. Define mutation and list four types.
2. Explain independent assortment as a source of genetic variation.
3. Explain how crossing over during meiosis generates new genetic combinations.
4. Define phenotypic plasticity and give one example.
5. Explain what a norm of reaction is and what crossing norms of reaction indicate.

## 2.4 The Modern Evolutionary Synthesis

### 2.4.1 Integrating genetics and Darwinian evolution

The Modern Evolutionary Synthesis (or New Synthesis) emerged in the 1930s to 1950s, integrating Darwin's theory of natural selection with Mendelian genetics and population genetics. Key architects: Ronald Fisher (The Genetical Theory of Natural Selection, 1930); Sewall Wright (genetic drift, adaptive landscapes); J.B.S. Haldane (mathematical population genetics); Theodosius Dobzhansky (Genetics and the Origin of Species, 1937; bridge between lab genetics and fieldwork); Ernst Mayr (Systematics and the Origin of Species, 1942; BSC); G.G. Simpson (palaeontology and evolution).

Before the Synthesis, naturalists and geneticists were divided: naturalists (Darwinian) argued that evolution was gradual and continuous; early geneticists argued that evolution proceeded by large mutations (saltations). The Synthesis resolved this by showing that: Mendelian inheritance provides the particulate inheritance that Darwin lacked; small mutations with quantitative effects



on phenotype could produce the continuous variation Darwin observed; natural selection acting on this variation could produce the gradual change the fossil record shows.

Fill in the blank: The Modern Evolutionary \_\_\_\_\_ integrated Darwin's natural selection with Mendelian genetics; key architects included Fisher, Wright, Haldane, Dobzhansky, Mayr, and Simpson; it established population genetics as the mathematical foundation of evolutionary biology.

#### **2.4.2 Microevolution and macroevolution**

Microevolution refers to changes in allele frequencies within a population over time; it operates at the level of populations and is driven by the four mechanisms: natural selection, genetic drift, mutation, and gene flow. Microevolution is directly observable (antibiotic resistance; industrial melanism) and is mathematically modelled by population genetics. The Modern Synthesis emphasised that macroevolution is simply the accumulation of microevolutionary changes over long time periods.

Macroevolution refers to evolutionary change at and above the species level: speciation (the origin of new species), anagenesis (gradual transformation of a lineage), cladogenesis (splitting of lineages), extinction, and long-term evolutionary trends (e.g. the trend toward increasing brain size in the hominin lineage). Some biologists argue that macroevolution involves processes (species selection, evolutionary constraints, developmental biases) not fully explained by microevolution alone (the Extended Evolutionary Synthesis debate).

Fill in the blank: \_\_\_\_\_ evolution refers to changes in allele frequencies within populations; \_\_\_\_\_ evolution refers to evolutionary change at and above the species level including speciation, extinction, and long-term evolutionary trends.

#### **2.4.3 Non-selective mechanisms of evolution**

Genetic drift is the random change in allele frequencies due to chance sampling in finite populations; its effect is strongest in small populations. Two special cases: founder effect (a small number of individuals colonise a new area and carry only a subset of the original



population's alleles; the new population has reduced genetic diversity and different allele frequencies; e.g. the Afrikaner population in South Africa has high frequency of specific genetic diseases traceable to a small 17th-century founder group).

Bottleneck effect: a drastic reduction in population size (e.g. due to disease, drought, or hunting) followed by recovery; genetic diversity is reduced because only a random subset of alleles survive; e.g. the cheetah (*Acinonyx jubatus*) has extremely low genetic diversity due to a severe population bottleneck approximately 10,000 years ago. Mutation: provides new alleles but is too slow a process alone to explain observed evolutionary rates. Gene flow: can introduce new alleles and homogenise allele frequencies; can counteract local adaptation by swamping local alleles with immigrant alleles.

Fill in the blank: The \_\_\_\_\_ effect occurs when a small number of individuals found a new population; the founders carry only a subset of the original gene pool, reducing genetic diversity and causing random allele frequency differences from the source population.

| <u><b>Mechanism</b></u>         | <b>Effect on Genetic Diversity</b>                                                                 | <b>Effect on Allele Frequencies</b>                        | <b>Key Notes</b>                                                                                              |
|---------------------------------|----------------------------------------------------------------------------------------------------|------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------|
| <u><b>Natural Selection</b></u> | Can reduce diversity by favoring certain alleles; may maintain diversity under balancing selection | Changes frequencies based on fitness advantage             | Adaptive process; alleles that improve survival/reproduction increase in frequency                            |
| <u><b>Genetic Drift</b></u>     | Reduces diversity, especially in small populations                                                 | Random changes; may fix or lose alleles                    | Non-adaptive; chance events drive allele frequency shifts (e.g., bottlenecks, founder effect)                 |
| <u><b>Mutation</b></u>          | Increases diversity by introducing new alleles                                                     | Usually small changes; provides raw material for evolution | Ultimate source of genetic variation; effects depend on whether mutations are beneficial, neutral, or harmful |



|                  |                                                                                 |                                                          |                                                                          |
|------------------|---------------------------------------------------------------------------------|----------------------------------------------------------|--------------------------------------------------------------------------|
| <u>Gene Flow</u> | Increases diversity within populations; reduces differences between populations | Introduces new alleles or homogenizes allele frequencies | Migration between populations; can counteract drift and local adaptation |
|------------------|---------------------------------------------------------------------------------|----------------------------------------------------------|--------------------------------------------------------------------------|

Box 2.1: Summary of the four mechanisms of evolutionary change

#### Pilot questions 2.4

1. State the key figures of the Modern Evolutionary Synthesis and their contributions.
2. Distinguish between microevolution and macroevolution.
3. Explain the founder effect and give one example.
4. Explain the bottleneck effect and give one example.
5. Explain how gene flow can oppose local adaptation.

### Series Summary

This Series covered natural selection and variation. Darwin (1859) proposed four postulates: variation, heritability, differential survival, and selection; Wallace co-discovered the theory. Evidence: industrial melanism (*Biston betularia*); antibiotic and pesticide resistance; artificial selection; fossil record. Modes of selection: directional (shifts mean; antibiotic resistance); stabilising (reduces variance; human birth weight); disruptive (increases variance; *Pyrenestes* beak size); balancing (maintains polymorphism; heterozygote advantage in sickle-cell; negative frequency-dependent selection).

Sources of variation: mutation (ultimate source; point mutations, chromosomal mutations, polyploidy; random with respect to fitness); recombination (independent assortment:  $2^n$  combinations; crossing over: new allele combinations). Phenotypic plasticity: single genotype



produces different phenotypes in different environments; norm of reaction describes phenotype across environments; G x E interaction from crossing norms. Modern Evolutionary Synthesis (1930s-50s; Fisher, Wright, Haldane, Dobzhansky, Mayr, Simpson): unified natural selection with Mendelian genetics. Microevolution (allele frequency change in populations) vs macroevolution (speciation, extinction, evolutionary trends). Non-selective mechanisms: genetic drift (random; strongest in small populations); founder effect; bottleneck effect; gene flow (homogenises allele frequencies). By completing this Series, you should achieve all six SLOs (2.1 to 2.6).

## Glossary of Terms

- **Balancing selection:** natural selection that maintains two or more alleles in a population at stable frequencies above those attributable to mutation alone; includes heterozygote advantage and frequency-dependent selection.
- **Bottleneck effect:** the loss of genetic diversity that follows a drastic reduction in population size; the surviving population represents a random, often unrepresentative subset of the original gene pool.
- **Canalization:** the tendency of development to produce a consistent phenotype despite genetic or environmental variation; low phenotypic plasticity.
- **Directional selection:** natural selection that consistently favours individuals at one phenotypic extreme, shifting the population mean over time.
- **Disruptive selection:** natural selection that favours both phenotypic extremes and acts against intermediate phenotypes; increases phenotypic variance.
- **Founder effect:** the reduction in genetic diversity that occurs when a new population is established by a small number of individuals carrying only a subset of the original population's alleles.



- **Genetic drift:** random changes in allele frequencies in a population, arising from chance sampling; more pronounced in small populations; can fix or eliminate alleles regardless of their fitness.
- **Gene flow:** the movement of alleles between populations through migration and reproduction; homogenises allele frequencies and reduces genetic differentiation.
- **Genotype-by-environment interaction (G x E):** the phenomenon where different genotypes respond differently to the same range of environmental conditions; detected by crossing norms of reaction.
- **Heritability ( $h^2$ ):** the proportion of phenotypic variance in a trait that is attributable to genetic (additive) variation; determines how strongly a trait can respond to selection.
- **Heterozygote advantage (overdominance):** a form of balancing selection in which the heterozygote Aa has higher fitness than either homozygote AA or aa; maintains both alleles in the population.
- **Industrial melanism:** the increase in frequency of dark (melanic) forms of the peppered moth (*Biston betularia*) in industrially polluted areas where soot-darkened bark provided camouflage for dark moths; a classic example of directional selection.
- **Macroevolution:** evolutionary change at or above the species level; includes speciation, extinction, anagenesis, cladogenesis, and long-term evolutionary trends.
- **Microevolution:** changes in allele frequencies within a population over time; driven by natural selection, genetic drift, mutation, and gene flow.
- **Modern Evolutionary Synthesis:** the theoretical integration of Darwinian natural selection with Mendelian genetics and population genetics, developed in the 1930s to 1950s.
- **Mutation:** a heritable change in DNA sequence; includes point mutations, chromosomal mutations, and polyploidy; the ultimate source of all new genetic variation.
- **Negative frequency-dependent selection:** selection that favours rare phenotypes or alleles; the rarer a morph, the higher its relative fitness; maintains polymorphism.



- **Norm of reaction:** a graph showing how the phenotype of a specific genotype changes across a range of environmental conditions.
- **Phenotypic plasticity:** the ability of a single genotype to produce different phenotypes in response to different environmental conditions.
- **Polyplidity:** the condition of having more than two complete sets of chromosomes; very common in plant evolution and crop domestication.
- **Recombination:** the exchange of DNA segments between homologous chromosomes during meiosis I (crossing over), producing chromosomes with new allele combinations.
- **Stabilising selection:** natural selection that favours intermediate phenotypes and acts against both extremes; reduces phenotypic variance without shifting the mean.

## Concept Check Questions [Series 2]

### Objective Questions

1. Darwin published On the Origin of Species in 1859; the theory was independently developed by Alfred Russel \_\_\_\_\_ in 1858. (Linked to SLO 2.1)
2. The four postulates of natural selection are: variation, heritability, differential survival, and \_\_\_\_\_ (change in trait frequency over generations). (Linked to SLO 2.1)
3. \_\_\_\_\_ selection favours intermediate phenotypes and reduces phenotypic variance without shifting the mean; human birth weight is the classic example. (Linked to SLO 2.3)
4. The sickle-cell polymorphism is maintained in malaria-endemic Nigeria by \_\_\_\_\_ advantage; HbA/HbS heterozygotes have higher fitness than either homozygote. (Linked to SLO 2.3)
5. The Modern Evolutionary \_\_\_\_\_ integrated Darwin's natural selection with Mendelian genetics and population genetics in the 1930s to 1950s. (Linked to SLO 2.5)



### Short-Answer Questions

6. State the four postulates of natural selection and explain why all four must hold. (Linked to SLO 2.1)
7. Distinguish between directional, stabilising, and disruptive selection in terms of their effects on the population mean and variance. (Linked to SLO 2.3)
8. Define mutation and state three types. (Linked to SLO 2.4)
9. Distinguish between the founder effect and the bottleneck effect. (Linked to SLO 2.6)
10. Explain phenotypic plasticity and give one example. (Linked to SLO 2.4)

### Long-Answer Questions

11. Describe Darwin's theory of natural selection; state its four postulates; and describe three pieces of evidence for natural selection. (Linked to SLOs 2.1, 2.2)
12. Describe and distinguish between directional, stabilising, disruptive, and balancing selection; give one example of each. (Linked to SLO 2.3)
13. Describe the sources of genetic variation (mutation, recombination); explain phenotypic plasticity and the norm of reaction; and describe the Modern Evolutionary Synthesis and non-selective mechanisms of evolution. (Linked to SLOs 2.4, 2.5, 2.6)

### Answers to Concept Check Questions [Series 2]

#### Objective Questions

1. Wallace.
2. Selection.
3. Stabilising.
4. Heterozygote.
5. Synthesis.



### Short-Answer Questions

6. (1) Variation within populations; (2) heritability of variation; (3) differential survival and reproduction; (4) trait frequency changes over generations. All four must hold: without heritability, selected traits cannot be passed on; without fitness differences, no selection occurs; without variation, there is nothing to select.
7. Directional: shifts mean in one direction; reduces variance. Stabilising: mean unchanged; variance reduced (eliminates extremes). Disruptive: mean unchanged; variance increased (both extremes favoured; intermediate eliminated).
8. Mutation is a heritable change in DNA sequence. Three types: point mutation (substitution, insertion, or deletion of one or a few bases); chromosomal mutation (deletion, duplication, inversion, or translocation of chromosomal segments); polyploidy (multiplication of entire chromosome sets).
9. Founder effect: a small group founds a new population carrying a subset of the source gene pool; allele frequencies differ from the source by chance. Bottleneck effect: an existing population is drastically reduced in size; genetic diversity is lost because only a random subset of alleles survives the bottleneck.
10. Phenotypic plasticity: the ability of a single genotype to produce different phenotypes in different environmental conditions. Example: a tree of one genotype grown in a windy exposed site develops a shorter, more compact form than the same genotype grown in a sheltered forest.

### Long-Answer Questions

11. Historical context: Darwin observed diversity in geographically isolated regions (Galapagos) and drew on Malthus's observation that populations grow faster than resources, implying competition. Wallace independently developed the same theory; Darwin and Wallace jointly presented the theory in 1858; *On the Origin of Species* published 1859. Four postulates: (1) variation within populations; (2) heritability of



variation; (3) differential survival and reproduction (fitness differences); (4) traits of the fitter individuals become more common over generations. Evidence: (1) industrial melanism in *Biston betularia* (dark form increased under soot-darkened bark; reversed after Clean Air Acts); (2) antibiotic resistance (bacterial populations evolve resistance when exposed to antibiotics; selection favours resistant genotypes); (3) pesticide resistance in *Anopheles gambiae* in Nigeria (populations in areas of high insecticide use show high frequencies of resistance alleles; direct microevolutionary response to selection).

12. Directional selection: favours one extreme; shifts population mean; reduces variance; examples: antibiotic resistance in bacteria; beak size in Galapagos finches during drought when only large seeds are available; industrial melanism. Stabilising selection: favours intermediate phenotypes; mean unchanged; variance reduced; example: human birth weight (very low and very high birth weight have higher infant mortality; intermediate 3-4 kg has highest survival). Disruptive selection: favours both extremes; mean unchanged; variance increased; can produce bimodal distribution; example: seed-cracker finch *Pyrenestes ostrinus* in Cameroon (very small and very large beaks are efficient at different seed sizes; intermediate beaks are less efficient at either). Balancing selection: maintains multiple alleles at stable frequencies; examples: heterozygote advantage in sickle-cell polymorphism (HbA/HbS heterozygotes have highest fitness in malaria-endemic Nigeria); negative frequency-dependent selection in snail shell polymorphism (rare colour morphs are less recognised by predators).
13. Mutation: ultimate source of all new genetic variation; includes point mutations (substitutions, insertions, deletions); chromosomal mutations (deletion, duplication, inversion, translocation); polyploidy (multiplication of chromosome sets; very common in crop plants). Most mutations are neutral or deleterious; rare beneficial mutations are the raw material for selection. Recombination: independent assortment at meiosis I produces  $2^n$  gamete chromosome combinations; crossing over (chiasmata in prophase I) produces recombinant chromosomes with new allele combinations; recombination is the primary source of new allele combinations per generation. Phenotypic plasticity: single genotype produces different phenotypes in different environments; norm of reaction describes phenotype of a genotype across an environmental gradient; crossing norms of



reaction indicate genotype-by-environment interaction (G x E). Modern Evolutionary Synthesis (1930s-50s): unified Darwin's natural selection with Mendelian genetics; key architects: Fisher, Wright, Haldane (mathematical framework); Dobzhansky (linked lab genetics to field biology); Mayr (BSC and speciation); Simpson (palaeontology). Established that macroevolution = accumulated microevolution. Non-selective mechanisms: genetic drift (random allele frequency change; strongest in small populations; can fix or eliminate alleles); founder effect (new population founded by small group; reduced diversity; random allele frequency differences; e.g. Afrikaner population); bottleneck effect (population drastically reduced; reduced diversity; e.g. cheetah bottleneck approximately 10,000 years ago); gene flow (introduces alleles from other populations; homogenises frequencies; can oppose local adaptation).

## Answers to Pilot Questions [Series 2]

### Part 2.1

1. (1) Variation: individuals within a population differ from one another in their traits (morphological, physiological, and behavioural); (2) Heritability: at least some of the variation is genetically inherited and can be passed from parent to offspring; (3) Differential survival and reproduction: individuals with certain trait variants survive and reproduce more successfully than others in a given environment (fitness differences); (4) Selection: because of fitness differences and heritability, traits of more successful individuals become more common in the population over successive generations.
2. Thomas Malthus observed in his 1798 Essay on the Principle of Population that human (and other animal) populations have the potential to grow geometrically (exponentially), doubling each generation, while food supply can only grow arithmetically (linearly); this means population growth will always outpace food supply, producing inevitable competition, struggle, and mortality. Darwin applied this insight to natural populations: if more individuals are produced than can survive, those with heritable traits that improve



survival or reproduction will leave more offspring than others, driving evolutionary change through differential reproductive success.

3. Industrial melanism in the peppered moth (*Biston betularia*): before industrialisation in 19th century Britain, the pale (typica) form was common because it was camouflaged against lichen-covered tree bark and therefore less visible to bird predators; the rare dark (carbonaria) melanic form was conspicuous and more often eaten. After industrial pollution killed lichens and coated bark with black soot, the dark form was better camouflaged; predation on pale moths increased; dark moth frequencies rose from less than 1% to over 90% in some industrial areas within decades. After the UK Clean Air Acts (1950s-1970s) reduced pollution, lichen returned and pale form frequencies increased again. This documents a complete directional selection episode responding to an environmental change.
4. Before antibiotics, bacterial populations contained rare random mutants carrying resistance alleles; these were selectively neutral or even slightly disadvantageous (resistance mechanisms have metabolic costs). When antibiotics are introduced, susceptible bacteria are killed; resistant bacteria survive and reproduce; their resistance alleles are inherited by all daughter cells; within a few generations, the population is dominated by resistant bacteria. This is textbook natural selection: heritable variation (resistance alleles), fitness difference (resistant bacteria survive antibiotic treatment), and change in allele frequency (resistance alleles increase to near-fixation). Antibiotic resistance in *Staphylococcus aureus* (MRSA) and in *Mycobacterium tuberculosis* causing drug-resistant TB are major public health problems in Nigerian hospitals.
5. All four postulates must hold simultaneously for natural selection to produce evolutionary change. If variation is absent (all individuals are identical for the trait), selection has nothing to act on. If variation is present but not heritable (all variation is due to the environment rather than genes), selected individuals cannot pass their advantageous traits to offspring and no evolutionary change occurs. If all variants have equal fitness (no differential survival or reproduction), there is no selection pressure. If differential reproduction occurs but trait differences are not heritable, the trait frequencies will not change from generation to generation. Only when variation exists, is heritable,



and is associated with differential fitness will allele frequencies change predictably over generations.

## Part 2.2

1. Directional selection favours individuals at one extreme of the phenotypic distribution, causing the population mean to shift toward that extreme while reducing variance. Two examples: (1) Antibiotic resistance: selection consistently favours bacteria carrying resistance alleles; susceptible individuals are eliminated; resistance allele frequency increases toward fixation in every generation of antibiotic exposure; (2) Beak size in Galapagos finches (*Geospiza fortis*) during the 1977 drought in the Galapagos: when small soft seeds were exhausted, only hard large seeds remained; birds with larger, deeper beaks could crack these seeds and survived; after the drought, mean beak size in the population was significantly larger than before (documented by Peter and Rosemary Grant).
2. Stabilising selection favours intermediate phenotypes and eliminates both extremes of the phenotypic distribution, thereby reducing variance without changing the mean. Classic example: human birth weight. Very low birth weight babies (under approximately 2.5 kg) have higher neonatal mortality due to immaturity, poor thermoregulation, and immune deficiency; very high birth weight babies (over approximately 4.5 kg) have higher mortality from delivery complications (obstructed labour, injury). Babies with intermediate birth weights (approximately 3 to 4 kg) have the highest survival. Before modern obstetric care, this selection pressure was very strong; stabilising selection has thus maintained a consistent average birth weight in human populations.
3. Disruptive selection favours both extreme phenotypes simultaneously and acts against individuals with intermediate phenotypes; it increases phenotypic variance in the population and can produce a bimodal (two-peaked) distribution. One consequence: disruptive selection can promote the maintenance of polymorphism within a population (two distinct morphs persist because both extremes are favoured); if combined with assortative mating (individuals mating preferentially with others of the same morph), it



can eventually drive the two extreme morphs toward reproductive isolation, initiating sympatric speciation (speciation without geographic separation).

4. Heterozygote advantage (overdominance) is a form of balancing selection in which the heterozygote (Aa) has higher fitness than either homozygote (AA or aa), resulting in both alleles being maintained in the population indefinitely. Sickle-cell example in Nigeria: HbA/HbA homozygotes (normal) have normal red blood cells but are susceptible to severe falciparum malaria; HbS/HbS homozygotes have sickle-cell disease, which causes chronic anaemia and organ damage and reduces survival; HbA/HbS heterozygotes (sickle-cell trait) have mostly normal blood but the sickling of a small proportion of red blood cells in low-oxygen conditions in the spleen kills Plasmodium falciparum parasites, giving significant protection against severe malaria. In malaria-endemic regions of Nigeria, both HbA and HbS alleles are maintained by this fitness advantage of the heterozygote.
5. Directional selection: shifts the population mean (moves the average value of the trait toward the favoured extreme); reduces variance (the disfavoured extreme is eliminated, narrowing the distribution). Stabilising selection: does not shift the population mean (the intermediate phenotype, which is already near the current mean, is favoured; the mean stays constant); reduces variance (both extremes are eliminated, making the distribution taller and narrower). In terms of the phenotypic frequency distribution plotted as a bell curve: directional selection moves the entire curve in one direction; stabilising selection makes the curve steeper and narrower without moving it.

### Part 2.3

1. Mutation is any heritable change in the DNA sequence of an organism. Four types: (1) Point mutation: a change in a single nucleotide base; can be a substitution (one base replaced by another; synonymous if it does not change the amino acid; non-synonymous if it changes the amino acid), an insertion (one or more bases added), or a deletion (one or more bases removed); insertions and deletions cause a frameshift mutation that alters the reading frame of the entire downstream sequence. (2) Chromosomal deletion: loss of a



chromosomal segment; can remove entire genes. (3) Chromosomal duplication: a segment is copied and repeated; provides raw material for new gene function evolution.

(4) Polyploidy: multiplication of the entire chromosome set (e.g. tetraploidy = 4 sets); extremely common in plant evolution; most cultivated crops are polyploids (wheat, cotton, coffee, sugarcane).

2. Independent assortment is the random orientation of homologous chromosome pairs at the metaphase I plate during meiosis I; because each pair aligns independently of all other pairs, the maternal and paternal chromosomes of each pair are distributed to gametes independently. For an organism with  $n$  pairs of chromosomes, there are  $2^n$  possible chromosome combinations in the gametes; for humans with  $n = 23$ , this gives  $2^{23} =$  approximately 8.4 million different chromosomal combinations from independent assortment alone. This means every gamete is likely to have a unique combination of maternal and paternal chromosomes, and every zygote formed by fertilisation will have a unique combination of all parental chromosomes.
3. Crossing over (recombination) occurs during prophase I of meiosis when homologous chromosomes pair up (synapsis) and physical exchange of DNA segments between non-sister chromatids occurs at points called chiasmata. Each chiasma is a site where a chromatid from one homologous chromosome has broken and rejoined to the corresponding chromatid of the other homologue, exchanging the segment distal to the chiasma. This produces recombinant chromatids that carry combinations of alleles (e.g. AB and ab from parental chromosomes can give aB and Ab recombinants) that were not present in either parent; these novel allele combinations may produce new phenotypes for selection to act on. Crossing over can also break up unfavourable allele combinations (negative linkage disequilibrium) and allow individually beneficial alleles to be assembled on the same chromosome.
4. Phenotypic plasticity is the capacity of a single genotype to produce different phenotypes in response to variation in environmental conditions, without any change in the underlying DNA sequence. Example: the water flea *Daphnia pulex* develops a prominent defensive helmet and tail spine in the presence of chemical signals (kairomones) released by predatory midge larvae; in the absence of predator cues, the same genotype produces individuals without these structures. The helmet and tail spine increase survival when



predators are present but are metabolically costly when predators are absent; the plastic response allows the same genotype to be well-adapted to both predator-present and predator-absent environments.

5. A norm of reaction is a graph that plots the phenotypic value of a specific genotype on the y-axis against a gradient of environmental conditions (e.g. temperature, food availability, light) on the x-axis; the resulting line shows how that genotype's phenotype responds across the environmental gradient. Different genotypes may have different slopes (reaction norm slopes) and different shapes. When the norms of reaction for two different genotypes cross each other (i.e. genotype A produces a higher phenotype than genotype B in one environment but a lower phenotype in another environment), this is called a genotype-by-environment interaction ( $G \times E$ ). Crossing norms of reaction indicate that the relative ranking of genotypes changes across environments, meaning no single genotype is universally superior and selection will favour different genotypes in different environments.

#### Part 2.4

1. Key figures and contributions to the Modern Evolutionary Synthesis: Ronald Fisher (The Genetical Theory of Natural Selection, 1930): showed mathematically that Mendelian inheritance of many genes with small effects could produce the continuous variation Darwin observed; reconciled Mendelism with Darwinian gradualism. Sewall Wright: developed the concept of genetic drift and effective population size; introduced the adaptive landscape metaphor. J.B.S. Haldane: provided mathematical models of selection acting on Mendelian genes; computed selection coefficients for observable evolution. Theodosius Dobzhansky (Genetics and the Origin of Species, 1937): demonstrated that chromosomal polymorphisms in wild *Drosophila* populations could be explained by natural selection; bridged laboratory genetics and field natural history. Ernst Mayr (Systematics and the Origin of Species, 1942): introduced the Biological Species Concept; explained allopatric speciation. G.G. Simpson (Tempo and Mode in Evolution,



1944): showed that palaeontological patterns were consistent with the gradual change predicted by population genetics.

