La-Net

BIO 303

BIOGEOGRAPHY AND SOIL BIOLOGY

Course code: BIO 303

Course title: Biogeography and Soil Biology

Course credit load: 2 Units

Series 1: Continental Drift and Gondwanaland

- **Part 1.1: The Theory of Continental Drift**
    - Sub Part 1.1.1: Wegener and the continental drift hypothesis
    - Sub Part 1.1.2: Evidence for continental drift
    - Sub Part 1.1.3: Plate tectonics as the mechanism
- **Part 1.2: Gondwanaland and Laurasia**
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- **Part 1.4: Continental Drift and Biogeography**
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Introduction

Biogeography asks why organisms are distributed where they are across the surface of the Earth. The answers require understanding not only the biology of the organisms themselves but also the geological history of the planet, since the positions of continents, the presence or absence of land connections, and the opening and closing of ocean barriers have profoundly shaped which species could reach which parts of the world and when. Continental drift is the foundational geological process that biogeographers must understand.

This Series introduces Alfred Wegener continental drift hypothesis, the evidence that supports it, and plate tectonics as the underlying mechanism; the history of the supercontinent Pangaea and its Gondwanaland and Laurasian components; the theory of land bridges and their role