2. Microevolution refers to changes in allele frequencies within a population over time; it occurs at the population level; it is directly observable within human lifetimes (antibiotic resistance evolution, industrial melanism); it is driven by the four mechanisms: natural selection, genetic drift, mutation, and gene flow; it is mathematically modelled by the Hardy-Weinberg framework and population genetics. Macroevolution refers to evolutionary change at and above the species level, occurring over geological timescales; it includes speciation (origin of new species), anagenesis (gradual transformation of an entire lineage), cladogenesis (branching of lineages), extinction, and long-term evolutionary trends such as the increase in body size in the horse lineage over 50 million years. The Modern Synthesis argued that macroevolution is simply the extrapolation of microevolutionary processes over long time periods.
3. The founder effect occurs when a small number of individuals ("founders") leave a large source population and establish a new population in a new location; the founders carry only a random sample of the alleles present in the source population, so the new population will have: reduced overall genetic diversity; allele frequencies that differ from the source population by chance; possible high frequency of alleles that were rare in the source population (if a founder happened to carry them). Example: the Afrikaners of South Africa descended largely from a small group of Dutch settlers in the 17th century; this small founding population had a high frequency of the allele causing Huntington's disease-like condition known as Huntington's disease and other genetic conditions that are unusually common in the Afrikaner population today, reflecting the founder effect.
4. The bottleneck effect occurs when a large population undergoes a dramatic reduction in size due to a catastrophic event (disease epidemic, severe drought, over-hunting, habitat destruction), then subsequently recovers in numbers; the bottleneck means that only a random and typically unrepresentative subset of alleles from the original population passes through to the survivors and their descendants; genetic diversity in the recovered population is much lower than in the original population; this reduction in diversity limits the evolutionary potential of the recovered population. Classic example: the cheetah (*Acinonyx jubatus*). Molecular genetic studies show that cheetah populations have



extremely low genetic diversity (individuals are almost as similar genetically as inbred laboratory mice); this is attributed to a severe population bottleneck approximately 10,000 years ago, possibly from a combination of climate change and human hunting at the end of the last ice age.

5. Gene flow is the movement of alleles from one population to another through migration and subsequent reproduction of immigrants. It can oppose local adaptation by introducing alleles from other populations that may have been selected against in the local environment; these immigrant alleles dilute the local, well-adapted allele combinations. For example, if a population of mice in a rocky, pale-substrate environment evolves pale coat colour (camouflage) by local selection, but is connected by gene flow to a neighbouring population on dark substrate that has evolved dark coat colour, the influx of dark alleles from the other population will counteract the local selection for pale coats. High gene flow (relative to selection intensity) swamps local adaptation; populations connected by extensive gene flow cannot diverge greatly in allele frequencies and cannot easily speciate.

## References and Attributions [Series 2]

### Textual References (Books and External Sources)

- Darwin, C. (1859). On the origin of species by means of natural selection. John Murray.
- Futuyma, D. J., & Kirkpatrick, M. (2017). Evolution (4th ed.). Sinauer Associates.
- Hartl, D. L., & Clark, A. G. (2007). Principles of population genetics (4th ed.). Sinauer Associates.
- FAO (Food and Agriculture Organization of the United Nations). (2025). Guidelines for sustainable agriculture. FAO.

### Figures, Plates, Tables, and Boxes



- Figure 2.1: Industrial melanism in the peppered moth diagram Attribution: AI generated. Suggested OER search string: "industrial melanism peppered moth Biston betularia natural selection directional diagram OER".
- Figure 2.2: Modes of natural selection phenotypic distribution graphs Attribution: AI generated. Suggested OER search string: "natural selection modes directional stabilising disruptive phenotypic distribution graphs OER".
- Figure 2.3: Independent assortment and crossing over as sources of variation Attribution: AI generated. Suggested OER search string: "independent assortment crossing over meiosis genetic variation recombination diagram OER".
- Box 2.1: Four mechanisms of evolutionary change comparison table Attribution: AI generated. Suggested OER search string: "evolutionary mechanisms comparison table natural selection genetic drift mutation gene flow OER box".



**Course code: BIO 302**

**Course title: Population Biology and Evolution**

**Course credit load: 2 Units**

## **Series 3: Isolation Mechanisms and Evolutionary Pathways**

- **Part 3.1: Reproductive Isolation Mechanisms**
  - Sub Part 3.1.1: Prezygotic isolation mechanisms
  - Sub Part 3.1.2: Postzygotic isolation mechanisms
  - Sub Part 3.1.3: The breakdown of isolation: hybridisation
- **Part 3.2: Modes of Speciation**
  - Sub Part 3.2.1: Allopatric speciation
  - Sub Part 3.2.2: Sympatric and parapatric speciation
  - Sub Part 3.2.3: Polyploidy and speciation in plants
- **Part 3.3: Adaptation and the Origin of Life**
  - Sub Part 3.3.1: Adaptation: types and mechanisms
  - Sub Part 3.3.2: Origin of life: major hypotheses
  - Sub Part 3.3.3: Early evolution of cells
- **Part 3.4: Origin of Species and Adaptive Radiation**
  - Sub Part 3.4.1: The origin of new species
  - Sub Part 3.4.2: Adaptive radiation



- Sub Part 3.4.3: Convergent evolution and evolutionary constraints

## Introduction

Speciation, the origin of new species, is the central event of macroevolution. It requires the evolution of reproductive isolation between diverging lineages. Understanding the mechanisms that prevent interbreeding, the geographic modes of speciation, and the broader pathways by which life diversifies are key topics in evolutionary biology. This Series also addresses the deep history of life: the origin of life itself, the first cells, and the explosive diversification of lineages through adaptive radiation.

Building on the species concepts and selection mechanisms of Series 1 and 2, this Series covers prezygotic and postzygotic isolation, hybridisation, allopatric and sympatric speciation, polyploidy, adaptation, origin of life hypotheses, early cellular evolution, the origin of species, adaptive radiation, convergent evolution, and evolutionary constraints.

## Series Learning Outcomes

Upon completing this Series, you should be able to:

- **SLO 3.1** classify and describe the major prezygotic and postzygotic reproductive isolation mechanisms (Linked to Part 3.1),
- **SLO 3.2** explain hybridisation as a breakdown of isolation and describe its evolutionary consequences (Linked to Part 3.1),
- **SLO 3.3** distinguish between allopatric, sympatric, and parapatric speciation and explain polyploidy as a speciation mechanism (Linked to Part 3.2),
- **SLO 3.4** define adaptation and describe the major hypotheses for the origin of life and early cellular evolution (Linked to Part 3.3),
- **SLO 3.5** explain how new species arise from existing species (Linked to Part 3.4), and



- **SLO 3.6** describe adaptive radiation and explain convergent evolution and evolutionary constraints (Linked to Part 3.4).

### 3.1 Reproductive Isolation Mechanisms

#### 3.1.1 Prezygotic isolation mechanisms

Reproductive isolation mechanisms are biological barriers that prevent two species from interbreeding and producing fertile offspring. Prezygotic mechanisms act before fertilisation.

Habitat isolation: two species occupy different habitats in the same geographic area and rarely encounter each other (e.g. two warthog species using different vegetation types in savanna).

Temporal isolation: species reproduce at different times (seasons, times of day); e.g. two frog species in Nigeria breeding at different points in the rainy season.

Behavioural (ethological) isolation: species do not recognise each other as mates; different mating calls, courtship displays, or chemical signals; most important in animals (e.g. different bird song dialects in West African sunbirds). Mechanical isolation: structural incompatibility prevents copulation or pollen transfer (e.g. flower shape matches only a specific pollinator; genital morphology prevents copulation between insect species). Gametic isolation: gametes of two species fail to attract or fertilise each other even if mating occurs (e.g. species-specific proteins on sea urchin egg surfaces prevent cross-species fertilisation).

Fill in the blank: \_\_\_\_\_ isolation prevents two species from interbreeding because they mate at different seasons, times of day, or years; it is a form of prezygotic isolation that does not require direct contact between individuals.



## REPRODUCTIVE ISOLATION MECHANISMS: PREZYGOTIC vs. POSTZYGOTIC BARRIERS

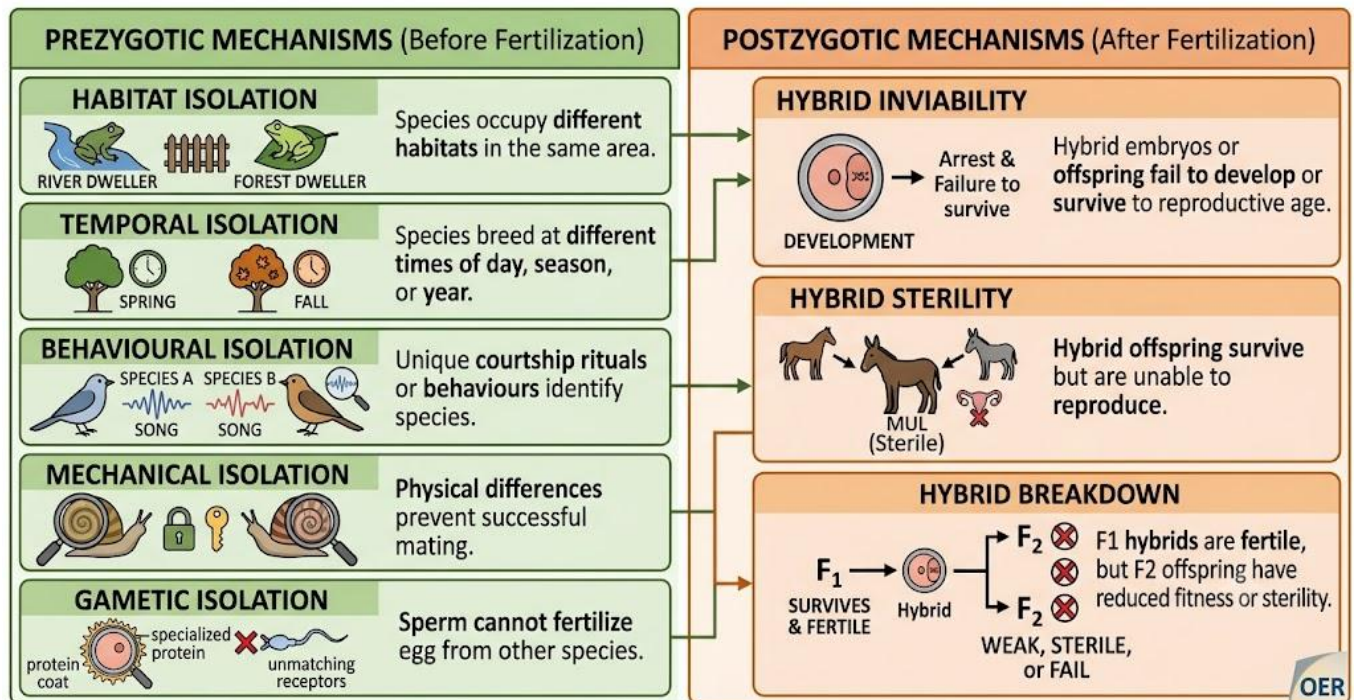


Figure 3.1: Diagram summarising prezygotic and postzygotic reproductive isolation mechanisms

### 3.1.2 Postzygotic isolation mechanisms

Postzygotic mechanisms reduce the fitness of hybrids after fertilisation has occurred. Hybrid inviability: hybrid embryos fail to develop normally or die before reaching reproductive age; genetic incompatibilities between parental genomes disrupt development; e.g. crosses between many frog species produce inviable embryos. Hybrid sterility: hybrids develop normally but are sterile; the most famous example is the mule (horse x donkey cross): mules are vigorous but cannot produce gametes because the parental chromosomes (horse  $2n=64$ ; donkey  $2n=62$ ) cannot pair properly at meiosis.

Hybrid breakdown: F<sub>1</sub> hybrids are viable and fertile, but F<sub>2</sub> or backcross offspring have reduced viability or fertility; the parental genomes interact normally in F<sub>1</sub> but deleterious combinations are exposed in later generations. The genetic basis of postzygotic isolation is partly explained by Dobzhansky-Muller incompatibilities: alleles that evolved independently in two lineages may be



incompatible when brought together in hybrids, causing developmental or reproductive failure. Postzygotic isolation is generally considered a later-evolving barrier than prezygotic isolation.

Fill in the blank: The mule (horse x donkey hybrid) is an example of hybrid \_\_\_\_\_ ; the mule is vigorous and viable but cannot produce gametes because the horse and donkey chromosomes cannot pair correctly at meiosis.

### 3.1.3 The breakdown of isolation: hybridisation

Hybridisation occurs when reproductive isolation breaks down and individuals of two different species or populations interbreed. It is very common in plants (estimated 25% of plant species hybridise with at least one congener) and in some animal groups (e.g. cichlid fish in African Great Lakes; West African primates). Hybridisation can have several outcomes: reinforcement (increased selection for stronger premating isolation, driving the two species further apart); fusion (the two populations merge back into one); hybrid speciation.

Homoploid hybrid speciation: a new species arises from hybridisation without polyploidy; rare but documented (e.g. *Heliconius* butterfly species in South America). Allopolyploid speciation: hybridisation combined with polyploidy produces a new species (common in plants; covered in 3.2.3). Hybrid zones: geographic areas where two species meet and produce hybrids; they provide natural experiments on reproductive isolation; their width and stability reflect the balance between dispersal (which widens them) and selection against hybrids (which narrows them). In Nigeria, hybrid zones between subspecies of forest birds occur where forest patches meet.

Fill in the blank: \_\_\_\_\_ is the evolutionary process by which selection strengthens prezygotic isolation in areas where two species meet and produce less-fit hybrids; it drives the two species further apart over time.

#### Pilot questions 3.1

1. Define reproductive isolation and name five prezygotic mechanisms.



2. Explain the difference between hybrid inviability and hybrid sterility with one example each.
3. Explain Dobzhansky-Muller incompatibilities.
4. Define hybridisation and state three possible evolutionary outcomes.
5. Explain what a hybrid zone is and what determines its width.

## 3.2 Modes of Speciation

### 3.2.1 Allopatric speciation

Allopatric speciation is the most common mode of speciation; it occurs when a geographic barrier divides a single population into two or more isolated populations that then diverge through selection, drift, and mutation until reproductive isolation evolves. The barrier may be a river, mountain range, sea, or desert. Vicariance allopatry: the habitat is split by a new geographic barrier (e.g. a river changes course, dividing a forest-dwelling species into two populations).

Peripatric speciation: a small peripheral population becomes isolated at the edge of the species range (e.g. a small colonising population on an island); the founder effect reduces genetic diversity and may accelerate divergence. Classic examples: Darwin's finches (Galapagos Islands; 14 species derived from a single ancestral finch that colonised the archipelago); cichlid fish in African Great Lakes (Lake Victoria alone has over 500 endemic cichlid species, largely the result of allopatric speciation within the lake during past drying events combined with sexual selection).

Fill in the blank: \_\_\_\_\_ speciation, the most common mode, occurs when a geographic barrier divides a population into isolated groups that diverge through selection and drift until reproductive isolation evolves; Darwin's finches on the Galapagos are a classic example.



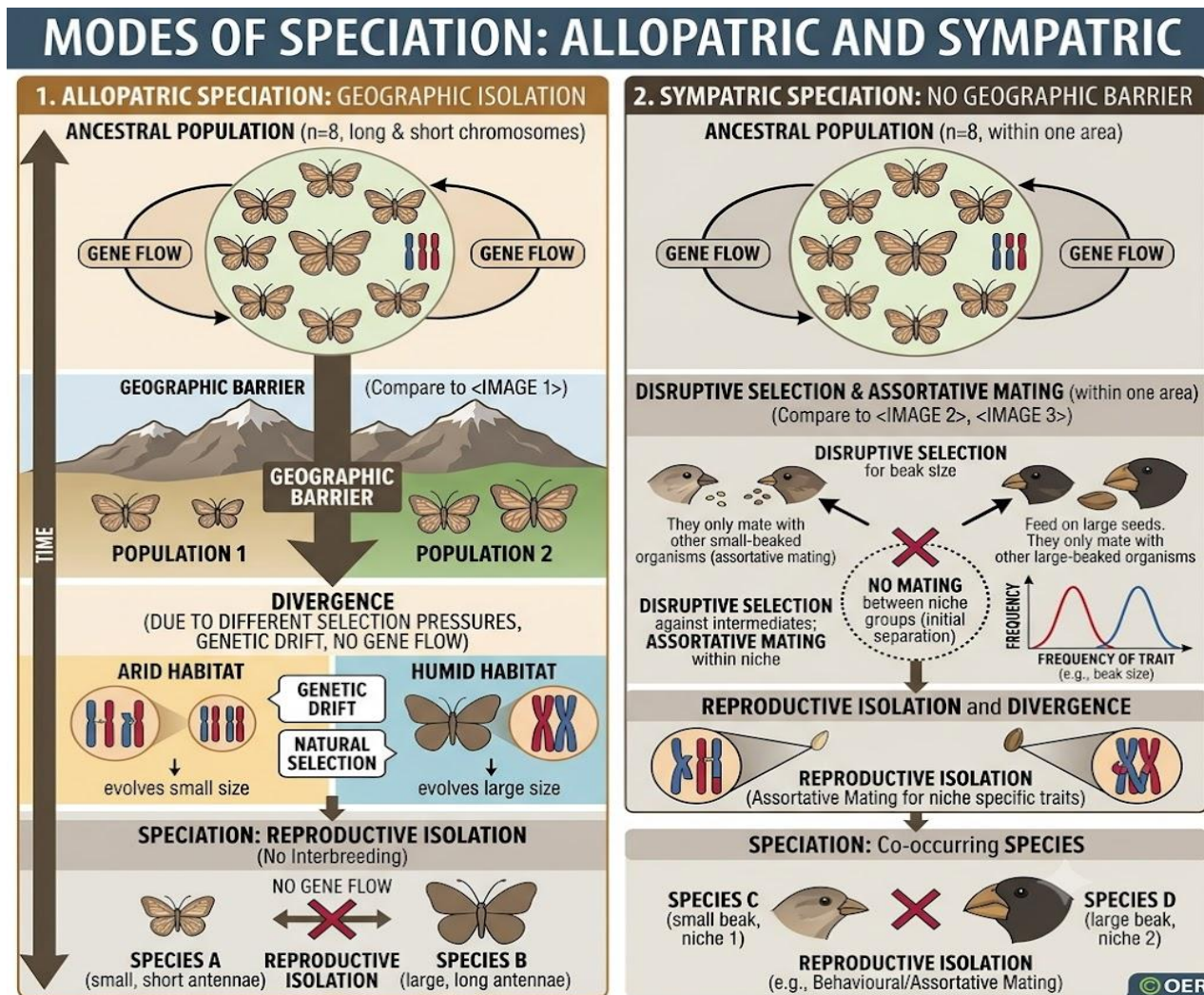


Figure 3.2: Diagram illustrating allopatric and sympatric speciation pathways

### 3.2.2 Sympatric and parapatric speciation

Sympatric speciation occurs within a single geographic population without a physical barrier; it requires some form of disruptive selection and assortative mating to maintain the diverging groups in contact. It is controversial because gene flow within the same area should prevent divergence. Proposed mechanisms: ecological divergence (two groups specialise on different resources; selection favours reduced interbreeding because hybrids are poorly adapted to either resource); host-race formation in phytophagous insects (e.g. *Rhagoletis pomonella* apple maggot fly in North America).



Parapatric speciation: populations are adjacent with a narrow contact zone and limited gene flow between them; divergence occurs across an environmental gradient or cline; e.g. two populations of a grass species on either side of a mine spoil tip, where one population has evolved metal tolerance. In parapatric speciation, selection is strong enough to maintain divergence despite some gene flow across the contact zone. The continuum of speciation modes (allopatric → parapatric → sympatric) reflects decreasing geographic isolation and increasing reliance on ecological selection to drive divergence.

Fill in the blank: \_\_\_\_\_ speciation occurs between adjacent populations with limited gene flow; divergence occurs across an environmental gradient, with selection strong enough to maintain differentiation despite some interbreeding across the contact zone.

### 3.2.3 Polyploidy and speciation in plants

Polyplody is the multiplication of entire chromosome sets; it is the most common mechanism of instantaneous (single-generation) speciation and is especially important in plant evolution.

Autopolyploidy: polyploidy within a single species (e.g. a tetraploid  $4n$  arising from a diploid  $2n$  parent by failure of cell division); autopolyploids can be reproductively isolated from their diploid parents immediately because crosses between  $4n$  and  $2n$  produce  $3n$  triploids that are sterile. Allopolyploidy: polyploidy following hybridisation between two different species.

Allopolyploidy is extremely common in crop plants: bread wheat (*Triticum aestivum*) is a hexaploid ( $6n = 42$ ) combining chromosomes of three ancestral diploid grass species; cotton (*Gossypium hirsutum*) is a tetraploid; sugarcane (*Saccharum officinarum*) is an octoploid; most edible banana varieties are sterile triploid hybrids of two diploid *Musa* species. In allopolyploids, hybridisation provides genetic variation from two species, while polyploidy restores fertility (each chromosome now has a homologue from the same original species to pair with at meiosis).

Fill in the blank: Bread wheat (*Triticum aestivum*) is a \_\_\_\_\_ ( $6n = 42$ ) that arose by allopolyploidy, combining the chromosome sets of three ancestral diploid grass species; allopolyploidy is the most common mechanism of instantaneous speciation in plants.



## Pilot questions 3.2

1. Define allopatric speciation and explain how it produces new species.
2. Distinguish between vicariance and peripatric speciation.
3. Explain sympatric speciation and state one documented example.
4. Distinguish between autopolyploidy and allopolyploidy.
5. Explain why allopolyploids are immediately reproductively isolated from their parental species.

## 3.3 Adaptation and the Origin of Life

### 3.3.1 Adaptation: types and mechanisms

An adaptation is a heritable trait that increases an organism's fitness in its environment as a result of natural selection. Three categories: structural adaptations (physical features; e.g. streamlined body of fish; thick waxy cuticle of xerophytes; haemoglobin oxygen affinity matched to altitude); physiological adaptations (internal biochemical or metabolic features; e.g. sickle-cell trait in malaria-endemic regions; salt glands in mangrove trees; antifreeze proteins in arctic fish); behavioural adaptations (actions improving survival or reproduction; e.g. migration, hibernation, nocturnal activity in desert mammals).

Convergent adaptations arise independently in unrelated lineages facing similar selective pressures (e.g. streamlined body shape evolving independently in fish, dolphins, and ichthyosaurs). Adaptive convergence is strong evidence that natural selection drives predictable solutions to common environmental challenges. Exaptation: a trait that evolved for one function is co-opted for a different function (e.g. bird feathers evolved first for insulation or display, and were later co-opted for flight; the ossicles of the mammalian middle ear are exapted jaw bones of ancestral synapsids).



Fill in the blank: An \_\_\_\_\_ is a heritable trait that increases fitness as a result of natural selection; convergent adaptations arise independently in unrelated lineages responding to similar selective pressures.

### 3.3.2 Origin of life: major hypotheses

Life is estimated to have originated approximately 3.5 to 4.0 billion years ago (Ga). The Oparin-Haldane hypothesis (1920s): the early Earth atmosphere was reducing ( $H_2$ ,  $CH_4$ ,  $NH_3$ ,  $H_2O$ ); organic molecules could be synthesised abiotically from these gases using UV radiation and lightning as energy sources; these molecules accumulated in a warm dilute "primordial soup" in early oceans and eventually assembled into self-replicating systems. The Miller-Urey experiment (1953) provided direct support by synthesising amino acids from a simulated reducing atmosphere.

RNA world hypothesis: RNA was the first self-replicating and catalytic molecule; RNA can both store information (like DNA) and catalyse reactions (ribozymes); small self-replicating RNA molecules arose first, later acquiring protein enzymes (more efficient catalysts) and DNA (more stable information storage). Hydrothermal vent hypothesis: life originated at deep-sea alkaline hydrothermal vents where natural proton gradients across mineral membranes could drive ATP synthesis; this does not require a reducing atmosphere. Panspermia: life or organic molecules were delivered to Earth from space (extraterrestrial origin); supported by detection of amino acids in meteorites.

Fill in the blank: The Miller-Urey experiment (1953) tested the Oparin-Haldane hypothesis by synthesising \_\_\_\_\_ acids and other organic molecules from a simulated reducing atmosphere; it demonstrated that the building blocks of life could form abiotically.

### 3.3.3 Early evolution of cells

The earliest life forms were prokaryotes (cells without a membrane-bound nucleus). Fossil evidence: stromatolites (layered structures formed by cyanobacterial mats) are preserved from approximately 3.5 Ga in Western Australia. The Great Oxidation Event (approximately 2.4 Ga): cyanobacteria evolved oxygenic photosynthesis, releasing  $O_2$  that transformed the atmosphere



from reducing to oxidising, driving the evolution of aerobic metabolism and eventually enabling complex multicellular life.

The endosymbiotic theory (Lynn Margulis): eukaryotic organelles (mitochondria and chloroplasts) are derived from free-living prokaryotes engulfed by a host cell that failed to be digested; evidence includes: double membranes in both organelles; own circular DNA similar to bacterial chromosomes; own ribosomes (70S, like bacteria); division by binary fission independent of the host cell. Eukaryotes arose approximately 1.8 to 2.0 Ga. Multicellularity evolved independently multiple times (plants, animals, fungi, algae) after eukaryotic cell evolution.

Fill in the blank: The \_\_\_\_\_ theory proposes that mitochondria and chloroplasts are derived from free-living prokaryotes that were engulfed by a host cell; evidence includes their double membranes, circular DNA, 70S ribosomes, and binary fission.

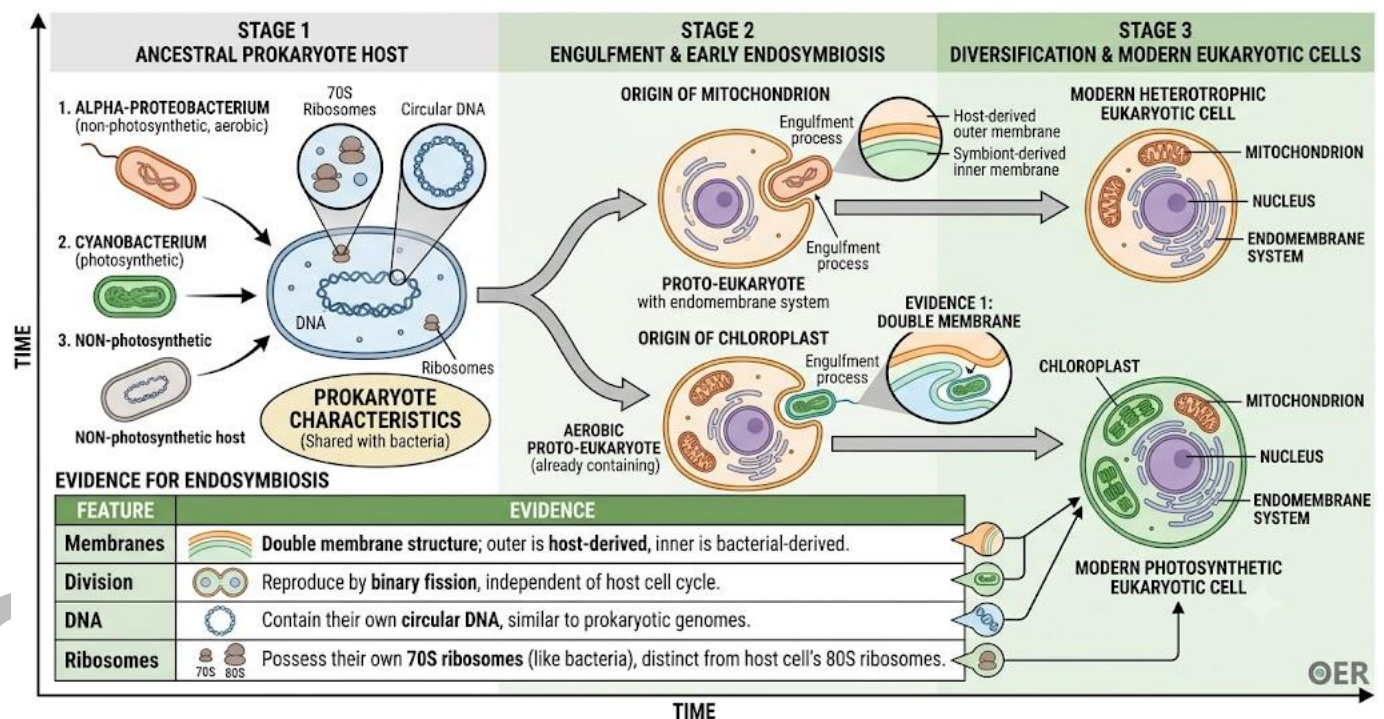


Figure 3.3: Diagram of the endosymbiotic origin of eukaryotic organelles



### Pilot questions 3.3

1. Distinguish between structural, physiological, and behavioural adaptations with one example each.
2. Explain what an exaptation is and give one example.
3. Describe the Oparin-Haldane hypothesis and state what the Miller-Urey experiment demonstrated.
4. Describe the RNA world hypothesis.
5. State four pieces of evidence for the endosymbiotic origin of mitochondria.

## 3.4 Origin of Species and Adaptive Radiation

### 3.4.1 The origin of new species

New species arise from existing species through the gradual (or occasionally rapid) accumulation of genetic differences that eventually result in reproductive isolation. The general sequence: (1) a single ancestral population is divided or parts of it diverge ecologically; (2) the diverging populations accumulate genetic differences through selection, drift, and mutation; (3) these genetic differences eventually produce reproductive isolation (prezygotic or postzygotic); (4) the populations are now reproductively isolated species that can coexist without merging even if the geographic barrier disappears.

Rates of speciation vary enormously. Gradualism: speciation is slow and gradual, consistent with the slow accumulation of small genetic changes under selection (Darwin's original view).

Punctuated equilibrium (Eldredge and Gould, 1972): most species show morphological stasis (little change) for most of their existence in the fossil record, punctuated by rapid bursts of change associated with speciation events; these rapid bursts may be too fast to be captured in detail by the fossil record but represent tens of thousands to hundreds of thousands of years.



Fill in the blank: The theory of \_\_\_\_\_ equilibrium (Eldredge and Gould, 1972) proposes that species show long periods of morphological stasis punctuated by rapid bursts of change associated with speciation events, explaining the pattern seen in many fossil lineages.

### 3.4.2 Adaptive radiation

Adaptive radiation is the rapid diversification of a single ancestral lineage into many ecologically distinct species, each adapted to a different niche or resource. It typically occurs when: a lineage colonises a new environment with many unfilled ecological niches; a key innovation evolves that opens up many new ecological opportunities; a mass extinction removes competitors. Classic examples: Darwin's finches (one colonising finch species diversified into 14 species on the Galapagos with beaks adapted to different food types); cichlid fish in African Great Lakes.

East African cichlid fish are the most spectacular example of adaptive radiation: Lake Victoria alone contains approximately 500 endemic cichlid species that diversified from a single ancestral species in approximately 15,000 years (an extraordinarily fast rate). The radiation was driven by sexual selection (female preference for male coloration drove rapid divergence in male pigmentation and assortative mating) and ecological specialisation (different jaw and tooth morphologies for different food types). The Nigerian freshwater systems contain diverse cichlid assemblages, including tilapia (*Oreochromis*) and *Hemichromis* species.

Fill in the blank: \_\_\_\_\_ radiation is the rapid diversification of a single ancestral lineage into many ecologically distinct species; it typically follows colonisation of a new environment with many unfilled niches or the evolution of a key innovation.



# CLADOGRAM OF DARWIN'S GALAPAGOS FINCH ADAPTIVE RADIATION: 14 SPECIES

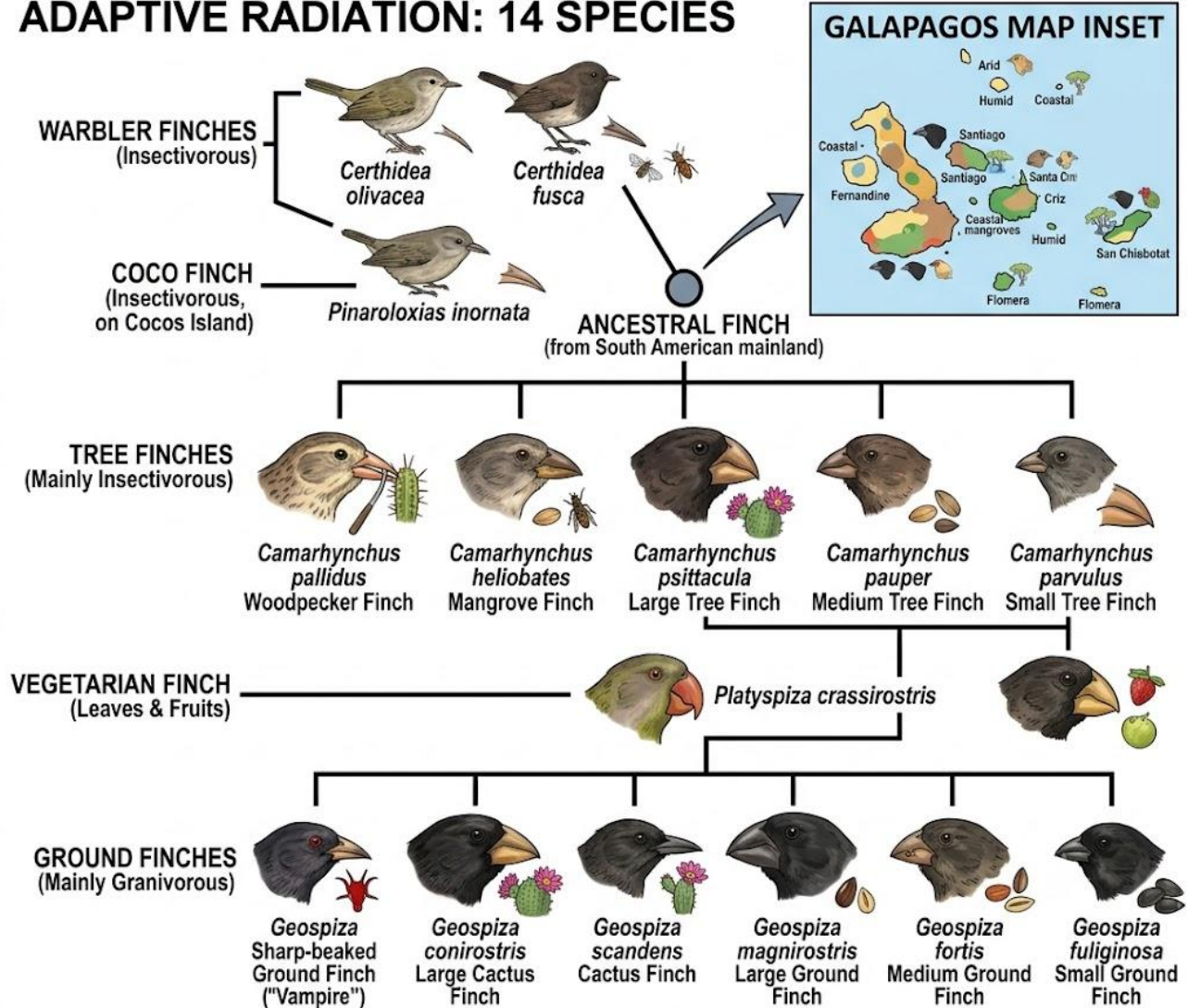


Figure 3.4: Diagram of adaptive radiation in Darwin's finches on the Galapagos Islands

## 3.4.3 Convergent evolution and evolutionary constraints

Convergent evolution occurs when unrelated lineages independently evolve similar traits in response to similar selective pressures. Classic examples: streamlined (fusiform) body shape in fish, dolphins, and ichthyosaurs (extinct marine reptiles); wings in birds, bats, pterosaurs, and insects; succulence and spines in American cacti and African euphorbias; the marsupial-placental mammal parallels (marsupial thylacine and placental wolf; marsupial sugar glider and placental



flying squirrel). Convergence demonstrates that natural selection produces predictable solutions to common adaptive challenges.

Evolutionary constraints are limits on the range of phenotypes that can be produced by evolution, imposed by: phylogenetic constraints (the ancestral body plan limits what descendants can become; insects have six legs because the hexapod body plan is deeply conserved); developmental constraints (some phenotypes are difficult to produce due to developmental system properties; e.g. the vertebrate limb develops from a conserved developmental programme that limits digit number variation); genetic constraints (pleiotropy: one gene affects many traits simultaneously, making it difficult to change one trait without affecting others; genetic correlations between traits).

Fill in the blank: \_\_\_\_\_ evolution occurs when unrelated lineages independently evolve similar traits in response to similar selective pressures; the streamlined body shape of fish, dolphins, and ichthyosaurs is a classic example.

#### Pilot questions 3.4

1. Describe the general sequence of events in the origin of a new species.
2. Distinguish between gradualism and punctuated equilibrium as models of speciation rate.
3. Define adaptive radiation and state the conditions that favour it.
4. Describe the cichlid adaptive radiation in African Great Lakes.
5. Define convergent evolution and give two examples.

#### Series Summary

This Series covered isolation mechanisms and evolutionary pathways. Prezygotic isolation: habitat, temporal, behavioural, mechanical, and gametic mechanisms prevent fertilisation.



Postzygotic isolation: hybrid inviability, hybrid sterility, and hybrid breakdown reduce fitness after fertilisation. Hybridisation occurs when isolation breaks down; outcomes include reinforcement, fusion, or hybrid speciation. Speciation modes: allopatric (geographic barrier; most common; Darwin's finches; African Great Lakes cichlids); sympatric (disruptive selection within one area; *Rhagoletis pomonella*); parapatric (adjacent populations across an environmental gradient); polyploidy (instantaneous speciation; allopolyploidy common in crops: bread wheat, cotton, banana).

Adaptation types: structural, physiological, behavioural; convergent adaptations; exaptation. Origin of life: Oparin-Haldane hypothesis (primordial soup; Miller-Urey experiment); RNA world; hydrothermal vent hypothesis; panspermia. Early cellular evolution: stromatolites from 3.5 Ga; Great Oxidation Event 2.4 Ga; endosymbiotic theory (mitochondria from alpha-proteobacteria; chloroplasts from cyanobacteria; evidence: double membranes, circular DNA, 70S ribosomes). Speciation: gradualism vs punctuated equilibrium. Adaptive radiation: rapid diversification into unfilled niches (Darwin's finches; cichlids; Lake Victoria approximately 500 species in 15,000 years). Convergent evolution: similar traits from similar selection (fish/dolphin/ichthyosaur body shape). Evolutionary constraints: phylogenetic, developmental, genetic. By completing this Series, you should achieve all six SLOs (3.1 to 3.6).

## Glossary of Terms

- **Adaptive radiation:** the rapid diversification of a single ancestral lineage into many ecologically distinct species, each adapted to a different niche; typically follows colonisation of a new environment or evolution of a key innovation.
- **Allopatric speciation:** speciation that occurs when a geographic barrier divides a population into isolated groups that diverge through natural selection and genetic drift until reproductive isolation evolves.
- **Allopolyploidy:** polyploidy that follows hybridisation between two different species; the hybrid retains the chromosome sets of both parents; very common in plant evolution and crop domestication.



- **Autopolyploidy:** polyploidy arising within a single species when chromosome sets are doubled by failure of cell division; produces individuals that are immediately reproductively isolated from their diploid parents.
- **Behavioural (ethological) isolation:** a prezygotic isolation mechanism in which species do not recognise each other as potential mates due to differences in courtship signals, mating calls, or chemical cues.
- **Convergent evolution:** the independent evolution of similar traits in unrelated lineages exposed to similar selective pressures; demonstrates the predictability of natural selection.
- **Dobzhansky-Muller incompatibilities:** genetic incompatibilities between alleles that evolved independently in two lineages; when brought together in hybrids, they cause developmental or reproductive failure, contributing to postzygotic isolation.
- **Endosymbiotic theory:** the hypothesis that mitochondria and chloroplasts arose from free-living prokaryotes engulfed by a host cell; supported by double membranes, bacterial-type ribosomes, circular DNA, and binary fission.
- **Evolutionary constraint:** a limit on the range of phenotypes that can be produced by evolution, imposed by phylogenetic history, developmental systems, or genetic architecture.
- **Exaptation:** a trait that originally evolved for one function but was later co-opted for a different function; e.g. bird feathers originally evolved for insulation and later co-opted for flight.
- **Gametic isolation:** a prezygotic isolation mechanism in which the gametes of two species fail to attract or fertilise each other, even if mating is attempted.
- **Great Oxidation Event:** the dramatic rise in atmospheric oxygen approximately 2.4 billion years ago caused by oxygenic photosynthesis in cyanobacteria; transformed early Earth's atmosphere and enabled aerobic life.



- **Habitat isolation:** a prezygotic isolation mechanism in which two species occupy different habitats in the same geographic area and rarely encounter each other.
- **Hybrid breakdown:** a postzygotic isolation mechanism in which F1 hybrids are viable and fertile, but later generations (F2 or backcrosses) have reduced viability or fertility.
- **Hybrid inviability:** a postzygotic isolation mechanism in which hybrid offspring fail to develop normally or die before reproducing.
- **Hybrid sterility:** a postzygotic isolation mechanism in which hybrid offspring develop normally but are sterile; the mule is the classic example.
- **Hybrid zone:** a geographic area where two species or populations meet and produce hybrids; its width reflects the balance between dispersal and selection against hybrids.
- **Key innovation:** a novel trait that opens new ecological opportunities for a lineage, often triggering adaptive radiation; e.g. the development of flowers and fruits in angiosperms.
- **Mechanical isolation:** a prezygotic isolation mechanism in which structural incompatibilities prevent copulation or pollen transfer between species.
- **Parapatric speciation:** speciation between adjacent populations with limited gene flow across a contact zone; divergence is maintained by strong selection across an environmental gradient.
- **Peripatric speciation:** a form of allopatric speciation in which a small peripheral population becomes isolated at the edge of the species range; the founder effect accelerates divergence.
- **Polyploidy:** the condition of having more than two complete chromosome sets; a common mechanism of instantaneous speciation in plants.
- **Prezygotic isolation:** reproductive isolation mechanisms that prevent fertilisation; includes habitat, temporal, behavioural, mechanical, and gametic isolation.
- **Postzygotic isolation:** reproductive isolation mechanisms that reduce fitness after fertilisation; includes hybrid inviability, hybrid sterility, and hybrid breakdown.



- **Punctuated equilibrium:** the model of macroevolution (Eldredge and Gould, 1972) proposing that species show long periods of morphological stasis punctuated by rapid bursts of change at speciation events.
- **Reinforcement:** the strengthening of prezygotic isolation mechanisms by selection in areas where two species meet and produce less-fit hybrids; drives the two species further apart.
- **RNA world:** the hypothesis that RNA was the first self-replicating and catalytic molecule in the origin of life, before the evolution of DNA and proteins.
- **Stromatolite:** a layered sedimentary structure formed by cyanobacterial mats; fossil stromatolites from 3.5 billion years ago are the oldest evidence of life.
- **Sympatric speciation:** speciation that occurs within a single geographic population without a physical barrier; requires disruptive selection and assortative mating.
- **Temporal isolation:** a prezygotic isolation mechanism in which two species breed at different times (seasons, hours, or years), preventing interbreeding.
- **Vicariance:** the division of a previously continuous habitat by a new geographic barrier, isolating populations and promoting allopatric speciation.

### Concept Check Questions [Series 3]

#### Objective Questions

1. \_\_\_\_\_ isolation prevents interbreeding by causing two species to breed at different times or seasons; it is a prezygotic isolation mechanism. (Linked to SLO 3.1)
2. The mule (horse x donkey) is an example of hybrid \_\_\_\_\_ ; the mule is vigorous but sterile because horse and donkey chromosomes cannot pair at meiosis. (Linked to SLO 3.1)



3. \_\_\_\_\_ speciation, the most common mode, occurs when a geographic barrier divides a population into isolated groups that diverge until reproductive isolation evolves. (Linked to SLO 3.3)
4. The Miller-Urey experiment demonstrated that \_\_\_\_\_ acids and other organic molecules could be synthesised abiotically from a simulated reducing atmosphere. (Linked to SLO 3.4)
5. The \_\_\_\_\_ theory proposes that mitochondria and chloroplasts arose from free-living prokaryotes engulfed by an ancestral eukaryotic host cell. (Linked to SLO 3.4)

#### Short-Answer Questions

- Name and briefly describe five prezygotic isolation mechanisms. (Linked to SLO 3.1)
- Distinguish between allopatric and sympatric speciation. (Linked to SLO 3.3)
- Explain why allopolyploid hybrids are immediately reproductively isolated from their parental species. (Linked to SLO 3.3)
- Describe the RNA world hypothesis. (Linked to SLO 3.4)
- Define adaptive radiation and give one example. (Linked to SLO 3.6)

#### Long-Answer Questions

1. Describe the major prezygotic and postzygotic reproductive isolation mechanisms; explain hybridisation and its evolutionary outcomes; and describe the concept of reinforcement. (Linked to SLOs 3.1, 3.2)
2. Distinguish between allopatric, sympatric, and parapatric speciation; explain polyploidy as a speciation mechanism; and describe the origin of life hypotheses and early cellular evolution. (Linked to SLOs 3.3, 3.4)
3. Explain how new species arise; describe adaptive radiation with an African example; and explain convergent evolution and evolutionary constraints. (Linked to SLOs 3.5, 3.6)



## Answers to Concept Check Questions [Series 3]

### Objective Questions

6. Temporal.
7. Sterility.
8. Allopatric.
9. Amino.
10. Endosymbiotic.

### Short-Answer Questions

11. Habitat (different habitats in same area; no encounter); temporal (different breeding seasons or times of day); behavioural/ethological (different mating calls or displays; no mate recognition); mechanical (structural incompatibility prevents copulation or pollen transfer); gametic (gametes fail to attract or fertilise each other even after mating).
12. Allopatric: geographic barrier physically separates the population; divergence occurs in isolation; most common mode; e.g. Darwin's finches. Sympatric: within a single population in the same location; no physical barrier; requires disruptive selection and assortative mating; controversial; e.g. *Rhagoletis pomonella* host races.
13. Allopolyploids are produced by hybridisation between two species (AB), then chromosome doubling produces AABB. When an allopolyploid (e.g.  $4n$  AABB) crosses with either parental species (e.g.  $2n$  AA or  $2n$  BB), the offspring have odd chromosome sets that cannot pair properly at meiosis and are sterile; the allopolyploid therefore cannot interbreed with either parent and is reproductively isolated from both immediately upon formation.
14. The RNA world hypothesis proposes that RNA was the first self-replicating and catalytic molecule before DNA or proteins evolved. RNA can both store genetic information (like DNA) and catalyse chemical reactions (as ribozymes). Small RNA molecules capable of



self-replication arose first; they gradually recruited protein enzymes (more efficient catalysts) and DNA (more stable information storage) as the complexity of early life increased.

15. Adaptive radiation is the rapid diversification of a single ancestral lineage into many ecologically distinct species, each adapted to a different niche; it typically follows colonisation of a new environment with unfilled ecological niches. Example: Darwin's finches (Geospizinae) on the Galapagos Islands, where 14 species with different beak shapes evolved from a single ancestral finch, each adapted to a different food type.

### Long-Answer Questions

1. Prezygotic mechanisms (before fertilisation): habitat isolation (two species in different habitats in same area; rarely encounter); temporal isolation (different breeding times: seasons, daily; e.g. two frog species breeding at different points in the Nigerian rainy season); behavioural/ethological isolation (different mating calls, courtship displays, or chemical signals; e.g. West African sunbird song dialects; most important in animals); mechanical isolation (structural incompatibility prevents copulation or pollen transfer; e.g. flower shape matching specific pollinator anatomy); gametic isolation (gametes fail to fuse even after mating; species-specific egg-surface proteins; e.g. sea urchins).  
Postzygotic mechanisms (after fertilisation): hybrid inviability (hybrid embryos die before reproductive age; genetic incompatibilities disrupt development); hybrid sterility (hybrids develop normally but are sterile; mule: horse x donkey; chromosomes cannot pair at meiosis); hybrid breakdown (F1 hybrids are fertile but later generations have reduced viability; Dobzhansky-Muller incompatibilities exposed in F2). Hybridisation: breakdown of isolation when two species interbreed; common in plants (approximately 25% hybridise); outcomes: reinforcement (selection strengthens prezygotic isolation; two species diverge further); fusion (populations merge back into one); hybrid speciation (new species arises: homoploid hybrid speciation without polyploidy; allopolyploid speciation with polyploidy). Hybrid zones: geographic areas where two species produce hybrids; width reflects balance between dispersal and selection against hybrids.



2. Allopatric speciation (most common): geographic barrier divides population; isolated populations diverge through selection, drift, mutation; reproductive isolation evolves; e.g. Darwin's finches (Galapagos); African Great Lakes cichlids; vicariance (new barrier splits habitat) vs peripatric (small peripheral founder population; founder effect accelerates divergence). Sympatric speciation: within a single geographic population; no physical barrier; requires disruptive selection and assortative mating; e.g. *Rhagoletis pomonella* apple vs hawthorn host races; controversial because gene flow should prevent divergence. Parapatric speciation: adjacent populations with limited gene flow; divergence across environmental gradient; e.g. grass populations on/off mine spoil tips. Polyploidy: multiplication of chromosome sets; autopolyploidy (within one species;  $4n$  from  $2n$  parent; immediately isolated because  $4n \times 2n = \text{sterile } 3n$ ); allopolyploidy (hybridisation + chromosome doubling; very common in crop plants; bread wheat: hexaploid  $6n = 42$  from three diploid species; cotton, sugarcane, banana; allopolyploid is immediately isolated from both parents). Origin of life: Oparin-Haldane (reducing atmosphere; primordial soup; organic synthesis; Miller-Urey 1953 confirmed amino acid synthesis); RNA world (RNA both codes and catalyses; ribozymes; RNA first; then proteins and DNA added); hydrothermal vent hypothesis (alkaline vents; proton gradients drove ATP synthesis; does not require reducing atmosphere); panspermia (extraterrestrial delivery; amino acids in meteorites). Early cellular evolution: earliest prokaryotes from approximately 3.5 Ga (stromatolites); Great Oxidation Event 2.4 Ga (cyanobacteria oxygenic photosynthesis transformed atmosphere); endosymbiotic theory (Margulis): mitochondria from alpha-proteobacteria; chloroplasts from cyanobacteria; evidence: double membranes, circular bacterial-type DNA, 70S ribosomes, binary fission; eukaryotes arose approximately 1.8 to 2.0 Ga; multicellularity evolved multiple times independently.
3. Origin of species: ancestral population diverges (via isolation or ecological divergence); genetic differences accumulate (selection, drift, mutation); reproductive isolation evolves (prezygotic or postzygotic); populations coexist as distinct species. Rate: gradualism (slow, continuous accumulation; Darwin's original view); punctuated equilibrium (Eldredge and Gould 1972; stasis punctuated by rapid bursts; pattern seen in many fossil lineages). Adaptive radiation: rapid diversification from single ancestor into many



ecologically distinct species; conditions: many unfilled niches (new environment; key innovation; competitor extinction); examples: Darwin's finches (14 species from one coloniser; beak shapes adapted to different food types; Galapagos); cichlid fish in African Great Lakes (Lake Victoria approximately 500 endemic species in approximately 15,000 years; driven by sexual selection for male coloration and ecological specialisation in jaw/tooth morphology; present in Nigerian freshwaters as *Oreochromis*, *Hemichromis*). Convergent evolution: similar traits evolve independently in unrelated lineages facing similar selective pressures; examples: streamlined body shape in fish, dolphins, ichthyosaurs; wings in birds, bats, pterosaurs, insects; succulent cactus-like adaptations in American Cactaceae and African Euphorbiaceae; marsupial-placental mammal parallels. Evolutionary constraints: limits on phenotypic evolution; phylogenetic (ancestral body plan restricts descendants; all insects have six legs); developmental (conserved developmental programmes constrain variant production; vertebrate limb digit number variation limited); genetic (pleiotropy: one gene affects many traits; correlated traits constrain independent evolution).

## Answers to Pilot Questions [Series 3]

### Part 3.1

6. Reproductive isolation mechanisms are biological barriers that prevent two species from interbreeding and producing fertile offspring. Five prezygotic mechanisms: (1) Habitat isolation: two species occupy different microhabitats within the same geographic area and rarely encounter each other; (2) Temporal isolation: two species breed at different seasons, different times of day, or in different years, so they never encounter potential mates of the other species at the same time; (3) Behavioural (ethological) isolation: species do not recognise each other as mates because of differences in species-specific courtship signals (calls, colour patterns, dances, or pheromones); (4) Mechanical isolation: anatomical or structural incompatibilities physically prevent copulation or pollen transfer between species; (5) Gametic isolation: even if mating occurs, the gametes



of two species fail to attract each other or fertilise each other because of species-specific molecular recognition proteins on their surfaces.

7. Hybrid inviability: hybrid offspring are formed (fertilisation occurs) but fail to complete normal development and die before reaching reproductive age; the incompatibility is expressed during embryonic or larval development; e.g. crosses between many frog species produce embryos that begin development but die at early stages. Hybrid sterility: hybrid offspring develop into adults that are anatomically normal and often vigorous, but they cannot produce functional gametes and are therefore sterile; they cannot transmit their genes to the next generation; the classic example is the mule (equine hybrid between *Equus caballus*, horse,  $2n = 64$ , and *Equus asinus*, donkey,  $2n = 62$ ); the mule has 63 chromosomes and is vigorous but sterile because the unpaired chromosomes cannot segregate properly at meiosis.
8. Dobzhansky-Muller incompatibilities are genetic incompatibilities that arise when two alleles (or gene combinations) that evolved independently in two diverging lineages are brought together in hybrids. In lineage A, allele A2 evolved in combination with the ancestral allele B1; in lineage B, allele B2 evolved in combination with ancestral allele A1; neither combination has ever been tested by selection together. When A2 and B2 are combined in an AB hybrid, they may interact negatively because they have never co-evolved; this can cause developmental disruption, sterility, or inviability. The key point is that neither A2 nor B2 is deleterious on its own in its own lineage; the problem only arises in hybrids that bring novel allele combinations together.
9. Hybridisation occurs when reproductive isolation breaks down and individuals of two different species interbreed and produce offspring. Three possible evolutionary outcomes: (1) Reinforcement: when the two species meet in a hybrid zone and hybrids have lower fitness, selection favours individuals that avoid mating with the other species; this strengthens prezygotic isolation mechanisms over time, driving the two species further apart; (2) Fusion: if hybrid fitness is high relative to the parental types, the two populations merge back into a single interbreeding population; (3) Hybrid speciation: the hybrid individuals become a distinct new species, either by allopolyploidy (hybridisation combined with polyploidy; common in plants) or homoploid hybrid speciation (without polyploidy; rare but documented in *Heliconius* butterflies).



10. A hybrid zone is a geographic area where two species or well-differentiated populations meet and produce hybrids at the zone of contact; it may be narrow (a sharp transition over a few kilometres) or wide (a broad cline over hundreds of kilometres). The width of a hybrid zone reflects the balance between two opposing forces: dispersal (individuals from both species moving into the contact zone widens the zone by introducing parental-type individuals further into hybrid territory) and selection against hybrids (if hybrids have lower fitness than either parental type, selection removes hybrids from the population, narrowing the zone); a wide, stable hybrid zone indicates that hybrids have relatively high fitness (weak selection against them); a narrow zone indicates strong selection against hybrids.

### Part 3.2

11. Allopatric speciation is the mode of speciation in which a single ancestral population is divided into two or more geographically isolated groups by a physical barrier (a river, mountain range, desert, ocean, or ice sheet); the isolated populations can no longer interbreed, so they diverge independently through natural selection acting on local conditions, genetic drift, and the accumulation of new mutations; over sufficient time, the genetic divergence leads to the evolution of reproductive isolation mechanisms (prezygotic and/or postzygotic); when the geographic barrier disappears or is surmounted, the two populations can coexist without merging because they are now reproductively isolated distinct species.
12. Vicariance allopatry: the ancestral range is divided by the appearance of a new geographic barrier within the habitat (e.g. a river changes course and bisects a forest, dividing a tree-dwelling mammal population into two isolated groups; or a land bridge is submerged by rising sea levels, separating an island population from the mainland); the barrier prevents gene flow and the two populations diverge in isolation. Peripatric speciation: a small subset of individuals from the main population colonises or becomes isolated at the peripheral margin of the species range (e.g. a small group of birds reaches a distant island); because the founding group is small, it carries only a random subset of



the source population's alleles (founder effect), resulting in reduced genetic diversity and random allele frequency differences; these genetic peculiarities, combined with selection in the novel peripheral environment, may accelerate divergence and speciation compared with ordinary allopatric speciation.

13. Sympatric speciation occurs within a single geographic population without any physical barrier separating the diverging lineages; all individuals live in the same area and potentially encounter each other at every generation. The most widely cited mechanism is the evolution of host-plant formation in phytophagous (plant-eating) insects: *Rhagoletis pomonella* (apple maggot fly) in North America originally bred only on hawthorn (*Crataegus*); when European settlers introduced apple trees (*Malus*), some flies began laying eggs on apples; over about 150 years, two reproductively partially isolated host races have evolved (hawthorn race and apple race), differing in emergence timing (temporal isolation), host preference (habitat isolation), and allele frequencies at several genes; this is considered an incipient case of sympatric speciation still in progress.
14. Autopolyploidy arises within a single species when the chromosome set is accidentally doubled (usually by failure of cell division during meiosis or mitosis), producing an individual with twice the normal chromosome number (e.g.  $4n$  from  $2n$  parents); examples include many grasses and some potatoes. Allopolyploidy arises when two different species hybridise and the hybrid chromosome sets are then doubled; the hybrid initially has one set from each parental species (e.g.  $n = A + B$  from species with  $n = A$  and  $n = B$ ); doubling produces an allotetraploid with two sets from each parent ( $2n = 2A + 2B$ ); examples include bread wheat (combining chromosomes of three ancestral diploid grasses), cotton, and many other crop species. Allopolyploidy provides genetic variation from two different species and restores meiotic fertility by giving each chromosome a homologue to pair with.
15. An allopolyploid arises from hybridisation between two parental species (species A with genome AA and species B with genome BB); the initial hybrid is AB (one set from each parent); when the chromosome set is doubled, the allopolyploid becomes AABB (two sets of each parental genome). When the allopolyploid (AABB,  $4n$ ) tries to cross with parental species A (AA,  $2n$ ), the offspring has three chromosome sets: one A set from the allopolyploid and one B set from the allopolyploid, plus two A sets from species A; this is



an irregular genome (e.g. AAB or ABB) with an odd number of some chromosomes that cannot pair properly at meiosis; the offspring are sterile. Similarly, crosses with species B are sterile. The allopolyploid can only reproduce successfully with other allopolyploids of the same type; it is therefore immediately reproductively isolated from both parental species from the moment it arises.

### Part 3.3

1. Structural adaptations: heritable physical features of the body; e.g. the pneumatophores (aerial roots) of mangrove trees (*Avicennia africana*) in the Niger Delta, which project upward above the anaerobic mud to absorb oxygen for root respiration. Physiological adaptations: heritable internal biochemical or metabolic features; e.g. sickle-cell trait (HbA/HbS heterozygosity) in Nigerians from malaria-endemic regions; the sickling response under low oxygen conditions in the spleen destroys *Plasmodium falciparum*, providing partial malaria protection. Behavioural adaptations: heritable actions or activity patterns that improve survival or reproduction; e.g. diurnal variation in activity of Nigerian savanna animals, with many large mammals resting in shade during the peak midday heat and becoming active in the cooler morning and late afternoon hours to reduce heat stress.
2. An exaptation is a trait that originally evolved for one function (and was therefore shaped by selection for that original function) but is subsequently used for a completely different function; the trait was not originally selected for its current use. Classic example: bird feathers. Molecular and fossil evidence indicates that feathers first evolved in theropod dinosaur ancestors of birds, where they probably served for thermoregulation (insulation) or display (species recognition, sexual selection) rather than flight; the earliest feathered dinosaurs (e.g. *Microaptor*, *Sinosauropteryx*) had feathers but could not fly; only after feathers were already present did lineages evolve that used them for aerial locomotion; the use of feathers for flight is therefore an exaptation of a structure originally evolved for insulation or display.



3. The Oparin-Haldane hypothesis (independently proposed by Alexander Oparin in 1924 and J.B.S. Haldane in 1929) proposes that the early Earth had a reducing atmosphere rich in hydrogen, methane, ammonia, and water vapour but lacking free oxygen; under the energy input of ultraviolet radiation and lightning, these gases reacted to form simple organic molecules (amino acids, sugars, nucleotides) abiotically; these accumulated in early oceans (and possibly tidal pools) to form a warm, dilute "primordial soup"; over billions of years, these organic molecules polymerised and self-assembled into increasingly complex structures, eventually forming self-replicating systems that mark the origin of life. The Miller-Urey experiment (Stanley Miller and Harold Urey, 1953) tested this hypothesis by simulating the proposed reducing atmosphere in a sealed apparatus with electrical discharges as an energy source; after one week, they detected significant quantities of amino acids and other organic molecules; this demonstrated that the building blocks of proteins could form abiotically under early Earth conditions, providing the first experimental support for the Oparin-Haldane hypothesis.
4. The RNA world hypothesis proposes that the first self-replicating and catalytic molecules in the origin of life were RNA molecules, not DNA or proteins. The key insight is that RNA is unique among known biological molecules in being able to both: (1) store genetic information in its nucleotide sequence (like DNA serves in modern cells); and (2) catalyse chemical reactions (RNA enzymes called ribozymes have been discovered; the ribosomal RNA that catalyses peptide bond formation is a ribozyme). A small RNA molecule that could replicate itself would have the properties needed to undergo Darwinian evolution; it could act as its own template for copying and could catalyse the reactions needed for its own replication; as complexity increased, RNA recruited protein molecules (which are more efficient catalysts) and eventually DNA (which is more chemically stable for information storage); the modern cell thus represents a later stage where DNA has taken over information storage, proteins have taken over most catalysis, and RNA serves in the middle role (mRNA, tRNA, rRNA).
5. Four pieces of evidence for the endosymbiotic origin of mitochondria: (1) Double membranes: mitochondria are bounded by two lipid bilayers; the outer membrane is derived from the host cell's engulfment vesicle; the inner membrane is derived from the original bacterial cell membrane; no other eukaryotic organelle that arose by de novo



membrane formation has two complete membranes in this configuration. (2) Circular DNA: mitochondria contain their own small circular DNA chromosome that resembles bacterial chromosomes in structure, organisation, and gene content; it is distinct from the linear nuclear chromosomes of the eukaryotic host. (3) 70S ribosomes: mitochondria have their own ribosomes, which are bacterial-type 70S ribosomes (composed of 30S and 50S subunits), not the larger 80S ribosomes of the eukaryotic cytoplasm; mitochondrial ribosomes are sensitive to the same antibiotics that inhibit bacterial (but not eukaryotic) ribosomes. (4) Binary fission: mitochondria divide independently of the host cell nucleus by binary fission (pinching in half), exactly as bacteria do, rather than by the mitotic spindle mechanism that divides the nucleus.

#### Part 3.4

1. The general sequence of events in the origin of a new species: (1) An ancestral population either becomes geographically divided by a barrier (allopatric) or experiences strong ecological divergent selection within a single geographic area (sympatric/parapatric); (2) The diverging populations accumulate genetic differences through natural selection acting on local conditions, genetic drift (especially in small isolated populations), and the accumulation of new mutations unique to each population; (3) Over time, the genetic differences begin to cause reproductive incompatibilities between the populations: prezygotic mechanisms (different mating times, different mate recognition signals, different habitat preferences) or postzygotic mechanisms (hybrid sterility, inviability) evolve; (4) When reproductive isolation is complete, the two groups can be brought into secondary contact without merging; they coexist as distinct, reproductively isolated species.
2. Gradualism: the model proposed by Darwin and supported by the Modern Synthesis, in which speciation and evolutionary change are slow and continuous; species change gradually and imperceptibly over long time periods through the accumulation of many small genetic changes under natural selection; this predicts that the fossil record should show smooth, continuous transitions between ancestral and descendant forms with many



intermediate stages. Punctuated equilibrium (Niles Eldredge and Stephen Jay Gould, 1972): an alternative model proposing that species show long periods of morphological stasis (little or no change; lasting millions of years) punctuated by geologically brief bursts of rapid morphological change associated with speciation events; the pattern observed in many fossil lineages (species appear suddenly in the fossil record, persist largely unchanged for millions of years, then disappear or are replaced abruptly) supports this model; the rapid bursts are not instantaneous but represent tens of thousands to hundreds of thousands of years, which is rapid geologically but can be modelled by microevolutionary processes.

3. Adaptive radiation is the rapid diversification of a single ancestral lineage into multiple ecologically distinct species, each adapted to a different resource, microhabitat, or ecological role in an environment with multiple unfilled niches. Conditions that favour adaptive radiation: (1) Colonisation of a new environment with many unfilled niches and few competing species (e.g. an island archipelago or a newly formed lake); (2) Mass extinction of previous dominant groups creates ecological opportunity for the surviving lineage (e.g. the mammal radiation following dinosaur extinction 66 million years ago); (3) Evolution of a key innovation that opens new ecological opportunities (e.g. the evolution of the pharyngeal jaw in cichlid fish, allowing them to process a wider variety of food types; the evolution of flowers in angiosperms that enabled new pollinator interactions).
4. The cichlid fish (family Cichlidae) of the African Great Lakes represent the most spectacular documented adaptive radiation in vertebrate history. Lake Victoria alone (shared between Uganda, Kenya, and Tanzania) contains approximately 500 to 600 endemic cichlid species that have evolved from a single ancestral cichlid lineage that colonised the lake approximately 15,000 years ago (when it last refilled after drying out); this represents an average speciation rate of one new species every 25 to 30 years. The radiation was driven primarily by two forces: sexual selection (female cichlids in Lake Victoria show strong preference for specific male coloration; even small differences in colour drive assortative mating and rapid reproductive isolation); and ecological specialisation (cichlids have evolved remarkably diverse jaw and tooth morphologies adapted for different food types: algae scrapers; invertebrate crushers; scale eaters;



piscivores; egg robbers; insect pickers). Nigerian freshwaters support diverse cichlid assemblages, including tilapia species (*Oreochromis niloticus*, widely farmed) and colourful jewel cichlids (*Hemichromis* species).

5. Convergent evolution occurs when two or more unrelated lineages independently evolve similar or identical traits in response to similar selective pressures in their environments; the similar traits arise by independent evolutionary events rather than from a common ancestor. Two examples: (1) Streamlined (fusiform) body shape in fish (sharks, tuna), dolphins and other cetaceans, ichthyosaurs (extinct marine reptiles), and penguins; all these very different vertebrate groups independently evolved a similar teardrop-shaped body profile that minimises water resistance for efficient locomotion in water; this is strong evidence that natural selection produces predictable optimal solutions to common physical challenges. (2) Succulent water-storing stems with spines (reduced leaves) in American Cactaceae (cacti; monocot family) and African Euphorbiaceae (spurge; dicot family); these two unrelated plant families have independently evolved nearly identical-looking morphologies as adaptations to arid environments; both have thick fleshy water-storing stems, reduced or absent leaves to minimise transpiration, and spines derived from different tissues (stipules in cacti; modified stipules or leaves in euphorbias).

## References and Attributions [Series 3]

### Textual References (Books and External Sources)

1. Futuyma, D. J., & Kirkpatrick, M. (2017). *Evolution* (4th ed.). Sinauer Associates.
2. Coyne, J. A., & Orr, H. A. (2004). *Speciation*. Sinauer Associates.
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4. FAO (Food and Agriculture Organization of the United Nations). (2025). *Guidelines for sustainable agriculture*. FAO.



## Figures, Plates, Tables, and Boxes

1. Figure 3.1: Prezygotic and postzygotic reproductive isolation mechanisms diagram  
Attribution: AI generated. Suggested OER search string: "reproductive isolation mechanisms prezygotic postzygotic diagram habitat temporal behavioural mechanical gametic hybrid OER".
2. Figure 3.2: Allopatric and sympatric speciation diagrams Attribution: AI generated.  
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3. Figure 3.3: Endosymbiotic theory diagram Attribution: AI generated. Suggested OER search string: "endosymbiotic theory diagram mitochondria chloroplasts prokaryote engulfment evidence double membrane OER".
4. Figure 3.4: Darwin's finch adaptive radiation cladogram Attribution: AI generated.  
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Course code: BIO 302

Course title: Population Biology and Evolution

# Series 4: Evolution of Plants, Animals, and Humans

- **Part 4.1: Major Events in Plant Evolution**
  - Sub Part 4.1.1: Origin and diversification of land plants
  - Sub Part 4.1.2: Evolution of the seed and flower
  - Sub Part 4.1.3: Coevolution of plants and animals
- **Part 4.2: Major Events in Animal Evolution**
  - Sub Part 4.2.1: Origin of animal body plans
  - Sub Part 4.2.2: Vertebrate evolution
  - Sub Part 4.2.3: Evolution of mammals
- **Part 4.3: Primate and Hominin Evolution**
  - Sub Part 4.3.1: Primate origins and classification
  - Sub Part 4.3.2: The hominin fossil record
  - Sub Part 4.3.3: Key adaptations in human evolution
- **Part 4.4: Molecular and Genomic Evolution**
  - Sub Part 4.4.1: Molecular evolution and neutral theory
  - Sub Part 4.4.2: Genome evolution
  - Sub Part 4.4.3: Molecular evidence for human evolution



## Introduction

The history of life on Earth is recorded in the fossil record and in the genomes of living organisms. Plants colonised the land approximately 470 million years ago and diversified into the lineages that feed almost all terrestrial life. Animals evolved diverse body plans, vertebrates colonised land, and mammals diversified explosively after the dinosaur extinction. The most recent chapter is the evolution of the human lineage from African primate ancestors.

This Series traces the major evolutionary events in the history of plants, animals, and humans, and introduces molecular and genomic approaches to understanding evolutionary history. These topics integrate the mechanisms of Series 2 and 3 with the deep time perspective of the fossil record and molecular phylogenetics.

## Series Learning Outcomes

Upon completing this Series, you should be able to:

- **SLO 4.1** describe the major events in plant evolution from algal ancestors to angiosperms (Linked to Part 4.1),
- **SLO 4.2** explain the evolution of the seed and flower and describe plant-animal coevolution (Linked to Part 4.1),
- **SLO 4.3** describe the origin of animal body plans and trace vertebrate and mammal evolution (Linked to Part 4.2),
- **SLO 4.4** describe primate classification and trace the hominin fossil record (Linked to Part 4.3),
- **SLO 4.5** describe the key anatomical adaptations in human evolution (Linked to Part 4.3), and
- **SLO 4.6** explain neutral theory, describe genome evolution, and evaluate molecular evidence for human evolution (Linked to Part 4.4).



## 4.1 Major Events in Plant Evolution

### 4.1.1 Origin and diversification of land plants

Land plants (Embryophyta) evolved from charophyte green algae approximately 470 million years ago (Ma) during the Ordovician period. The colonisation of land required major adaptations: a waxy cuticle to prevent desiccation; stomata for controlled gas exchange; a vascular system (xylem and phloem) to transport water and nutrients; structural support against gravity (lignified cell walls); and spores or seeds for reproduction on land without requiring water.

Major plant lineages in evolutionary order: Bryophytes (mosses, liverworts, hornworts): non-vascular; no true roots or leaves; require water for fertilisation; approximately 470 Ma.

Pteridophytes (ferns, horsetails): first vascular plants; true roots, stems, and leaves; reproduce by spores; dominated Carboniferous forests (300 Ma). Gymnosperms (conifers, cycads, ginkgo): seed plants; no fruit; pollen eliminates dependence on water for fertilisation; dominated Mesozoic (250-66 Ma). Angiosperms (flowering plants): seeds enclosed in fruit; flowers; most diverse plant group; dominated from approximately 100 Ma to present.

Fill in the blank: Land plants evolved from \_\_\_\_\_ green algae approximately 470 million years ago; their colonisation of land required key adaptations including a waxy cuticle, stomata, vascular tissue, and structural support against gravity.

### 4.1.2 Evolution of the seed and flower

The seed was a key innovation in plant evolution. Unlike spores, a seed contains a protected embryo with its own food reserve (endosperm or cotyledons) and a protective seed coat; it can remain dormant through unfavourable conditions and disperse over long distances. The evolution of pollen (the male gametophyte) eliminated the requirement for liquid water for fertilisation; gymnosperms achieved this first, approximately 360 Ma.



Flowers evolved in the angiosperms approximately 130 Ma (Early Cretaceous); they are derived from modified leaves that form the sepals, petals, stamens (male), and carpels (female). The evolution of the flower co-occurred with the diversification of insect pollinators and bird pollinators; the resulting tight coevolution between flower morphology and pollinator biology produced an extraordinary diversity of flower forms. The angiosperms now comprise approximately 300,000 species, making them the most species-rich plant group; most Nigerian food crops (cassava, yam, cowpea, maize, rice) are angiosperms.

Fill in the blank: The seed was a key plant innovation because, unlike a spore, it contains a protected embryo with a food \_\_\_\_\_ (endosperm or cotyledons) and can remain dormant and disperse over long distances without requiring liquid water.

#### **4.1.3 Coevolution of plants and animals**

Plants and animals have profoundly shaped each other's evolution through reciprocal selective pressures. Pollination coevolution: flowering plants provide nectar or pollen as reward; pollinators (bees, butterflies, moths, birds, bats) provide pollen transfer; tight coevolution has produced precisely matching flower morphology and pollinator anatomy (e.g. African sunbirds and tubular flowers; hawkmoths and white night-blooming flowers). Many Nigerian crops (cocoa *Theobroma cacao*; cowpea *Vigna unguiculata*) depend on specific pollinators.

Seed dispersal coevolution: plants provide fleshy nutritious fruit to attract animal seed dispersers; the disperser benefits from the food and the plant benefits from having seeds carried to new locations. Fruit-eating (frugivorous) birds, bats, and primates are major seed dispersers in Nigerian forests. Plant-herbivore coevolution: plants evolve chemical defences (alkaloids, tannins, terpenes) against herbivores; herbivores evolve detoxification mechanisms; this reciprocal arms race drives the enormous chemical diversity of plants and the specialised diets of many insects and other herbivores.

Fill in the blank: \_\_\_\_\_ coevolution between plants and their pollinators has produced precisely matching flower morphology and pollinator anatomy; reciprocal selection in both partners drives increasing specialisation over evolutionary time.



# TIMELINE OF MAJOR PLANT EVOLUTION EVENTS: FROM LAND TAKEOFF TO PRESENT

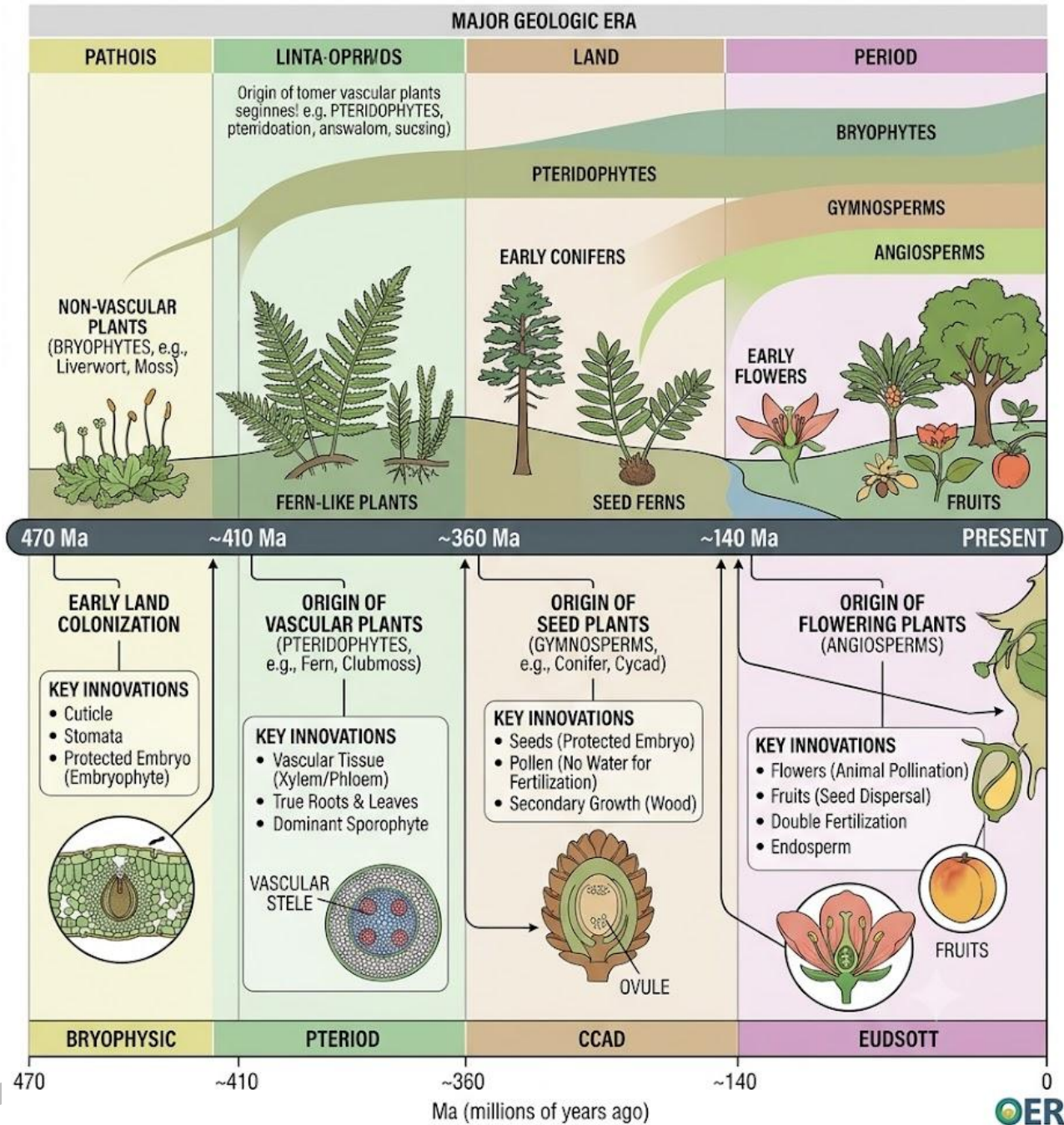


Figure 4.1: Timeline of major events in plant evolution



## Pilot questions 4.1

- State four adaptations that allowed plants to colonise land.
- List the four major plant groups in evolutionary order and state one distinguishing feature of each.
- Explain why the evolution of the seed was a key innovation in plant history.
- Explain pollination coevolution with one Nigerian example.
- Describe how plant-herbivore coevolution generates chemical diversity in plants.

## 4.2 Major Events in Animal Evolution

### 4.2.1 Origin of animal body plans

Animals (Metazoa) are multicellular, heterotrophic eukaryotes; they evolved approximately 600 to 800 Ma from unicellular flagellate ancestors. The Cambrian Explosion (approximately 541-525 Ma) was the rapid diversification of animal body plans over about 25 million years; most major animal phyla appear in the fossil record at this time. Key Cambrian animal groups: Porifera (sponges); Cnidaria; Platyhelminthes; Annelida; Mollusca; Arthropoda (the most species-rich phylum); Echinodermata; Chordata.

Animal body plans are defined by key developmental characters: symmetry (radial: Cnidaria, Echinodermata; bilateral: all Bilateria); body cavity (acoelomate: Platyhelminthes; pseudocoelomate: Nematoda; eucoelomate: Annelida, Mollusca, Arthropoda, Chordata); segmentation (Annelida, Arthropoda, Chordata); and presence of the notochord (Chordata). Hox genes are the master developmental switches that control body plan organisation along the anterior-posterior axis; they are highly conserved across all bilaterians and changes in their expression underlie much of the diversity of animal body plans.

Fill in the blank: \_\_\_\_\_ genes are master developmental regulators that control body plan organisation along the anterior-posterior axis; they are highly conserved across all bilaterians and changes in their expression underlie much of animal body plan diversity.



### 4.2.2 Vertebrate evolution

Vertebrates (Subphylum Vertebrata) are chordates with a vertebral column. Key steps in vertebrate evolution: first vertebrates appeared in Cambrian-Ordovician (approximately 500 Ma); jawless fish (Agnatha: lampreys, hagfish); Devonian Period (approximately 420-360 Ma): jawed fish (gnathostomes) with paired fins evolved; lobe-finned fish (Sarcopterygii) gave rise to tetrapods; the first tetrapods (Acanthostega, Ichthyostega) evolved approximately 375 Ma and show a mosaic of fish and land characteristics.

Subsequent vertebrate evolution: Amphibians (first fully terrestrial vertebrates; approximately 350 Ma; still require water for reproduction); Reptiles (amniote egg evolved approximately 310 Ma; full independence from water; dinosaurs dominated Mesozoic 252-66 Ma); Birds (evolved from theropod dinosaurs approximately 150 Ma; Archaeopteryx is the transitional fossil); Mammals (evolved from synapsid reptiles approximately 225 Ma; diversified explosively after the K-Pg extinction 66 Ma). Nigeria's vertebrate fauna reflects this evolutionary history: representatives of all vertebrate classes are present.

Fill in the blank: The amniote egg, which evolved approximately 310 Ma, was a key innovation that allowed reptiles to reproduce \_\_\_\_\_ from water; it enclosed the embryo in a fluid-filled membrane (amnion) protecting it from desiccation on land.

### 4.2.3 Evolution of mammals

Mammals (Class Mammalia) evolved from a synapsid lineage during the Triassic (approximately 225 Ma); the earliest mammals were small, insectivorous, and mostly nocturnal. Defining mammalian features: hair; mammary glands; endothermy (warm-bloodedness); three middle ear ossicles (malleus, incus, stapes: evolved from ancestral jaw bones, evidenced by the fossil series from Cynognathus through Morganucodon to modern mammals); the neocortex of the brain; and predominantly viviparity.

After the K-Pg mass extinction 66 Ma, the loss of non-avian dinosaurs freed ecological niches and mammals underwent a spectacular adaptive radiation. Within approximately 10 to 15 million years, most modern mammalian orders appeared: primates, carnivores, perissodactyls (horses),



artiodactyls (cattle, pigs), cetaceans (whales, from terrestrial artiodactyl ancestors), rodents, and bats. Nigeria supports a diverse mammal fauna including 274 species, of which several are endemic or near-endemic, including the Cross River gorilla (*Gorilla gorilla diehli*), the world's most endangered great ape.

Fill in the blank: Mammals underwent a rapid adaptive radiation after the K-Pg mass extinction \_\_\_\_\_ Ma, when the loss of non-avian dinosaurs freed ecological niches; most modern mammalian orders appeared within approximately 10 to 15 million years.



# PHYLOGENETIC TIMELINE OF VERTEBRATE EVOLUTION

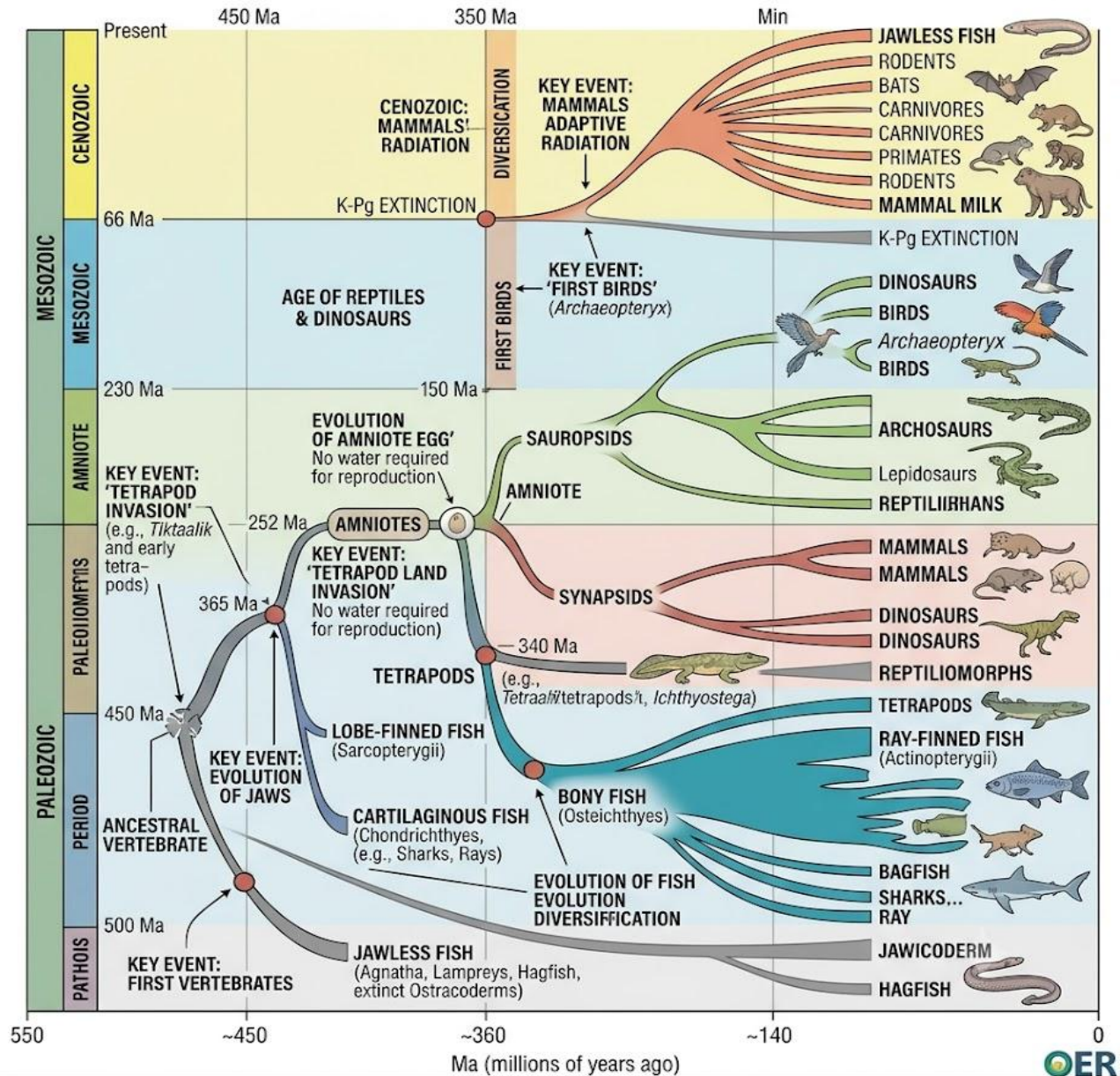


Figure 4.2: Timeline of major vertebrate evolution events

## Pilot questions 4.2

- Describe the Cambrian Explosion and state its significance for animal evolution.
- Explain the role of Hox genes in animal body plan evolution.
- Trace the key steps in vertebrate evolution from jawless fish to tetrapods.
- Explain why the evolution of the amniote egg was a key vertebrate innovation.



- Describe the mammalian adaptive radiation after the K-Pg extinction.

### 4.3 Primate and Hominin Evolution

#### 4.3.1 Primate origins and classification

Primates (Order Primates) evolved approximately 65 Ma from small arboreal (tree-dwelling) insectivore-like ancestors shortly after the K-Pg extinction. Key primate characters: grasping hands and feet (opposable thumb; nails instead of claws); forward-facing eyes (binocular stereoscopic vision); large brain relative to body size; social complexity; reduced litter size with extended parental care. These features are adaptations to an arboreal lifestyle and manipulative feeding.

Primate classification: Strepsirrhini (wet-nosed primates: lemurs, lorises, galagos); Haplorhini (dry-nosed primates: tarsiers, and Simiiformes). Simiiformes split into Platyrrhini (New World monkeys; South America) and Catarrhini (Old World monkeys + apes). Catarrhini include Cercopithecidae (Old World monkeys: vervet, baboon, colobus, mangabey) and Hominoidea (apes: gibbons, orangutan, gorilla, chimpanzee, and humans). Nigeria has approximately 20 primate species; forests of Cross River State harbour chimpanzees, gorillas (*Gorilla gorilla diehli*), red colobus (*Piliocolobus epieni*), and drills (*Mandrillus leucophaeus*).

Fill in the blank: Catarrhini (Old World primates) are divided into Cercopithecidae (Old World monkeys) and \_\_\_\_\_ (apes), which include gibbons, orangutans, gorillas, chimpanzees, and humans.

#### 4.3.2 The hominin fossil record

The hominin lineage (humans and their extinct relatives after divergence from the chimpanzee lineage) diverged approximately 6 to 7 Ma in Africa. Major hominin fossils in chronological order: *Sahelanthropus tchadensis* (approximately 7 Ma; Chad; possible earliest hominin; small brain; possibly bipedal); *Ardipithecus ramidus* (approximately 4.4 Ma; Ethiopia; partially



bipedal; still arboreal); *Australopithecus afarensis* (approximately 3.9-3.0 Ma; Lucy skeleton 3.2 Ma; bipedal but small brain approximately 400-550 cc).

*Homo habilis* (approximately 2.4-1.4 Ma; first member of genus *Homo*; brain approximately 600-700 cc; made Oldowan stone tools); *Homo erectus* (approximately 1.9-0.1 Ma; larger brain approximately 900 cc; made Acheulean hand axes; first to leave Africa; reached Asia); *Homo heidelbergensis* (approximately 700-200 ka; intermediate between *Homo erectus* and modern humans; controlled use of fire); *Homo neanderthalensis* (approximately 400-40 ka; Europe and western Asia; large brain approximately 1,500 cc; made Mousterian tools; interbred with anatomically modern humans); *Homo sapiens* (approximately 300 ka to present; originated in Africa; fully modern anatomy; Saharan Africa included Nigeria's ancestors).

Fill in the blank: *Australopithecus afarensis* (the species of the "Lucy" skeleton, approximately 3.2 Ma) was bipedal but had a small brain of approximately \_\_\_\_\_ cc; it preceded the genus *Homo* in the African hominin fossil record.



## TIMELINE OF HOMININ EVOLUTION: SPECIES, BRAIN, TOOLS, AND DISPERSALS

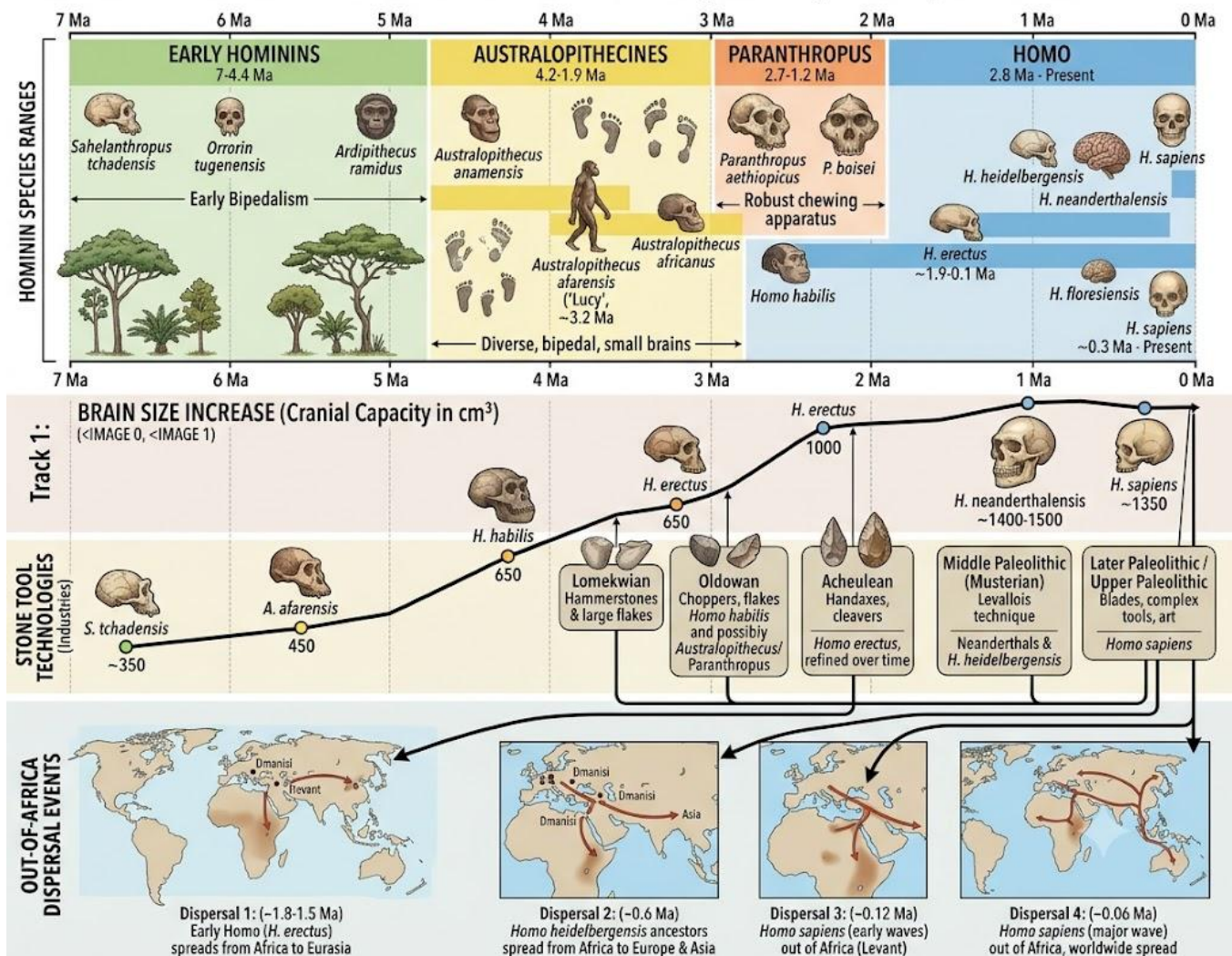


Figure 4.3: Timeline of the hominin fossil record showing key species and brain size increase

### 4.3.3 Key adaptations in human evolution

**Bipedalism:** the adoption of upright walking on two legs is the earliest and most diagnostic hominin adaptation; it appears in the fossil record before brain size increase; it freed the forelimbs for carrying and tool use; pelvis and lower limb anatomy changed substantially; the foramen magnum shifted from the back to the base of the skull. Evidence from fossils: knee joint angle, footprints (Laetoli trackways, 3.6 Ma), pelvic shape, and femur structure.

**Encephalisation:** the increase in brain size relative to body size, particularly the expansion of the prefrontal cortex; brain size increased from approximately 350 cc in *Australopithecus* to



approximately 1,400 cc in modern *Homo sapiens*; correlated with tool complexity, language, and social organisation. Reduced prognathism (facial flattening); reduction of canine teeth; increased manual dexterity (opposable thumb); prolonged developmental period (extended childhood); evolution of spoken language (hyoid bone shape, Broca's and Wernicke's areas); and use of fire (which reduces required gut length and may have increased available energy for brain growth).

Fill in the blank: \_\_\_\_\_ is the earliest and most diagnostic hominin adaptation; it preceded brain enlargement in the fossil record and is evidenced by fossil knee joints, the Laetoli trackways (3.6 Ma), pelvic morphology, and the position of the foramen magnum.

### Pilot questions 4.3

1. State five key primate characters and explain their adaptive significance.
2. Name the major primate groups of Nigeria and state the conservation status of one.
3. Trace the hominin fossil record from *Sahelanthropus* to *Homo sapiens*.
4. Explain why bipedalism is considered the most diagnostic early hominin adaptation.
5. Describe the trend of encephalisation in the hominin lineage.

## 4.4 Molecular and Genomic Evolution

### 4.4.1 Molecular evolution and neutral theory

Molecular evolution refers to the change in DNA, RNA, and protein sequences over evolutionary time. The neutral theory of molecular evolution (Motoo Kimura, 1968) proposes that most molecular variation within and among species is selectively neutral; the majority of DNA substitutions are neither beneficial nor deleterious and spread through populations by genetic drift rather than selection. Neutral variation accumulates at a rate approximately equal to the mutation rate, independent of population size.



Evidence for neutral theory: synonymous (silent) substitutions in protein-coding genes (those that do not change the amino acid sequence) accumulate approximately five times faster than non-synonymous substitutions, because they are not subject to purifying selection; intron sequences and pseudogenes evolve faster than coding sequences; the molecular clock (constant rate of neutral substitution) allows divergence time estimation. Positive selection (adaptive molecular evolution) can be detected when the ratio of non-synonymous to synonymous substitutions ( $dN/dS$ ) exceeds 1.0.

Fill in the blank: Kimura's neutral theory of molecular evolution proposes that most molecular variation is selectively \_\_\_\_\_ and spreads through populations by genetic drift; the resulting constant rate of neutral substitution forms the basis of the molecular clock.

#### 4.4.2 Genome evolution

Genomes evolve through several mechanisms beyond simple point mutation: gene duplication (a gene is copied to produce a duplicate; the duplicate can evolve new function by accumulating mutations without losing the original function; gene families such as globins and Hox genes arose by tandem duplication); genome duplication (polyploidy; especially important in plant evolution; the human genome shows evidence of two ancient whole-genome duplication events); horizontal gene transfer (movement of DNA between unrelated organisms, common in prokaryotes, also occurs in eukaryotes from organelle genomes).

Transposable elements (TEs; "jumping genes") make up approximately 45 to 80% of many eukaryotic genomes; they insert themselves into new positions, can disrupt gene function, and are a major driver of genome size variation. Genome size (C-value) varies enormously among organisms: from 0.003 pg in some fungi to over 300 pg in some lilies; this variation is not well correlated with organismal complexity (the C-value paradox), largely because TE content and polyploidy, not gene number, account for most variation. The human genome is approximately 3.2 Gb, of which only approximately 1.5% codes for proteins.

Fill in the blank: \_\_\_\_\_ duplication produces a copy of a gene; the duplicate can evolve a new function by accumulating mutations while the original gene maintains its ancestral function; gene families such as the haemoglobin globin genes arose by this mechanism.



### 4.4.3 Molecular evidence for human evolution

Molecular data provide powerful independent evidence for human evolutionary history.

**Mitochondrial DNA (mtDNA):** mtDNA is maternally inherited with no recombination; comparison of mtDNA sequences among human populations and great apes shows that humans are most closely related to chimpanzees; the human-chimpanzee divergence time is approximately 5 to 7 Ma (consistent with the fossil record); **mitochondrial Eve:** the most recent common matrilineal ancestor of all living humans, estimated to have lived approximately 100,000 to 200,000 years ago in Africa.

**Y-chromosome analysis:** the Y chromosome is paternally inherited and supports an African origin for modern human males approximately 200,000 years ago (Y-chromosomal Adam).

**Ancient DNA (aDNA):** DNA extracted from fossil bones of Neanderthals and Denisovans reveals that modern non-African humans carry approximately 1 to 4% Neanderthal DNA and some Asian populations carry Denisovan DNA, demonstrating interbreeding between modern humans and archaic hominins during the dispersal from Africa. **Human-chimpanzee genome comparison:** approximately 98.8% DNA sequence identity; major differences are in gene regulation, copy number variation, and LINE-1 transposable element content.

Fill in the blank: Analysis of mitochondrial DNA identified "mitochondrial \_\_\_\_\_", the most recent common matrilineal ancestor of all living humans, estimated to have lived approximately 100,000 to 200,000 years ago in Africa.

| <a href="#">Evidence</a>          | Key Insight                                  | Effect on Understanding Human Evolution    | Example/Notes                                            |
|-----------------------------------|----------------------------------------------|--------------------------------------------|----------------------------------------------------------|
| <a href="#">DNA Comparison</a>    | Humans share ~98–99% of DNA with chimpanzees | Confirms close evolutionary relationship   | Comparative genomics shows conserved and divergent genes |
| <a href="#">Mitochondrial Eve</a> | All humans trace maternal lineage to one     | Demonstrates common ancestry through mtDNA | mtDNA inherited maternally, no recombination             |



|                                         |                                                                         |                                            |                                                         |
|-----------------------------------------|-------------------------------------------------------------------------|--------------------------------------------|---------------------------------------------------------|
|                                         | woman ~150–200k years ago                                               |                                            |                                                         |
| <b><u>Y-Chromosome Adam</u></b>         | All men trace paternal lineage to one male ancestor ~200–300k years ago | Confirms shared paternal ancestry          | Y-chromosome passed father-to-son                       |
| <b><u>Ancient DNA: Neanderthals</u></b> | Modern humans share 1–4% of DNA with Neanderthals                       | Evidence of interbreeding                  | Sequenced Neanderthal genomes show introgression        |
| <b><u>Ancient DNA: Denisovans</u></b>   | Denisovan DNA found in Melanesian and Asian populations                 | Shows multiple archaic admixture events    | Up to 5% Denisovan DNA in some populations              |
| <b><u>Molecular Clock</u></b>           | Mutations accumulate at predictable rates                               | Estimates divergence times between species | Used to date human–chimp split (~5–7 million years ago) |
| <b><u>Pseudogene Evidence</u></b>       | Shared nonfunctional genes across species                               | Indicates common ancestry                  | Example: GULO pseudogene for vitamin C synthesis        |

Box 4.1: Key molecular evidence for human evolutionary relationships

#### Pilot questions 4.4

1. Explain Kimura's neutral theory of molecular evolution.
2. Explain how gene duplication contributes to genome evolution with one example.
3. Explain what the C-value paradox is.
4. Explain what mitochondrial Eve represents and what her existence tells us about human evolution.
5. Summarise the ancient DNA evidence for interbreeding between modern humans and archaic hominins.



## Series Summary

This Series covered the evolution of plants, animals, and humans. Plant evolution: land plants evolved from charophyte algae approximately 470 Ma; four groups in order (bryophytes, pteridophytes, gymnosperms, angiosperms); key innovations: vascular tissue, seed (embryo + food reserve + protective coat; eliminates water dependence for fertilisation), flower (130 Ma; coevolved with pollinators); plant-herbivore chemical arms race generates phytochemical diversity. Animal evolution: Cambrian Explosion 541-525 Ma established most animal phyla; Hox genes control body plans; vertebrate milestones: jawless fish (500 Ma), jawed fish, tetrapods from lobe-finned fish (375 Ma), amniote egg (310 Ma), mammals from synapsids (225 Ma), K-Pg extinction (66 Ma), mammal adaptive radiation.

Primate evolution: primates evolved approximately 65 Ma from arboreal insectivores; classified as Strepsirrhini and Haplorhini; Hominoidea includes apes and humans; Nigeria hosts approximately 20 primate species including the endangered Cross River gorilla. Hominin fossil record: diverged from chimpanzees approximately 6-7 Ma; key taxa: Sahelanthropus (7 Ma), Ardipithecus (4.4 Ma), Australopithecus afarensis/Lucy (3.2 Ma), Homo habilis (2.4 Ma; first tools), Homo erectus (1.9 Ma; first to leave Africa), Homo sapiens (300 ka; originated Africa). Key human adaptations: bipedalism (earliest adaptation; before brain expansion); encephalisation (350 to 1,400 cc); language; tool use. Molecular evolution: neutral theory (Kimura 1968; most variation is neutral; spreads by drift; molecular clock); genome evolution (gene duplication, polyploidy, TEs, C-value paradox); molecular evidence for human evolution (98.8% human-chimpanzee DNA identity; mitochondrial Eve approximately 100-200 ka Africa; ancient DNA: 1-4% Neanderthal in non-Africans). By completing this Series, you should achieve all six SLOs (4.1 to 4.6).

## Glossary of Terms

1. **Amniote egg:** an egg with internal membranes (amnion, chorion, allantois) that protect the embryo from desiccation; evolved approximately 310 Ma in early reptiles, enabling fully terrestrial reproduction.



2. **Ancient DNA (aDNA):** DNA extracted from fossil or archaeological specimens; used to reconstruct genomes of extinct species (Neanderthals, Denisovans) and trace population history.
3. **Angiosperms:** the flowering plants; the most species-rich plant group (approximately 300,000 species); seeds enclosed in fruit; evolved approximately 130 Ma.
4. **Australopithecus:** a genus of bipedal hominins that lived 4.2 to 1.8 Ma in Africa; small-brained (approximately 350-550 cc) but fully bipedal; *A. afarensis* includes the famous "Lucy" fossil.
5. **Bipedalism:** walking habitually on two hindlimbs; the earliest and most diagnostic adaptation in the hominin lineage; preceded major brain size increase.
6. **C-value paradox:** the observation that genome size (C-value) is not correlated with organismal complexity; due to variation in transposable element content and polyploidy rather than gene number.
7. **Cambrian Explosion:** the rapid diversification of animal body plans approximately 541 to 525 Ma; most major animal phyla appear in the fossil record during this period.
8. **Charophytes:** a group of freshwater green algae that are the closest living relatives of land plants; land plants evolved from a charophyte ancestor approximately 470 Ma.
9. **Denisovans:** an extinct archaic hominin group known from ancient DNA and a few fossils from Siberia; interbred with modern humans during the Out of Africa dispersal; some Asians carry Denisovan DNA.
10. **Encephalisation:** the evolutionary increase in brain size relative to body size; a major trend in the hominin lineage, from approximately 350 cc in *Australopithecus* to approximately 1,400 cc in *Homo sapiens*.
11. **Exaptation:** a trait that originally evolved for one function and was later co-opted for a new function (covered in Series 3; relevant here: mammalian ear ossicles are exapted jaw bones of ancestral synapsids).



12. **Gene duplication:** the copying of a gene to produce a duplicate; the duplicate can accumulate mutations and evolve a new function while the original retains its ancestral role.
13. **Gymnosperms:** seed plants in which seeds are borne naked on cones without being enclosed in fruit; include conifers, cycads, and ginkgo; dominated Mesozoic floras.
14. **Hominin:** the group comprising humans and all extinct relatives after the divergence from the chimpanzee lineage; all are bipedal.
15. **Homo erectus:** an extinct hominin species (approximately 1.9 to 0.1 Ma) with a brain of approximately 900 cc; made Acheulean stone tools; the first hominin to disperse out of Africa.
16. **Homo sapiens:** anatomically modern humans; originated in Africa approximately 300 ka; dispersed globally approximately 60 to 70 ka.
17. **Hox genes:** a conserved family of transcription factors that control body plan organisation along the anterior-posterior axis; found in all bilaterians.
18. **K-Pg extinction:** the Cretaceous-Palaeogene mass extinction event 66 Ma; caused by asteroid impact and volcanism; eliminated non-avian dinosaurs and approximately 75% of all species; followed by the mammalian adaptive radiation.
19. **Mitochondrial Eve:** the most recent common matrilineal ancestor (traced through mitochondrial DNA) of all living humans; estimated to have lived approximately 100,000 to 200,000 years ago in Africa.
20. **Neanderthals (Homo neanderthalensis):** an extinct archaic human species in Europe and western Asia (approximately 400-40 ka) with a large brain; interbred with modern humans; modern non-African humans carry approximately 1 to 4% Neanderthal DNA.
21. **Neutral theory:** Kimura's (1968) theory that most molecular variation within and among species is selectively neutral and spreads through populations by genetic drift rather than natural selection.



22. **Polyploidy:** the possession of more than two complete sets of chromosomes; a major driver of genome evolution and speciation in plants.
23. **Pteridophytes:** vascular plants that reproduce by spores (no seeds); include ferns and horsetails; dominated Carboniferous forests.
24. **Sahelanthropus tchadensis:** a possible earliest hominin (approximately 7 Ma) from Chad; the oldest candidate for a bipedal hominin ancestor.
25. **Synapsids:** the lineage of amniotes that includes both modern mammals and their extinct relatives (pelycosaurs, therapsids); mammals evolved from synapsids in the Triassic.
26. **Transposable elements (TEs):** DNA sequences that can move within a genome; make up approximately 45 to 80% of eukaryotic genomes; a major driver of genome size variation and evolution.

## Concept Check Questions [Series 4]

### Objective Questions

1. Land plants evolved from \_\_\_\_\_ green algae approximately 470 Ma; their colonisation of land required a waxy cuticle, stomata, vascular tissue, and lignified support structures. (Linked to SLO 4.1)
2. \_\_\_\_\_ genes are master developmental regulators that control body plan organisation along the anterior-posterior axis in all bilaterians. (Linked to SLO 4.3)
3. The amniote egg, which evolved approximately 310 Ma, allowed reptiles to reproduce independently of \_\_\_\_\_, enabling fully terrestrial life. (Linked to SLO 4.3)
4. \_\_\_\_\_ is the earliest and most diagnostic hominin adaptation; it preceded brain enlargement in the fossil record. (Linked to SLO 4.5)
5. Kimura's neutral theory proposes that most molecular variation is selectively \_\_\_\_\_ and spreads through populations by genetic drift rather than selection. (Linked to SLO 4.6)



### Short-Answer Questions

- List the four major plant groups in evolutionary order and state one key innovation associated with each. (Linked to SLO 4.1)
- Describe the Cambrian Explosion and state its significance for animal evolution. (Linked to SLO 4.3)
- Trace the hominin fossil record from Australopithecus to Homo sapiens. (Linked to SLO 4.4)
- Explain the neutral theory of molecular evolution. (Linked to SLO 4.6)
- Summarise the molecular evidence for an African origin of modern humans. (Linked to SLO 4.6)

### Long-Answer Questions

1. Describe the major events in plant evolution from algal ancestors to angiosperms; explain the significance of the seed and flower; and describe plant-animal coevolution. (Linked to SLOs 4.1, 4.2)
2. Describe the origin of animal body plans, trace vertebrate evolution from jawless fish to mammals, and explain the mammalian adaptive radiation. (Linked to SLO 4.3)
3. Describe primate classification and the hominin fossil record; explain key human anatomical adaptations; and describe the molecular evidence for human evolution. (Linked to SLOs 4.4, 4.5, 4.6)

### Answers to Concept Check Questions [Series 4]

#### Objective Questions

6. Charophyte.



7. Hox.
8. Water.
9. Bipedalism.
10. Neutral.

### Short-Answer Questions

11. Bryophytes (non-vascular; waxy cuticle and stomata); Pteridophytes (first vascular tissue: xylem and phloem); Gymnosperms (first seed: embryo with food reserve; pollen eliminates water for fertilisation); Angiosperms (flowers and fruit; coevolution with pollinators; seeds enclosed in fruit).
12. The Cambrian Explosion (approximately 541-525 Ma) was the rapid diversification of most major animal body plans in approximately 25 million years. Significance: it established the fundamental architectural blueprints (body plans) of essentially all living animal phyla; most animal evolution since has been variation within these basic body plans rather than the origin of new ones.
13. Australopithecus afarensis (approximately 3.2 Ma; Lucy; bipedal; brain approximately 400-550 cc); Homo habilis (approximately 2.4-1.4 Ma; first Homo; brain approximately 600-700 cc; Oldowan tools); Homo erectus (approximately 1.9-0.1 Ma; brain approximately 900 cc; Acheulean tools; first out of Africa); Homo heidelbergensis (700-200 ka; fire use); Homo neanderthalensis (400-40 ka; brain approximately 1,500 cc; Mousterian tools); Homo sapiens (approximately 300 ka-present; Africa; full modern anatomy).
14. The neutral theory (Kimura, 1968) proposes that most molecular variation within and among species is selectively neutral (neither beneficial nor deleterious); such variation spreads by genetic drift, not selection; neutral substitutions accumulate at a rate approximately equal to the mutation rate, forming the basis of the molecular clock.
15. Mitochondrial DNA places the most recent common matrilineal ancestor (mitochondrial Eve) in Africa approximately 100,000 to 200,000 years ago; Y-chromosome analysis places Y-chromosomal Adam in Africa approximately 200,000 years ago; ancient DNA



shows non-African humans carry approximately 1 to 4% Neanderthal DNA, indicating interbreeding occurred after leaving Africa; human-chimpanzee DNA is approximately 98.8% identical with divergence approximately 5 to 7 Ma.

### Long-Answer Questions

1. Plant evolution: land plants (Embryophyta) evolved from charophyte green algae approximately 470 Ma (Ordovician); required four key adaptations: cuticle (prevents desiccation); stomata (gas exchange); vascular tissue (xylem and phloem for water and nutrient transport); lignified cell walls (support against gravity). Four groups in order: Bryophytes (non-vascular; mosses/liverworts; require water for fertilisation; 470 Ma); Pteridophytes (vascular; ferns/horsetails; spore reproduction; dominated Carboniferous coal forests 300 Ma); Gymnosperms (seed plants; conifers/cycads; pollen eliminates water dependence; naked seeds on cones; dominated Mesozoic 250-66 Ma); Angiosperms (flowers; fruit; seeds enclosed; approximately 300,000 species; dominant from 100 Ma to present; most Nigerian crop plants). Seed significance: embryo + food reserve + protective seed coat; dormancy and long-distance dispersal; no water needed for fertilisation (pollen carries male gamete to ovule). Flower significance (130 Ma): evolved with insect and bird pollinators; extraordinary coevolution drove angiosperm diversification. Plant-animal coevolution: pollination (nectar/pollen reward; pollinators: bees, butterflies, sunbirds, bats; precise morphological match between flower and pollinator; Nigerian examples: cocoa, cowpea); seed dispersal (fleshy fruit attracts frugivorous birds, bats, primates; plant benefits from seed transport); plant-herbivore arms race (alkaloids, tannins, terpenes as plant defences; herbivores evolve detoxification; drives chemical diversity).
2. Animal body plans: animals evolved approximately 600-800 Ma; Cambrian Explosion (541-525 Ma) established most phyla; defined by: symmetry (radial vs bilateral); body cavity (acoelomate, pseudocoelomate, eucoelomate); segmentation; notochord. Hox genes control anterior-posterior body plan organisation; conserved across all bilaterians; their expression changes underlie body plan diversity. Vertebrate evolution: first



vertebrates (jawless fish Agnatha) approximately 500 Ma; jawed fish (gnathostomes) with paired fins evolved in Devonian (420-360 Ma); lobe-finned fish (Sarcopterygii) gave rise to tetrapods approximately 375 Ma (Acanthostega, Ichthyostega); amphibians (350 Ma; still water-dependent for reproduction); amniote egg evolved approximately 310 Ma (reptiles; fully terrestrial reproduction); dinosaurs dominated Mesozoic 252-66 Ma; birds evolved from theropod dinosaurs approximately 150 Ma (Archaeopteryx); mammals from synapsids approximately 225 Ma. Mammalian adaptive radiation: K-Pg extinction 66 Ma removed non-avian dinosaurs; within approximately 10-15 Ma, most mammalian orders appeared: primates, carnivores, artiodactyls (cattle, pigs, whales from terrestrial ancestors), perissodactyls, rodents, bats; Nigeria supports 274 mammal species including Cross River gorilla (most endangered great ape).

3. Primate classification: evolved approximately 65 Ma from arboreal insectivores; key characters: grasping hands (opposable thumb); forward-facing eyes (stereoscopic vision); large brain; social complexity; slow reproduction. Classification: Strepsirrhini (wet-nosed: lemurs, lorises, galagos) and Haplorhini (dry-nosed: tarsiers and Simiiformes); Simiiformes split into Platyrrhini (New World monkeys) and Catarrhini (Old World monkeys + Hominoidea); Hominoidea = gibbons, orangutans, gorillas, chimpanzees, and humans. Nigeria has approximately 20 primate species; Cross River State has chimpanzees, Cross River gorilla (approximately 250 individuals remaining; Critically Endangered), red colobus, drill. Hominin fossil record: diverged from chimpanzees approximately 6-7 Ma in Africa; Sahelanthropus tchadensis (7 Ma; Chad; possible first hominin); Ardipithecus ramidus (4.4 Ma; Ethiopia; partly bipedal); Australopithecus afarensis/Lucy (3.2 Ma; fully bipedal; brain approximately 400-550 cc); Homo habilis (2.4-1.4 Ma; first Homo; Oldowan tools; brain approximately 600-700 cc); Homo erectus (1.9-0.1 Ma; first out of Africa; Acheulean tools; brain approximately 900 cc); Homo neanderthalensis (400-40 ka; Mousterian tools; brain approximately 1,500 cc; interbred with Homo sapiens); Homo sapiens (approximately 300 ka to present; Africa; modern anatomy). Key adaptations: bipedalism (earliest; Laetoli trackways 3.6 Ma; foramen magnum position; pelvic and femur morphology; freed forelimbs for tool use); encephalisation (350 to 1,400 cc; prefrontal cortex expansion; linked to language, tools, social complexity); reduced prognathism; reduced canines; prolonged development;



language (hyoid bone; Broca's and Wernicke's areas); fire use. Molecular evidence: human-chimpanzee 98.8% DNA identity; divergence approximately 5-7 Ma; mitochondrial Eve approximately 100-200 ka Africa; Y-chromosomal Adam approximately 200 ka Africa; ancient DNA reveals approximately 1-4% Neanderthal in non-African modern humans and Denisovan DNA in some Asian populations; shared inactivated GULO pseudogene in humans and other apes (common ancestry; cannot synthesise vitamin C).

## Answers to Pilot Questions [Series 4]

### Part 4.1

6. Four adaptations for land colonisation: (1) Waxy cuticle (a layer of cutin covering the outer surface of aerial cells; prevents water loss through evaporation; the primary barrier against desiccation in a terrestrial environment where water is not continuously available as it is in aquatic habitats); (2) Stomata (pores in the epidermis controlled by guard cells; allow CO<sub>2</sub> and O<sub>2</sub> exchange while minimising water loss; permit regulation of gas exchange rather than the passive permeability of aquatic algae); (3) Vascular tissue (xylem and phloem; transports water, minerals, and organic solutes between organs separated in air; in aquatic plants, all cells are in contact with water; land plants need a transport system to supply cells far from water sources); (4) Lignified cell walls and structural support (gravity is a much greater challenge for a plant standing in air than one supported by water; lignin in xylem cell walls provides the rigidity needed to keep the plant upright against gravity).
7. Four major plant groups in evolutionary order: (1) Bryophytes (mosses, liverworts, hornworts; approximately 470 Ma; non-vascular; no true roots, stems, or leaves; reproduce by spores; require liquid water for fertilisation by swimming sperm; restricted to moist habitats); (2) Pteridophytes (ferns, horsetails, clubmosses; approximately 425 Ma; first vascular plants with true xylem and phloem; true roots, stems, and leaves; reproduce by spores; still need water for fertilisation by swimming sperm; dominated



Carboniferous coal forests); (3) Gymnosperms (conifers, cycads, ginkgo; approximately 360 Ma; first seed plants; seeds borne naked on cones; pollen eliminates water dependence for fertilisation; no flowers or fruit; dominated Mesozoic floras); (4) Angiosperms (flowering plants; approximately 130 Ma; seeds enclosed in fruit derived from the ovary wall; flowers attract pollinators; approximately 300,000 species; most dominant and diverse plant group on Earth).

8. The seed was a key plant innovation for three main reasons: (1) Protection of the embryo: the seed coat (testa) derived from the ovule integuments provides physical and chemical protection for the dormant embryo against desiccation, mechanical damage, and pathogen attack; a naked spore has no such protection. (2) Nutritional independence: the seed contains a food reserve (endosperm in most seeds; cotyledons in some) that provides the energy and organic nutrients the embryo needs to germinate and establish itself before photosynthesis becomes sufficient; a spore has no significant food reserve and must photosynthesize immediately. (3) Elimination of water for fertilisation: pollen (the male gametophyte in seed plants) is transported by wind or animals directly to the female reproductive structures; the sperm are delivered directly to the ovule without swimming through water; this freed seed plants from dependence on liquid water for sexual reproduction, allowing colonisation of much drier habitats than pteridophytes.
9. Pollination coevolution occurs when the reproductive fitness of both a plant and its animal pollinator is influenced by the traits of the other; selection in each partner is driven by the other, producing reciprocal evolutionary change that leads to increasingly precise morphological and behavioural matching. Nigerian example: the African sunbirds (Family Nectariniidae; Nectarinia, Cinnyris species) are nectar feeders that pollinate many tubular-flowered plants; plants with deep red or orange tubular flowers (which reflect light in wavelengths sunbirds perceive well) that hold nectar at the base of a tube matching the sunbird's curved bill are preferentially visited and pollinated; sunbirds with bill curves matching the flower tubes extract nectar more efficiently; over evolutionary time, selection favours more precise matching between flower tube length/curvature and bill morphology in both partners, producing the diversity of tubular flower forms and curved sunbird bills seen in African communities.



10. Plants produce a diverse arsenal of secondary metabolites (compounds not directly involved in primary metabolism) partly as chemical defences against herbivores: alkaloids (caffeine, nicotine, morphine, quinine) are toxic to most herbivores; tannins (complex polyphenols in bark and leaves) bind and precipitate digestive enzymes, reducing protein digestion efficiency; terpenes (essential oils, latex) are deterrents and toxins; glucosinolates (in cabbage family) release toxic isothiocyanates on cell damage. When herbivores evolve biochemical mechanisms (cytochrome P450 enzymes) to detoxify one class of compound, selection pressures intensify on plants to produce new or modified compounds that the detoxification system cannot handle; this reciprocal arms race, operating over millions of years, drives the extraordinary diversity of plant secondary chemistry and the parallel diversity of specialist herbivore detoxification pathways.

#### Part 4.2

11. The Cambrian Explosion was the geologically rapid diversification of most major animal body plans that occurred approximately 541 to 525 Ma, during the early Cambrian period; over approximately 25 million years (brief by geological standards), the fossil record records the first appearance of representatives of most animal phyla still alive today. Key Cambrian fossil sites: Burgess Shale (Canada) and Chengjiang biota (China) preserve soft-bodied animals in exceptional detail. Significance: (1) it established the basic architectural blueprints (body plans) of virtually all living animals; the fundamental symmetry, body cavity, segmentation, and organ system arrangements of modern animal phyla were essentially set during this event; (2) it represents the origin of complex animal ecosystems with predators and prey; (3) it demonstrates that body plan evolution (macroevolution) can proceed at rates far faster than background rates in appropriate ecological conditions (many unfilled niches).

12. Hox genes are a family of highly conserved transcription factor genes that specify positional identity along the anterior-posterior (head-to-tail) body axis of bilaterally symmetrical animals; they control which body part develops at which position during



embryogenesis. They encode homeodomain proteins that bind to DNA and activate or repress target genes. They are found in all bilaterians (from worms to flies to humans) and their order on the chromosome corresponds to their order of expression along the body axis (spatial and temporal colinearity). Changes in Hox gene expression are responsible for much of the diversity of animal body plans: the loss of legs in snakes resulted from changes in Hox gene expression domains in the trunk; the evolution of wings from legs in insect ancestors involved changes in Hox gene expression in the thorax; arthropod body plans (centipede vs insect vs crab) reflect differences in how many segments express particular Hox genes.

13. Key steps: (1) Earliest vertebrates (jawless fish/Agnatha: lampreys, hagfish; approximately 500 Ma Cambrian-Ordovician; bony plates instead of teeth; no paired fins; filter feeders); (2) Jawed fish/Gnathostomes evolved in Silurian-Devonian (approximately 420-360 Ma); jaws evolved from gill arches; paired pectoral and pelvic fins appeared; became dominant aquatic predators; (3) Lobe-finned fish (Sarcopterygii; includes lungfish and coelacanths as living relatives) evolved muscular paired fins supported by bones homologous to the tetrapod limb; approximately 375 Ma, tetrapods evolved from lobe-finned fish ancestors; transitional fossils *Acanthostega* and *Ichthyostega* (Greenland, approximately 375 Ma) have four limbs with digits but retain many fish characteristics (tail fin, gills, elongated body); they were probably primarily aquatic. The limbs of these early tetrapods are homologous to the paired fins of their fish ancestors.
14. The amniote egg evolved approximately 310 Ma in the lineage leading to modern reptiles; it contains a complete, self-contained aquatic environment for the embryo, enclosed within a shell: the amnion is a fluid-filled membrane that surrounds the embryo and prevents desiccation; the chorion facilitates gas exchange through the porous shell; the allantois stores waste products; the yolk sac provides nutrients. Before the amniote egg, tetrapods (amphibians) had to return to water to lay their unshelled eggs; fertilisation was external; the embryos could not survive outside water. The amniote egg freed vertebrates from this water dependence by providing the embryo with its own aquatic microenvironment on land; this opened the entire terrestrial biome to vertebrate colonisation; reptiles rapidly diversified and occupied habitats unavailable to amphibians.



The amniote egg was the most significant single evolutionary innovation in vertebrate history for enabling the radiation of terrestrial vertebrates.

15. The K-Pg mass extinction 66 Ma caused by the Chicxulub asteroid impact in Mexico (combined with Deccan Traps volcanism) eliminated approximately 75% of all species, including all non-avian dinosaurs; this catastrophic removal of the dominant terrestrial vertebrates freed an enormous range of previously occupied ecological niches. Mammals at this time were small (mostly under 1 kg), insectivorous, and nocturnal; there were few large-bodied or ecologically diverse mammals. Within approximately 10 to 15 million years after the extinction (Palaeocene and Eocene epochs), mammals underwent an explosive adaptive radiation: large herbivorous mammals occupying the grazing and browsing niches formerly held by dinosaurs; large carnivores occupying the predatory niches; bats evolving flight and echolocation; whales secondarily returning to the sea from terrestrial artiodactyl ancestors; primates diversifying in trees; rodents becoming the most species-rich mammalian order. Essentially all modern mammalian orders can be traced to this post-K-Pg radiation.

#### Part 4.3

1. Five key primate characters and adaptive significance: (1) Grasping hands and feet with opposable thumbs (or big toes in most species) and flat nails instead of claws: allows precise grasping of branches and food items; essential for arboreal locomotion and manipulation. (2) Forward-facing eyes producing binocular stereoscopic vision with large overlap of the visual fields of both eyes: provides precise depth perception for judging distances during leaping and reaching in trees; also important for fine visual discrimination of food. (3) Large brain relative to body size (high encephalisation quotient): supports complex social behaviour, learning, and problem-solving that are advantageous in the complex three-dimensional environment of forest canopies with long-lived social groups. (4) Social complexity with prolonged infant dependency and extended parental care: allows transmission of learned behaviour and social knowledge from experienced individuals to young; increases the survival probability of each



offspring. (5) Reduced litter size (usually one or two offspring per birth): allows concentration of parental investment in each offspring; compensated by high offspring survival due to intensive parental care and learning.

2. Major Nigerian primate groups: (1) Galagos (bushbabies; Strepsirrhini; *Galago* species; small, nocturnal; found in all forested regions of Nigeria); (2) Old World monkeys (Cercopithecidae): vervet monkeys (*Cercopithecus aethiops*); red colobus (*Piliocolobus badius epeni*, endemic to Niger Delta islands; Critically Endangered); drill (*Mandrillus leucophaeus*; Cross River State and Cameroon; Endangered); (3) Great apes (Hominidae): Nigeria-Cameroon chimpanzee (*Pan troglodytes ellioti*; distributed across Cross River and Taraba States); Cross River gorilla (*Gorilla gorilla diehli*). Conservation status of Cross River gorilla: Critically Endangered on the IUCN Red List; approximately 200 to 300 individuals remain in the forests of Cross River and Benue States and adjacent Cameroon; the most endangered great ape in the world; threats include habitat loss (deforestation for agriculture), hunting, and forest fragmentation.
3. Hominin fossil record from approximately 7 Ma to *Homo sapiens*: *Sahelanthropus tchadensis* (approximately 7 Ma; Chad; small brain approximately 320-380 cc; possible hominin based on position of foramen magnum suggesting bipedalism; one of the oldest potential hominin fossils); *Ardipithecus ramidus* (approximately 4.4 Ma; Ethiopia; partially bipedal on the ground but retained climbing adaptations for trees; brain similar to chimpanzee approximately 300-350 cc); *Australopithecus afarensis* (approximately 3.9-3.0 Ma; Ethiopia, Tanzania; the "Lucy" specimen 3.2 Ma; fully bipedal (evidenced by knee joint anatomy and the Laetoli footprint trackways 3.6 Ma); brain approximately 400-550 cc; no stone tools); *Homo habilis* (approximately 2.4-1.4 Ma; East Africa; brain approximately 600-700 cc; associated with the first stone tool industry: Oldowan tools; first member of genus *Homo*); *Homo erectus* (approximately 1.9 Ma to approximately 100 ka; Africa and Asia; brain approximately 800-1,000 cc; made Acheulean hand axes; first hominin to leave Africa and reach Asia; used fire); *Homo neanderthalensis* (approximately 400-40 ka; Europe and western Asia; brain approximately 1,400-1,500 cc, similar to modern humans; made Mousterian stone tools; interbred with *Homo sapiens*; modern non-African humans carry approximately 1-4% Neanderthal DNA); *Homo*



sapiens (approximately 300 ka to present; originated in Africa; fully modern anatomy; globally dispersed approximately 60-70 ka).

4. Bipedalism is considered the earliest and most diagnostic hominin adaptation because:  
(1) it appears in the fossil record before significant brain size increase; the Laetoli trackways (3.6 Ma) and the Lucy skeleton (3.2 Ma) show clear bipedal anatomy (bipedal knee joint angle, non-divergent big toe, obligate bipedal gait) in a species with a chimpanzee-sized brain (approximately 400 cc); this contradicts any view that brain expansion drove bipedalism; (2) all known hominin fossils are at least partially bipedal; there is no known hominin that had a significantly enlarged brain but was not bipedal; bipedalism thus defines the hominin lineage from its beginning; (3) the anatomical changes associated with bipedalism are extensive and diagnostic in fossil material: the foramen magnum (the hole where the spinal cord exits the skull) shifted from the posterior position (as in chimpanzees) to a position near the base of the skull (directly under the head, balancing it upright); the pelvis became shorter and broader (to support the abdominal organs in an upright stance and anchor the hip abductor muscles needed for bipedal walking); the femur angles inward from hip to knee (valgus angle) bringing the feet under the body's centre of gravity.
5. Encephalisation in the hominin lineage is the evolutionary increase in brain size relative to body size. The trend: Australopithecus (approximately 3-4 Ma): brain volume approximately 350 to 550 cc (similar to a chimpanzee at 350-450 cc); no stone tools; Homo habilis (approximately 2.4 Ma): approximately 600-700 cc; Oldowan stone tools appear at this time; Homo erectus (approximately 1.9 Ma): approximately 800-1,000 cc; more sophisticated Acheulean tools; fire use; out of Africa dispersal; Homo neanderthalensis (approximately 400-40 ka): approximately 1,400-1,500 cc; Homo sapiens (modern): approximately 1,350-1,400 cc average; The most rapid encephalisation occurred in the Homo lineage between approximately 2.5 and 0.5 Ma, when brain volume roughly tripled in approximately 2 million years; this is correlated with: increasing tool complexity; use of fire (which may have provided more calorie-dense food, reducing gut size and freeing energy for brain growth); expanding dietary breadth; increasing social group size; and the eventual evolution of language. Brain expansion was concentrated in the prefrontal cortex (associated with planning, decision-making, and social cognition),



the temporal lobes (language and memory), and the parietal lobes (spatial reasoning and tool use).

#### Part 4.4

1. Kimura's neutral theory of molecular evolution (1968) proposes that the vast majority of DNA sequence variation within and between species is selectively neutral: most nucleotide substitutions, insertions, and deletions are neither beneficial nor harmful to the organism and do not affect fitness significantly; because they are not subject to natural selection, these neutral variants accumulate and spread through populations solely by the random process of genetic drift; the rate at which neutral variants are fixed (become the only variant present in the population) is approximately equal to the mutation rate, independent of population size; this means that neutral molecular variants accumulate at an approximately constant rate over time in a lineage, forming the basis of the molecular clock. Evidence: synonymous (silent) substitutions in coding sequences that do not change the amino acid sequence accumulate much faster than non-synonymous substitutions that change the amino acid (because synonymous changes are invisible to selection while non-synonymous changes are often subject to purifying selection); non-coding sequences (introns, intergenic regions) evolve faster than coding sequences; pseudogenes (non-functional gene copies) evolve at the fastest rates, approaching the neutral mutation rate.
2. Gene duplication occurs when a copying error or unequal crossing over during recombination produces an extra copy of a gene within the genome; the organism now has two copies of the same gene, both functional. The duplicate gene is freed from purifying selection for its original function because the original copy continues to perform the ancestral role; random mutations accumulate in the duplicate; occasionally a mutation enables the duplicate to catalyse a related but distinct reaction or to be expressed in a different tissue or at a different developmental stage; if this new function is beneficial, selection fixes the mutation and the duplicate becomes a new gene with a new function. This process of neofunctionalization has generated many of the largest gene



families in eukaryotic genomes. Example: the haemoglobin gene family. Ancestral organisms had a single myoglobin-like oxygen-binding globin gene; repeated rounds of gene duplication have produced a family of related genes: alpha-globin, beta-globin (adult haemoglobin), gamma-globin (foetal haemoglobin; higher oxygen affinity for extracting oxygen from maternal blood), delta-globin, epsilon-globin (embryonic haemoglobin); each duplication was followed by divergence for expression in different tissues or at different developmental stages.

3. The C-value paradox is the observation that there is no positive correlation between the size of an organism's genome (its C-value, measured in picograms of DNA per haploid cell set or in base pairs) and the complexity or developmental sophistication of the organism. Simple organisms can have enormous genomes while complex organisms may have relatively small ones: some salamanders have genomes approximately 10 times larger than the human genome (approximately 3.2 Gb); some lilies have genome sizes over 100 times larger than the human genome; the lung fish has one of the largest animal genomes at approximately 130 Gb; yet these animals are not more complex than humans in any meaningful biological sense. The paradox is explained by the fact that most of the DNA in large eukaryotic genomes is not protein-coding sequence; instead, genome size differences are primarily due to: variation in transposable element content (TEs make up 45-80% of most eukaryotic genomes; species with recent TE bursts have much larger genomes); polyploidy (polyploid species have multiple copies of all chromosomes, directly multiplying genome size); and repetitive sequences. Gene number is actually relatively constant across many complex eukaryotes (humans approximately 20,000 genes; nematode approximately 19,000 genes; despite 30-fold difference in genome size).
4. Mitochondrial Eve is the most recent common matrilineal ancestor (traced exclusively through the maternal line via mitochondrial DNA) of all currently living human beings; she is not the only woman alive at her time (many other women lived contemporaneously), but she is the one whose mtDNA lineage has been transmitted without interruption to every living person; all other female lineages alive at her time have since died out by chance (genetic drift). Analysis of mtDNA sequences from geographically diverse human populations shows: the deepest branches (greatest divergence) are found among African populations, indicating the oldest lineages are in



Africa; populations outside Africa show lower mtDNA diversity, consistent with a more recent origin; phylogenetic analysis of these mtDNA sequences places the root of the human mtDNA tree in Africa approximately 100,000 to 200,000 years ago. Mitochondrial Eve therefore supports the "Out of Africa" model: modern Homo sapiens originated in Africa relatively recently and then dispersed globally, replacing archaic populations in other regions (with some interbreeding as revealed by ancient DNA).

5. Ancient DNA studies have extracted and sequenced DNA from fossil bone of Neanderthals (*Homo neanderthalensis*) and a related group called the Denisovans (known from a finger bone and teeth from Denisova Cave, Siberia). Key findings: (1) Neanderthal-modern human interbreeding: comparison of the Neanderthal genome (sequenced by Svante Paabo's team, 2010) with modern human genomes reveals that modern humans of non-African origin (Europeans, Asians, and Australasians) carry approximately 1 to 4% of their nuclear DNA from Neanderthal ancestors; African populations carry little to no Neanderthal DNA; this pattern is explained by interbreeding occurring after modern Homo sapiens left Africa (approximately 60-70 ka) but before dispersing widely, when they encountered Neanderthal populations in the Middle East or western Asia. (2) Denisovan-modern human interbreeding: modern Melanesian (Papua New Guinea and Pacific Islander) populations carry approximately 4 to 6% Denisovan-derived DNA; Aboriginal Australians also carry Denisovan DNA; this indicates a second interbreeding event between dispersing modern humans and Denisovan populations in Southeast Asia or Australasia. Both findings demonstrate that the emergence of modern Homo sapiens was not a clean replacement of archaic populations but involved multiple interbreeding events, and that some archaic hominin alleles persist in living humans (some Neanderthal-derived alleles affect immune function and metabolism in modern humans).



## References and Attributions [Series 4]

### Textual References (Books and External Sources)

1. Futuyma, D. J., & Kirkpatrick, M. (2017). *Evolution* (4th ed.). Sinauer Associates.
2. Johanson, D., & Wong, K. (2009). *Lucy's legacy: The quest for human origins*. Harmony Books.
3. Kimura, M. (1983). *The neutral theory of molecular evolution*. Cambridge University Press.
4. FAO (Food and Agriculture Organization of the United Nations). (2025). *Guidelines for sustainable agriculture*. FAO.

### Figures, Plates, Tables, and Boxes

1. Figure 4.1: Timeline of major plant evolution events Attribution: AI generated. Suggested OER search string: "plant evolution timeline bryophytes pteridophytes gymnosperms angiosperms major events OER".
2. Figure 4.2: Timeline of major vertebrate evolution events Attribution: AI generated. Suggested OER search string: "vertebrate evolution timeline jawless fish tetrapods amniote egg mammals adaptive radiation OER".
3. Figure 4.3: Hominin fossil record timeline Attribution: AI generated. Suggested OER search string: "hominin fossil record timeline brain size increase stone tools australopithecus homo species OER".
4. Box 4.1: Molecular evidence for human evolutionary relationships Attribution: AI generated. Suggested OER search string: "molecular evidence human evolution table mtDNA Neanderthal ancient DNA mitochondrial Eve OER box".



Course code: BIO 302

Course title: Population Biology and Evolution

# Series 5: Population Dynamics and Growth Factors

- **Part 5.1: Population Structure and Dynamics**
  - Sub Part 5.1.1: Population parameters and age structure
  - Sub Part 5.1.2: Population dispersion and sampling methods
  - Sub Part 5.1.3: Population genetics: allele frequency change over time
- **Part 5.2: Population Growth Models**
  - Sub Part 5.2.1: Exponential growth
  - Sub Part 5.2.2: Logistic growth and carrying capacity
  - Sub Part 5.2.3: Density-dependent and density-independent factors
- **Part 5.3: Intraspecific and Interspecific Interactions**
  - Sub Part 5.3.1: Competition and its evolutionary consequences
  - Sub Part 5.3.2: Predator-prey dynamics
  - Sub Part 5.3.3: Mutualism, parasitism, and coevolution
- **Part 5.4: Conservation Genetics and Applied Population Biology**
  - Sub Part 5.4.1: Small populations and extinction risk
  - Sub Part 5.4.2: Conservation genetics in practice
  - Sub Part 5.4.3: Sustainable use and population management



## Introduction

Population biology studies how populations grow, fluctuate, and interact, and how evolutionary forces change their genetic composition over time. These processes are directly relevant to wildlife conservation, pest management, fisheries, and human health. Understanding population dynamics connects the evolutionary mechanisms of earlier Series to the practical management of species and ecosystems.

This final Series integrates population ecology with population genetics, covering population parameters, growth models, species interactions, and the application of population biology principles to conservation. Nigerian examples are used throughout, linking the course to the biodiversity challenges facing West Africa.

## Series Learning Outcomes

Upon completing this Series, you should be able to:

- **SLO 5.1** describe the key parameters that characterise a population and explain how age structure influences population growth (Linked to Part 5.1),
- **SLO 5.2** describe exponential and logistic growth models and explain how density-dependent and density-independent factors regulate populations (Linked to Part 5.2),
- **SLO 5.3** describe competition, predation, and symbiotic interactions and explain their evolutionary consequences (Linked to Part 5.3),
- **SLO 5.4** explain the genetic risks facing small populations (Linked to Part 5.4),
- **SLO 5.5** describe conservation genetics approaches applicable to Nigerian species (Linked to Part 5.4), and
- **SLO 5.6** explain the principles of sustainable population use and wildlife management (Linked to Part 5.4).



## 5.1 Population Structure and Dynamics

### 5.1.1 Population parameters and age structure

A population is a group of individuals of the same species in the same area at the same time. Key parameters: population size (N); population density (N per unit area); birth rate (b); death rate (d); immigration rate; emigration rate; intrinsic rate of increase  $r = b \text{ minus } d$ . When  $r$  is positive the population grows; when  $r = 0$  it is stable; when  $r$  is negative it declines.

Age structure is the distribution of individuals among age classes. It is represented by an age pyramid. A broad-based pyramid (many young) indicates a growing population; a rectangular pyramid indicates a stable population; a narrow-based pyramid indicates a declining population. In wildlife management, age structure predicts future population trajectories and guides harvesting decisions. Sex ratio (proportion of males to females) also affects population growth; in polygynous species, fewer males are needed to maintain reproductive output.

Fill in the blank: The intrinsic rate of increase  $r$  equals birth rate minus \_\_\_\_\_ rate; when  $r$  is positive the population grows; a broad-based age pyramid with many young individuals indicates a \_\_\_\_\_ population.

### 5.1.2 Population dispersion and sampling methods

Population dispersion describes the spatial arrangement of individuals. Random: individuals distributed independently; rare in nature. Uniform: regular spacing from territorial competition; e.g. nesting birds. Clumped: individuals aggregated; the most common pattern; caused by resource patches, social behaviour, or clonal growth; e.g. savanna cattle at water points; colonial birds. Clumped dispersion is typical of most Nigerian wildlife species.

Population density is estimated by: direct count (census; feasible only for large conspicuous animals: elephants in aerial surveys); quadrat sampling (count individuals in randomly placed plots; used for plants and sessile invertebrates); line transect (count individuals within a strip along a line; used for birds and large mammals in Nigerian national parks); mark-recapture



(Lincoln-Petersen method:  $N = n_1 \times n_2 / m$ ; used for mobile animals; requires marked individuals to mix randomly with the unmarked population).

Fill in the blank: The Lincoln-Petersen mark-recapture estimate is  $N = n_1 \times n_2 / m$ , where  $n_1$  is the first sample size,  $n_2$  is the second sample size, and  $m$  is the number of \_\_\_\_\_ individuals recaptured in the second sample.

### 5.1.3 Population genetics: allele frequency change over time

Population genetics tracks how allele frequencies change over generations. The four mechanisms of change are: natural selection (directional, stabilising, disruptive, balancing; covered in Series 2); genetic drift (random change; strongest in small populations); mutation (ultimate source of new alleles; slow); and gene flow (transfer of alleles between populations by migration). These mechanisms were formalised in the Modern Evolutionary Synthesis and form the mathematical core of evolutionary theory.

Effective population size ( $N_e$ ) is the size of an idealised randomly mating population that would experience the same rate of genetic drift as the actual population; it is typically much smaller than the census population size  $N$  because of unequal sex ratios, variance in reproductive success, and fluctuating population sizes. Low  $N_e$  means faster drift and faster loss of heterozygosity. For the Cross River gorilla ( $N$  approximately 250),  $N_e$  is probably below 100, making genetic drift a serious threat to its long-term genetic health.

Fill in the blank: \_\_\_\_\_ population size ( $N_e$ ) is the size of an idealised randomly mating population that experiences the same rate of drift as the actual population; it is usually much smaller than census  $N$  because of unequal sex ratios and variance in reproductive success.



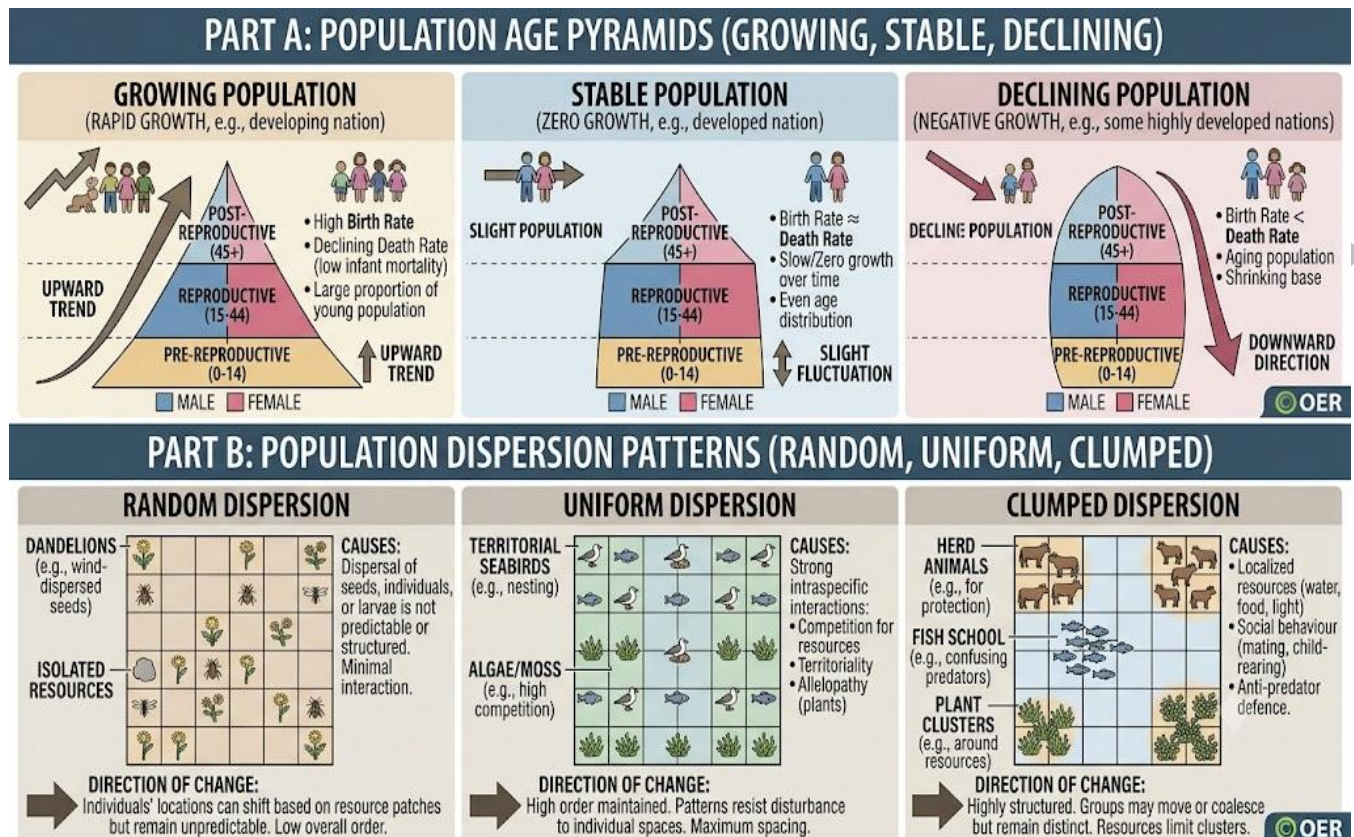


Figure 5.1: Diagrams of age pyramids (growing, stable, declining) and population dispersion patterns

### Pilot questions 5.1

- Define a population and state six key population parameters.
- Explain how age structure predicts future population growth.
- Describe the three patterns of population dispersion with one example each.
- Explain the mark-recapture method and state one assumption it requires.
- Define effective population size and explain why it matters for conservation.

## 5.2 Population Growth Models

### 5.2.1 Exponential growth

Exponential growth occurs when resources are unlimited; every individual reproduces at the same rate regardless of population size. The equation is  $dN/dt = rN$  ( $N$  = population size;  $r$  =



intrinsic rate of increase;  $t$  = time). This produces a J-shaped curve that accelerates continuously. It is observed in: newly colonising populations; populations recovering after a crash; invasive species in a new range; and bacteria in culture media.

Exponential growth is rarely sustained because resources are finite. The doubling time is  $t = 0.693 / r$ . Examples in Nigeria: water hyacinth (*Eichhornia crassipes*) showed near-exponential spread when first introduced into Nigerian waterways; locust swarms (*Schistocerca gregaria*) exhibit near-exponential population growth during outbreak conditions when food is abundant, then crash when vegetation is exhausted. Understanding exponential growth is critical for predicting pest outbreaks and planning early intervention.

Fill in the blank: Exponential growth is described by  $dN/dt = rN$  and produces a \_\_\_\_\_ - shaped curve; it occurs when resources are unlimited and each individual reproduces at the same rate regardless of population density.

### 5.2.2 Logistic growth and carrying capacity

Logistic growth models resource-limited population growth. The equation is  $dN/dt = rN[(K - N)/K]$ , where  $K$  is the carrying capacity (the maximum population size the environment can sustainably support). When  $N$  is small, growth is nearly exponential; as  $N$  approaches  $K$  the growth rate slows and stops. This produces an S-shaped (sigmoidal) curve. The growth rate is maximum at  $N = K/2$ ; this is the point of maximum sustainable yield in fisheries and wildlife management.

The carrying capacity  $K$  is set by the most limiting resource: food, water, nesting sites, or territory. It is not fixed; it changes with habitat conditions. Overshoot (when  $N$  briefly exceeds  $K$ ) leads to resource depletion and population crash. In Yankari National Park, the elephant population is managed to prevent overshoot of the carrying capacity set by dry-season water and vegetation availability; exceeding  $K$  causes degradation that lowers  $K$  further, producing a downward spiral.



Fill in the blank: In the logistic growth model, the carrying capacity  $K$  is the maximum population the environment can sustainably support; population growth rate is maximum at  $N = \underline{\hspace{2cm}}$ , which is the basis for the maximum sustainable yield concept.

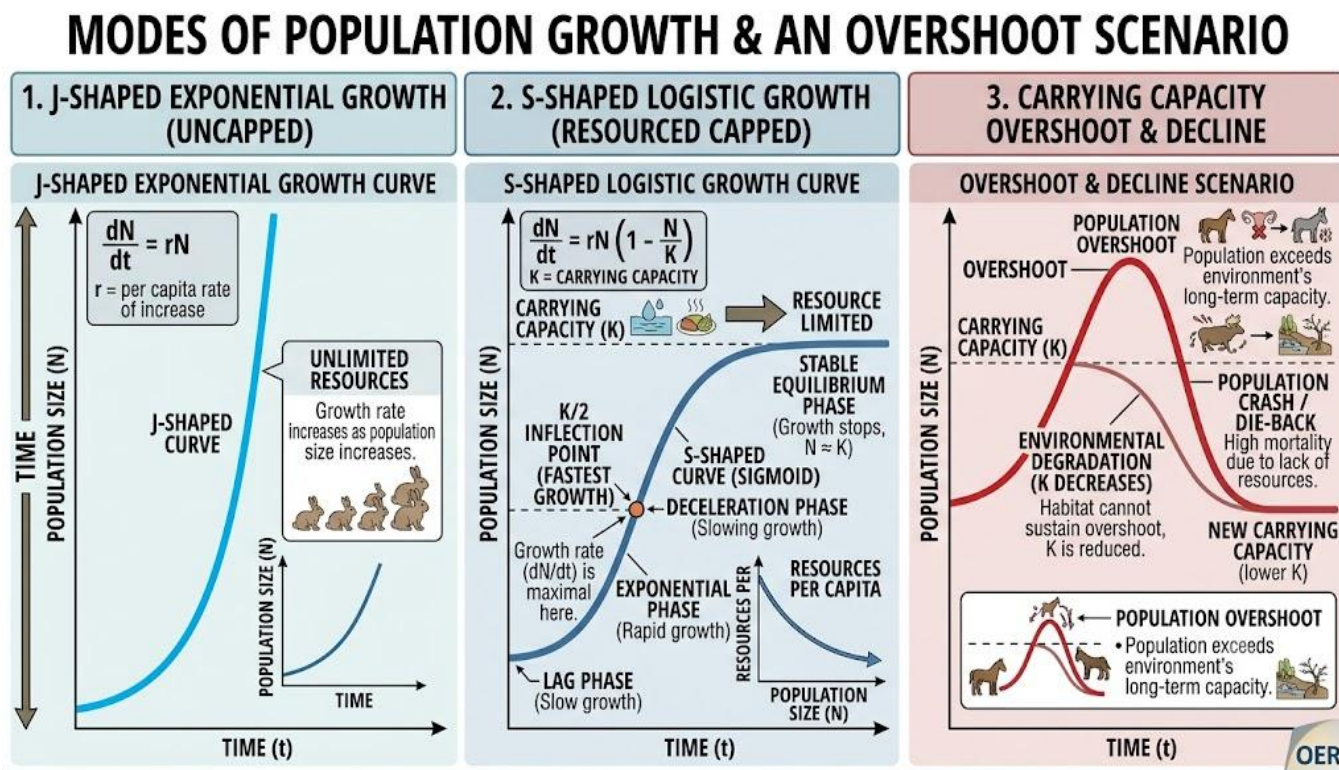


Figure 5.2: Exponential and logistic growth curves

### 5.2.3 Density-dependent and density-independent factors

Density-dependent factors: their effect on per capita growth rate intensifies as population density increases; they act as negative feedback mechanisms that slow growth as  $N$  approaches  $K$ .

Examples: food competition (less food per individual at high density); disease transmission (spreads faster in dense populations); predation (predators concentrate where prey is abundant); intraspecific competition for territory. These are the regulators in the logistic model.

Density-independent factors affect the population regardless of its size. They are typically abiotic: drought, fire, flood, extreme cold, or pollution. A catastrophic drought kills a proportion of a population whether it is large or small. In the Nigerian Sahel, drought-years cause livestock and wildlife population crashes independently of pre-drought density. Real populations are



regulated by both types; density-dependent factors dominate near  $K$ , while density-independent factors can override them during extreme events.

Fill in the blank: \_\_\_\_\_-dependent factors such as food competition and disease intensify in effect as population density rises; they act as negative feedback, slowing population growth as  $N$  approaches  $K$  in the logistic model.

### Pilot questions 5.2

- Describe exponential growth and state two conditions under which it occurs.
- Describe logistic growth and explain the significance of  $K$ .
- Distinguish between density-dependent and density-independent factors with one example each.
- Explain what happens when a population overshoots its carrying capacity.
- Explain why maximum sustainable yield occurs at  $N = K/2$ .

## 5.3 Intraspecific and Interspecific Interactions

### 5.3.1 Competition and its evolutionary consequences

Intraspecific competition: between individuals of the same species; always strong because all individuals have identical resource requirements; regulates population density (a density-dependent factor). Interspecific competition: between different species using the same limited resource; both species are harmed. The competitive exclusion principle (Gause's Law): two species with identical niches cannot coexist indefinitely; the inferior competitor will be excluded or displaced.

Evolutionary consequence: character displacement. When two competing species co-occur, selection favours individuals that use different resources from the competitor; over generations, the two species diverge in their resource-use characters (e.g. beak size in competing bird species becomes more different in sympatry than in allopatry). Resource partitioning: competing species in a community divide resources by time, space, or food type, reducing competition and allowing



coexistence. In Nigerian savanna, multiple antelope species partition the vegetation resource by feeding at different heights and on different plant parts.

Fill in the blank: \_\_\_\_\_ displacement is the evolutionary divergence of competing species in resource-use characters when they co-occur; selection favours individuals that differ from the competitor, reducing overlap in the realised niches of the two species.

### 5.3.2 Predator-prey dynamics

Predator-prey interactions regulate both populations. The Lotka-Volterra model predicts coupled oscillations: prey increases → predators increase → predation reduces prey → predators decline → prey recovers. These cycles are out of phase: prey peaks slightly before predator peaks. The model assumes: prey grows exponentially without predators; predator growth depends only on prey availability; both populations interact as their only limiting factor.

In practice, cycles are modified by: prey refuges (prey can hide at low densities, preventing extinction); alternative prey (predators switch to other food when one prey is scarce); predator satiation at high prey densities. In Nigerian savanna, kob (*Kobus kob*) population size fluctuates partly in response to lion and leopard predation pressure, though habitat change and human hunting complicate the dynamics. Predation also drives the evolution of prey antipredator defences (camouflage, warning colouration, thorns, toxic chemistry).

Fill in the blank: In the Lotka-Volterra predator-prey model, prey and predator populations show coupled \_\_\_\_\_; prey peaks slightly before predator peaks because predator numbers can only increase after prey abundance has risen.



## LOTKA-VOLTERRA PREDATOR-PREY OSCILLATION GRAPH AND NIGERIAN SAVANNA INTERACTION

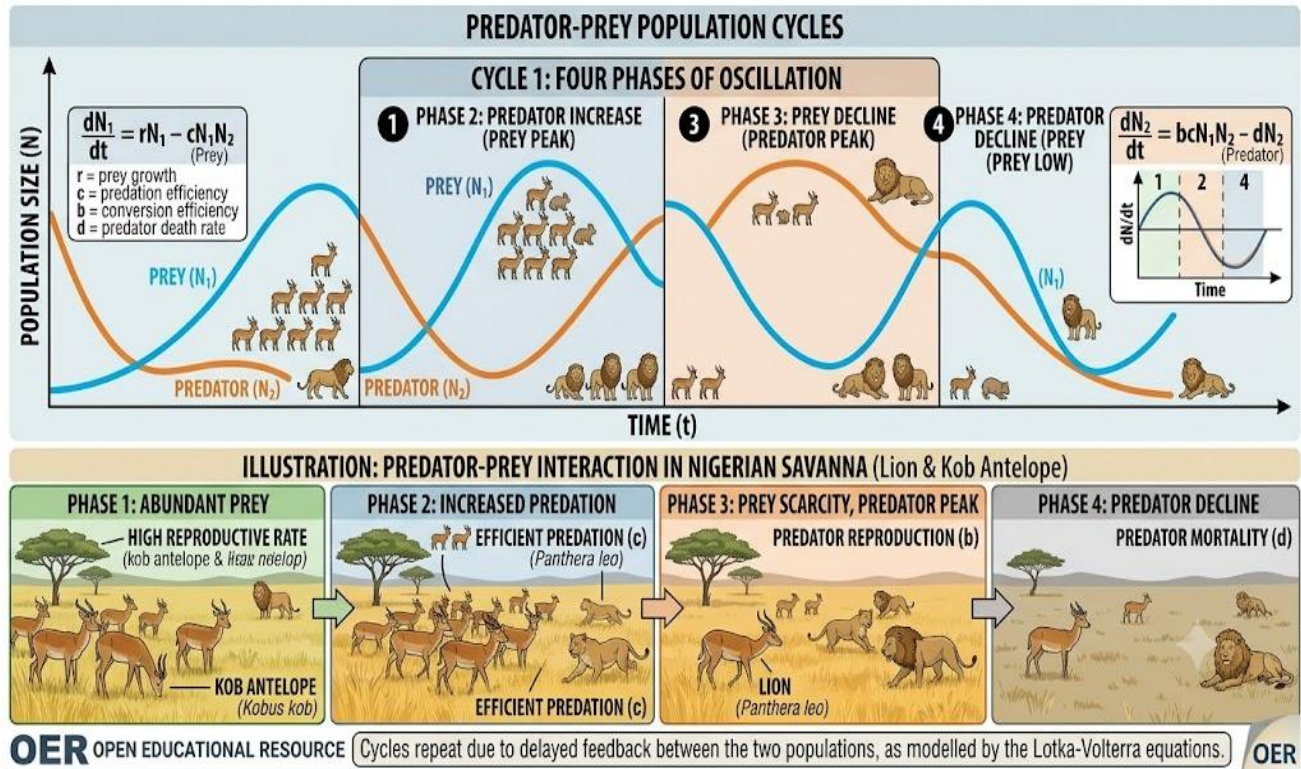


Figure 5.3: Lotka-Volterra predator-prey cycle graph and Nigerian savanna example

### 5.3.3 Mutualism, parasitism, and coevolution

**Mutualism:** both species benefit; often obligate (one or both partners cannot survive without the other). **Evolutionary consequence:** tight coevolution produces highly specialised partners that are increasingly dependent on each other. **Nigerian examples:** Rhizobium bacteria and cowpea (*Vigna unguiculata*) root nodules (bacteria fix  $N_2$ ; plant provides carbohydrates); mycorrhizal fungi and forest trees (fungi extend effective root surface; trees provide photosynthate); oxpecker birds and cattle.

**Parasitism:** the parasite benefits at the host's expense; the host is harmed but not immediately killed. Parasites evolve higher virulence when transmission is easy (dense host populations) and lower virulence when transmission is difficult. Hosts evolve resistance; parasites evolve to overcome it: a continuous coevolutionary arms race. **Nigerian examples:** Plasmodium falciparum (malaria parasite) and Anopheles gambiae (mosquito vector); Striga hermonthica (witch weed)



on sorghum and maize; cattle trypanosomiasis (sleeping sickness) caused by *Trypanosoma* and transmitted by tsetse flies (*Glossina*) in the Middle Belt.

Fill in the blank: *Rhizobium* bacteria and cowpea root nodules are an example of \_\_\_\_\_; the bacteria fix atmospheric  $N_2$  into ammonia that the plant uses; the plant provides carbohydrates to the bacteria in return.

### Pilot questions 5.3

1. State the competitive exclusion principle and explain character displacement.
2. Describe the Lotka-Volterra predator-prey model and the resulting population cycles.
3. Explain how parasitism drives coevolution between host and parasite.
4. Explain resource partitioning and give a Nigerian example.
5. Give two Nigerian examples of mutualism.

## 5.4 Conservation Genetics and Applied Population Biology

### 5.4.1 Small populations and extinction risk

Small populations face genetic and demographic risks that increase extinction probability.

Genetic risks: (1) Inbreeding depression: mating between close relatives increases homozygosity, exposing deleterious recessive alleles; reduces survival and reproductive success; documented in captive and wild populations of large mammals. (2) Loss of heterozygosity through genetic drift: small populations lose alleles by chance faster than new alleles are introduced by mutation; this reduces adaptive potential.

Demographic risks: (1) demographic stochasticity (random variation in birth and death rates has a larger effect in small populations; e.g. by chance all offspring in one year may be of one sex, reducing reproduction); (2) environmental stochasticity (random variation in environmental conditions; a single drought or disease outbreak can eliminate a small population entirely). The minimum viable population (MVP) concept estimates the minimum  $N$  needed for a population to



have a high probability of persisting for a defined time period; typically 50 to 500 individuals for demographic and genetic viability.

Fill in the blank: \_\_\_\_\_ depression is the reduced fitness resulting from mating between close relatives; it exposes deleterious recessive alleles by increasing homozygosity and is a major genetic risk in small and isolated wildlife populations.

### **5.4.2 Conservation genetics in practice**

Conservation genetics applies population genetic tools to the management of threatened species. Key tools: microsatellite and SNP markers to measure genetic diversity (heterozygosity, allelic richness) and population structure ( $F_{ST}$ ) in wild populations; mitochondrial DNA to trace maternal lineage diversity and population boundaries; landscape genetics (how landscape features affect gene flow); whole-genome sequencing of threatened species (e.g. Cross River gorilla) to detect inbreeding, identify distinct management units, and prioritise populations for protection.

Translocation and genetic rescue: moving individuals between isolated populations to restore gene flow and counteract inbreeding depression; well-documented for Florida panthers (where translocating Texas pumas increased fitness measurably). For Nigerian populations: genetic studies of the Cross River gorilla show that the approximately 10 forest fragment subpopulations have very low  $F_{ST}$ , suggesting recent connectivity, but corridor loss risks rapid isolation; genetic monitoring guides corridor protection priorities. Ex-situ conservation (zoos, seed banks) must manage pedigrees to minimise inbreeding.

Fill in the blank: \_\_\_\_\_ rescue is the improvement of fitness in a small inbred population by introducing individuals from another population, restoring gene flow and reducing inbreeding depression; it has been documented in Florida panthers and is applicable to fragmented Nigerian wildlife populations.

### **5.4.3 Sustainable use and population management**



Sustainable use means harvesting a population at a rate that does not exceed its renewal rate, maintaining the population and its habitat for future generations. The maximum sustainable yield (MSY) in the logistic model occurs at  $N = K/2$ , where population growth rate  $dN/dt$  is maximum; harvesting exactly the production at this point removes as many individuals as the population adds each generation. Harvesting above MSY drives the population below  $K/2$  and reduces the growth rate, potentially causing collapse.

Nigerian applications: fisheries management in Kainji Lake and coastal waters uses closed seasons and minimum mesh sizes to prevent overharvesting; the national shrimp fishery of the Niger Delta is managed under seasonal closures. Wildlife management in national parks uses population monitoring to set safe offtake levels for community hunts outside park boundaries; ivory and bushmeat trade regulations aim to keep elephant and large mammal harvests below MSY. Effective sustainable use requires population monitoring, strong governance, and community involvement.

Fill in the blank: The maximum sustainable yield in the logistic growth model occurs at  $N = K/2$ ; harvesting above the MSY drives the population \_\_\_\_\_  $K/2$  and reduces the intrinsic growth rate, potentially leading to population collapse.

| <u>Concept</u>            | <u>Equation / Definition</u>                                        | <u>Practical Application</u>                                                                     |
|---------------------------|---------------------------------------------------------------------|--------------------------------------------------------------------------------------------------|
| <u>Exponential Growth</u> | $N_t = N_0 e^{rt}$                                                  | Models population growth without limits; useful for microbes or invasive species in early stages |
| <u>Logistic Growth</u>    | $N_t = \frac{K}{1 + K - N_0 N_0 e^{-rt}}$                           | Describes growth with carrying capacity; predicts stabilization of populations                   |
| <u>Carrying Capacity</u>  | $K$ = maximum sustainable population size                           | Used in wildlife management and conservation to avoid overpopulation                             |
| <u>Sustainable Yield</u>  | Maximum harvest rate without reducing population size               | Guides fisheries and forestry management to balance use and regeneration                         |
| <u>Mark-Recapture</u>     | $N = M \times CR$ ( $M$ = marked, $C$ = captured, $R$ = recaptured) | Estimates population size of mobile species like fish or mammals                                 |



|                                  |                                    |                                                                            |
|----------------------------------|------------------------------------|----------------------------------------------------------------------------|
| <a href="#">Allele Frequency</a> | $p+q=1$ (Hardy-Weinberg principle) | Tracks genetic variation in populations; baseline for evolutionary studies |
|----------------------------------|------------------------------------|----------------------------------------------------------------------------|

Box 5.1: Summary of key population biology equations and concepts

#### Pilot questions 5.4

1. Define inbreeding depression and explain why it threatens small wildlife populations.
2. Explain the minimum viable population concept.
3. Explain genetic rescue and give one documented example.
4. Explain how maximum sustainable yield is derived from the logistic growth model.
5. Describe two population management tools used in Nigerian fisheries or wildlife.

### Series Summary

This Series examined how populations grow, what limits that growth, and how species interact with one another. A population is described by its size, density, birth rate, death rate, and intrinsic rate of increase ( $r = b$  minus  $d$ ); age pyramids reveal whether a population is growing, stable, or declining. Population growth follows two main models: exponential growth ( $dN/dt = rN$ ) produces a J-shaped curve when resources are unlimited, while logistic growth produces an S-shaped curve as the population approaches its carrying capacity ( $K$ ). Growth is regulated by density-dependent factors such as food, disease, and predation, which intensify as numbers rise, and by density-independent factors such as drought and fire, which act regardless of population size.

Species interactions further shape population dynamics. Intraspecific competition regulates density; interspecific competition can lead to competitive exclusion, character displacement, or resource partitioning. Predator-prey relationships produce coupled population cycles described by the Lotka-Volterra equations, with prey numbers peaking before predators. Mutualism benefits both partners (Rhizobium and cowpea; mycorrhizal fungi), while parasitism benefits the parasite at the host's expense, driving coevolutionary arms races (malaria, Striga,



trypanosomiasis). Small populations face inbreeding depression and loss of genetic diversity; a minimum viable population of roughly 50 to 500 individuals is needed for long-term survival. Sustainable harvesting of wild populations is guided by the principle of maximum sustainable yield, achieved when the population is maintained at half the carrying capacity ( $N = K/2$ ).

## Glossary of Terms

1. **Age structure:** the distribution of individuals among age classes in a population; a broad base indicates a growing population; a narrow base indicates a declining population.
2. **Carrying capacity (K):** the maximum population size an environment can sustainably support given available resources; the upper asymptote of logistic growth.
3. **Character displacement:** the evolutionary divergence of competing species in resource-use traits when they co-occur; reduces niche overlap and allows coexistence.
4. **Competitive exclusion principle (Gause's Law):** two species with identical niches cannot coexist indefinitely; the inferior competitor will be excluded or forced to shift its resource use.
5. **Demographic stochasticity:** random variation in individual birth and death events; its effect on population growth is proportionally larger in small populations.
6. **Density-dependent factor:** a population regulating factor whose per capita effect intensifies as population density increases; e.g. food competition, predation, disease.
7. **Density-independent factor:** a factor that affects a population regardless of its density; typically abiotic; e.g. drought, fire, flood.
8. **Effective population size ( $N_e$ ):** the size of an ideal randomly mating population that experiences the same rate of genetic drift as the actual population; usually much smaller than census  $N$ .
9. **Environmental stochasticity:** random variation in environmental conditions from year to year; can extinguish small populations through a single catastrophic event.



10. **Exponential growth:** population growth when resources are unlimited; described by  $dN/dt = rN$ ; produces a J-shaped curve.
11. **Genetic rescue:** the improvement of fitness in an inbred small population by introducing individuals from another population, restoring gene flow and heterozygosity.
12. **Inbreeding depression:** reduced fitness (survival, reproduction, health) resulting from matings between close relatives; caused by increased homozygosity that exposes deleterious recessive alleles.
13. **Intraspecific competition:** competition between individuals of the same species; intensity increases with population density; a key density-dependent regulating factor.
14. **Logistic growth:** population growth that decelerates as  $N$  approaches  $K$ ; described by  $dN/dt = rN[(K - N)/K]$ ; produces an S-shaped (sigmoidal) curve.
15. **Lotka-Volterra model:** a mathematical model of predator-prey interactions predicting coupled oscillations in which prey peaks slightly before predator peaks.
16. **Mark-recapture (Lincoln-Petersen):** a method for estimating population size:  $N = n_1 \times n_2 / m$ ; requires marked individuals to mix randomly with the unmarked population.
17. **Maximum sustainable yield (MSY):** the maximum harvest rate that can be maintained indefinitely without causing population decline; in logistic growth, occurs at  $N = K/2$ .
18. **Minimum viable population (MVP):** the minimum population size with a high probability of persisting for a defined time period; typically estimated at 50 to 500 individuals for demographic and genetic viability.
19. **Overshoot:** a situation where a population temporarily exceeds its carrying capacity  $K$ , followed by resource depletion and population decline or crash.
20. **Population density:** the number of individuals per unit area or volume; used instead of absolute size for comparing populations across different habitat areas.



21. **Resource partitioning:** the division of limited resources among competing species by differences in time of use, space, or food type; allows coexistence by reducing interspecific competition.
22. **Translocation:** the deliberate movement of individuals from one population to another to restore gene flow, reestablish a locally extinct population, or supplement a declining population.

### Concept Check Questions [Series 5]

#### Objective Questions

1. The intrinsic rate of increase  $r$  equals birth rate minus \_\_\_\_\_ rate; when  $r$  is positive the population is growing. (Linked to SLO 5.1)
2. Exponential growth produces a \_\_\_\_\_-shaped curve and is described by  $dN/dt = rN$ ; it occurs when resources are unlimited. (Linked to SLO 5.2)
3. In the logistic growth model, population growth rate is maximum at  $N = \_\_\_\_\_\_$ , which is the basis of the maximum sustainable yield concept. (Linked to SLO 5.2)
4. \_\_\_\_\_ depression is the reduced fitness caused by mating between close relatives; it increases homozygosity and exposes deleterious recessive alleles. (Linked to SLO 5.4)
5. Rhizobium bacteria and cowpea root nodules are an example of \_\_\_\_\_; both partners benefit from the association. (Linked to SLO 5.3)

#### Short-Answer Questions

- Distinguish between density-dependent and density-independent population factors. (Linked to SLO 5.2)
- Describe the Lotka-Volterra predator-prey model and state the resulting population pattern. (Linked to SLO 5.3)



- Define inbreeding depression and explain why it threatens small populations. (Linked to SLO 5.4)
- Define maximum sustainable yield and state at what population size it occurs in the logistic model. (Linked to SLO 5.6)
- Distinguish between exponential and logistic growth. (Linked to SLO 5.2)

### Long-Answer Questions

1. Describe the key parameters of a population; explain exponential and logistic growth models; and distinguish between density-dependent and density-independent regulatory factors. (Linked to SLOs 5.1, 5.2)
2. Describe intraspecific competition, interspecific competition, and predator-prey dynamics; explain character displacement; and give examples of mutualism and parasitism in Nigeria. (Linked to SLO 5.3)
3. Explain the genetic and demographic risks facing small populations; describe conservation genetics approaches; and explain sustainable use and MSY. (Linked to SLOs 5.4, 5.5, 5.6)

### Answers to Concept Check Questions [Series 5]

#### Objective Questions

6. Death.
7. J.
8.  $K/2$ .
9. Inbreeding.
10. Mutualism.



### Short-Answer Questions

11. Density-dependent: effect intensifies as density rises; negative feedback near  $K$ ; e.g. food competition. Density-independent: effect the same regardless of density; typically abiotic; e.g. drought killing a fixed proportion of a livestock population.
12. As prey increases, predators increase; predation then reduces prey; fewer prey reduces predator numbers; prey recovers. The result is coupled oscillations with prey peaks slightly before predator peaks.
13. Inbreeding depression is reduced fitness (survival, reproduction) from mating between close relatives; increased homozygosity exposes deleterious recessive alleles. Small isolated populations mate between relatives by necessity, reducing fitness and increasing extinction risk.
14. MSY is the maximum harvest rate that can be sustained indefinitely without population decline. In the logistic model it occurs at  $N = K/2$ , where the population growth rate  $dN/dt$  is at its maximum.
15. Exponential growth: unlimited resources;  $dN/dt = rN$ ; J-shaped curve; accelerates indefinitely. Logistic growth: resource-limited;  $dN/dt = rN[(K-N)/K]$ ; S-shaped curve; levels off at carrying capacity  $K$ .

### Long-Answer Questions

1. Population: group of same species in same area at same time. Parameters:  $N$  (size), density ( $N$  per unit area),  $b$  (birth rate),  $d$  (death rate),  $r = b$  minus  $d$ , immigration, emigration. Age structure: broad base = growing; rectangular = stable; narrow base = declining. Dispersion: random (rare); uniform (territorial competition); clumped (most common; resource patches or social behaviour). Mark-recapture:  $N = n_1 \times n_2 / m$ . Exponential growth:  $dN/dt = rN$ ; J-shaped; occurs under unlimited resources; rare in nature. Logistic growth:  $dN/dt = rN[(K-N)/K]$ ; S-shaped; growth slows as  $N$  approaches  $K$ ; levels off at  $K$ ; maximum growth at  $N = K/2$ . Density-dependent: food competition,



predation, disease; intensify with density; negative feedback near  $K$ . Density-independent: drought, fire, flood; affect population regardless of size; can override density-dependent regulation during extreme events.

2. Intraspecific competition: same species; always intense (identical resource needs); density-dependent regulator. Interspecific competition: different species sharing a resource; both harmed; competitive exclusion (Gause): identical niches cannot coexist indefinitely; inferior competitor excluded or shifts niche. Character displacement: co-occurring competitors diverge in resource-use traits by selection; allows coexistence; e.g. sympatric bird species with diverged beak sizes. Resource partitioning: competing species divide resources by time, space, or food type; Nigerian savanna antelope partition vegetation by feeding height. Predator-prey (Lotka-Volterra): prey increases providing food; predator population grows; predation reduces prey; predators decline; prey recovers; coupled oscillations; prey peaks slightly before predator. Mutualism (both benefit): *Rhizobium* and cowpea (N fixation + carbohydrates); mycorrhizal fungi and forest trees. Parasitism (parasite benefits; host harmed): *Plasmodium falciparum* causing malaria; *Striga hermonthica* (witch weed) on sorghum; *Trypanosoma* causing trypanosomiasis via tsetse flies in the Nigerian Middle Belt.
3. Genetic risks: inbreeding depression (close relatives mate; homozygosity rises; deleterious recessives exposed; reduced survival and reproduction); loss of heterozygosity by drift (small  $N_e$  loses alleles rapidly; reduces adaptive potential). Demographic risks: demographic stochasticity (random birth/death events destabilise small populations; e.g. all offspring one sex by chance); environmental stochasticity (single drought or disease can eliminate a small population). MVP: minimum  $N$  for high probability of persistence; approximately 50-500 individuals. Conservation genetics: microsatellite and SNP markers measure heterozygosity and  $F_{ST}$ ; mtDNA traces maternal lineages; landscape genetics maps gene flow barriers; whole-genome sequencing of Cross River gorilla (~250 individuals) identifies inbreeding and management units; translocation and genetic rescue (introduce individuals to restore gene flow; documented in Florida panther). Sustainable use: harvest at or below  $MSY$  ( $N = K/2$ ); Kainji Lake fisheries (closed seasons, mesh-size limits); Niger Delta shrimp (seasonal closures); wildlife offtake managed in national park buffer zones.



## Answers to Pilot Questions [Series 5]

### Part 5.1

6. A population is a group of individuals of the same species in the same geographic area at the same time, potentially interbreeding. Six parameters: (1)  $N$  (population size: total number of individuals); (2) population density ( $N$  per unit area or volume); (3) birth rate  $b$  (births per individual per unit time); (4) death rate  $d$  (deaths per individual per unit time); (5) immigration rate (individuals entering per unit time); (6) emigration rate (individuals leaving per unit time). The intrinsic rate of increase  $r = b$  minus  $d$  determines the direction of population change.
7. A broad-based age pyramid has many young individuals who will soon reach reproductive age, so birth rates will rise even if current conditions remain unchanged, producing rapid future growth. A rectangular pyramid indicates current births roughly equal current deaths (stable population). A narrow-based pyramid has few young relative to adults, so fewer individuals will enter the reproductive age class in the future; as older cohorts die without adequate replacement, the population declines.
8. Random: individuals are distributed independently with no attraction or repulsion; rare in nature; e.g. wind-dispersed seeds in open habitat. Uniform: individuals are regularly spaced due to strong intraspecific competition for territory or space; e.g. nesting colonies of weaver birds. Clumped: individuals aggregate in groups; the most common pattern; caused by resource patches, social behaviour, or clonal reproduction; e.g. cattle clustering around water points in dry-season savanna.
9. Mark-recapture: (1) capture a first sample ( $n_1$ ), mark each individual, and release; (2) after mixing, capture a second sample ( $n_2$ ) and count how many are marked ( $m$ ); (3) estimate  $N = n_1 \times n_2 / m$ . Key assumption: marked individuals must mix randomly with the unmarked population before the second sample is taken, so the proportion of marked



individuals in the second sample accurately reflects their proportion in the whole population.

10. Effective population size ( $N_e$ ) is the size of an idealised randomly mating population that experiences the same rate of genetic drift as the actual population; it is usually much smaller than census  $N$  because of unequal sex ratios (one breeding male and many females reduces  $N_e$ ), variance in reproductive success (a few individuals produce most offspring), and fluctuating  $N$  over time. For conservation: low  $N_e$  accelerates loss of heterozygosity and alleles by drift, reducing adaptive potential and increasing inbreeding depression; the Cross River gorilla ( $N$  approximately 250) likely has  $N_e$  below 100, making genetic monitoring and corridor protection critical.

## Part 5.2

11. Exponential growth is population growth at a constant per capita rate regardless of population size, described by  $dN/dt = rN$ ; it produces a J-shaped curve that accelerates continuously. Two conditions: (1) unlimited resources (food, water, space; no resource competition); (2) no predation, disease, or other density-dependent limits on survival or reproduction. It occurs in newly colonising populations, populations recovering from a crash, and invasive species that have escaped their natural enemies.
12. Logistic growth is resource-limited population growth described by  $dN/dt = rN[(K-N)/K]$ ; as  $N$  rises toward  $K$  the term  $(K-N)/K$  approaches zero, slowing growth to zero at  $N = K$ .  $K$  (carrying capacity) is the maximum population the environment can sustainably support, set by the most limiting resource. It is significant for management: it sets the upper sustainable limit for any population; overharvesting a population above  $MSY$  reduces  $K$ ; habitat degradation reduces  $K$ ; improving habitat increases  $K$ .
13. Density-dependent: the per capita effect intensifies as population density increases; they act as negative feedback reducing  $r$  as  $N$  rises; examples: food competition (at high density, less food per individual reduces reproductive rates and increases starvation mortality); disease transmission (density increases contact rates, spreading pathogens faster). Density-independent: affect a fixed proportion regardless of density; typically



abiotic catastrophes; example: the Sahelian droughts of 1972-74 and 1983-84 killed similar proportions of livestock and wildlife populations regardless of whether those populations were large or small.

14. When  $N$  exceeds  $K$ , the  $(K-N)/K$  term becomes negative, meaning  $dN/dt$  is negative: the population declines. Resources have been depleted below the level needed to sustain the population; birth rates fall and death rates rise above replacement. If resources are slow to recover, the population can crash well below  $K$ . Severe overshoot can permanently degrade habitat (overgrazing, soil compaction), lowering  $K$  itself and setting a downward spiral where  $K$  falls further below  $N$  in successive seasons.
15. In the logistic model, the growth rate  $dN/dt = rN[(K-N)/K]$  is a quadratic function of  $N$ ; it equals zero at  $N = 0$  and  $N = K$ , and reaches its maximum at the midpoint  $N = K/2$ . At  $N = K/2$  the population adds the most new individuals per unit time, so any harvest that removes exactly that production can be sustained indefinitely without depleting the population below  $K/2$ . Harvesting above  $MSY$  removes more individuals than the population produces at that density;  $N$  falls below  $K/2$ ; growth rate decreases further; continued overharvesting leads to collapse.

### Part 5.3

1. Competitive exclusion (Gause's Law): two species with identical niches cannot coexist indefinitely in the same community; the superior competitor excludes the inferior one unless the inferior species shifts its resource use or is kept below competitive exclusion levels by predation or disturbance. Character displacement: when two competing species are sympatric (co-occur), selection favours individuals that use resources less similar to those used by the competitor; over generations both species diverge in their resource-use traits (e.g. beak size in sympatric birds becomes more different than in allopatric populations of the same species); this divergence reduces niche overlap and allows stable coexistence.
2. The Lotka-Volterra model describes coupled dynamics of one predator and one prey species. When prey is abundant, predators have plentiful food and increase; rising



predation reduces prey numbers; with fewer prey, predators starve and decline; reduced predation pressure allows prey to recover; the cycle repeats. The resulting pattern is coupled sinusoidal oscillations in both populations, with prey peaks occurring slightly before predator peaks. The model assumes: prey grows exponentially without predators; predator growth depends only on prey consumption; interactions are the only limiting factors for both populations.

3. In parasitism, the parasite benefits by extracting resources from the host; the host evolves immune and behavioural resistance; the parasite then evolves mechanisms to overcome host resistance; this generates a continuous coevolutionary arms race. High host resistance selects for more virulent parasites; high parasite virulence selects for stronger host resistance; neither side wins permanently. In dense host populations, highly virulent strains spread easily and are favoured; in sparse host populations, less virulent strains that keep the host alive for longer are favoured.
4. Resource partitioning occurs when competing species divide a shared limiting resource by exploiting it at different times, in different microhabitats, or by consuming different food types or sizes; this reduces effective niche overlap below the level that would cause competitive exclusion and allows coexistence. Nigerian example: in the guinea savanna of the Middle Belt, multiple antelope species (kob, topi, roan, waterbuck) coexist by partitioning vegetation: kob feed on short grass in open areas; roan prefer taller grass near woodland edges; waterbuck stay close to permanent water and eat coarser vegetation; this division reduces direct competition for any single resource type.
5. Two Nigerian mutualism examples: (1) Rhizobium bacteria and cowpea (*Vigna unguiculata*): the bacteria colonise root nodules of cowpea plants, using the enzyme nitrogenase to convert atmospheric  $N_2$  into ammonia that the plant incorporates into amino acids and proteins; the bacteria receive carbohydrates produced by photosynthesis; both partners gain directly from the association; this is critical for nitrogen economy in Nigerian smallholder farming systems where synthetic fertiliser is expensive. (2) Mycorrhizal fungi and forest trees in Nigerian rainforest: the fungal hyphae extend the effective surface area of tree roots many-fold, dramatically increasing the uptake of phosphorus and other minerals from the soil; the tree provides the fungus with



photosynthetically fixed carbon (sugars); the association is especially critical in the highly phosphorus-deficient laterite soils of the Niger Delta and rainforest zones.

#### Part 5.4

1. Inbreeding depression is the reduction in fitness (survival, reproductive success, immune function, developmental stability) that results from mating between close relatives. Close relatives share many alleles by common descent; their offspring have elevated homozygosity, increasing the probability that two copies of a rare deleterious recessive allele are present in the same individual and expressed phenotypically. Small isolated wildlife populations inevitably mate between relatives over successive generations because the pool of unrelated mates shrinks; fitness declines progressively with each generation of inbreeding, reducing birth rates, increasing juvenile mortality, and lowering disease resistance, all of which accelerate the probability of extinction.
2. The minimum viable population (MVP) is the minimum population size at which a population has a specified high probability (typically 95 to 99%) of persisting for a defined time period (typically 100 years). It is estimated by population viability analysis (PVA), which models the combined effects of demographic stochasticity, environmental stochasticity, and genetic deterioration (inbreeding depression and loss of heterozygosity). Genetic considerations suggest  $N_e$  of at least 50 to avoid rapid inbreeding and 500 for long-term evolutionary adaptability; demographic considerations typically require larger actual  $N$  to buffer against stochastic events. MVP estimates are used to set minimum reserve sizes and conservation targets.
3. Genetic rescue is the deliberate introduction of individuals from one population into another genetically impoverished population to restore gene flow, increase heterozygosity, and reduce inbreeding depression. The introduced individuals bring new alleles that mask the deleterious homozygous combinations, directly improving fitness in the recipient population. Documented example: the Florida panther (*Puma concolor coryi*) population in South Florida was reduced to fewer than 30 individuals by the 1990s and was severely inbred; eight female Texas pumas (*Puma concolor stanleyana*) were



translocated in 1995; within two generations, kinked tails and heart defects associated with inbreeding declined markedly, and population growth rate increased significantly, demonstrating measurable genetic rescue.

4. In the logistic growth model,  $dN/dt = rN[(K-N)/K]$  is maximised at  $N = K/2$ ; differentiating  $dN/dt$  with respect to  $N$  and setting the derivative to zero confirms that the growth rate is greatest (the population adds the most new individuals per unit time) at half the carrying capacity. At this point, the population production (new individuals added) exactly equals the harvest that can be removed without causing net population decline; any harvest of that amount or less is sustainable indefinitely. Harvesting above this level removes more individuals than are produced; the population falls below  $K/2$ ; at lower  $N$  the growth rate is also lower; the population can no longer replace the harvested individuals and collapses unless harvesting is reduced.
5. Two Nigerian population management tools: (1) Closed fishing seasons in Kainji Lake (and coastal Niger Delta waters): the Nigerian Institute for Oceanography and Marine Research (NIOMR) and state fisheries agencies impose seasonal bans on fishing during peak spawning periods (typically 2 to 6 weeks per year); this allows fish populations to reproduce before being harvested, keeping  $N$  above  $K/2$  and maintaining production near  $MSY$ ; minimum mesh sizes are also enforced to allow juveniles to escape nets and reach reproductive maturity before harvest. (2) Wildlife offtake management in national park buffer zones: in Yankari National Park buffer communities, Nigeria National Park Service conducts aerial and ground population surveys of large mammals (elephants, buffalo, roan antelope, kob) to estimate  $N$  and compare it against  $K$ ; where populations are at or below  $K/2$ , hunting is prohibited or restricted; where populations are above  $K/2$  (producing surplus above  $MSY$ ), limited community harvesting is permitted under annual quota systems.



## References and Attributions [Series 5]

### Textual References (Books and External Sources)

1. Krebs, C. J. (2009). Ecology: The experimental analysis of distribution and abundance (6th ed.). Benjamin Cummings.
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4. FAO (Food and Agriculture Organization of the United Nations). (2025). Guidelines for sustainable agriculture. FAO.

### Figures, Plates, Tables, and Boxes

1. Figure 5.1: Age pyramid diagrams and population dispersion patterns Attribution: AI generated. Suggested OER search string: "population age pyramid growing stable declining dispersion random uniform clumped diagram OER".
2. Figure 5.2: Exponential and logistic population growth curves Attribution: AI generated. Suggested OER search string: "exponential logistic population growth J-shaped S-shaped curve carrying capacity K/2 inflection overshoot OER".
3. Figure 5.3: Lotka-Volterra predator-prey cycle graph Attribution: AI generated. Suggested OER search string: "Lotka-Volterra predator prey cycle graph oscillations phases Nigerian savanna kob antelope OER".
4. Box 5.1: Summary of key population biology equations and concepts Attribution: AI generated. Suggested OER search string: "population biology equations table exponential logistic growth carrying capacity sustainable yield mark-recapture OER box".

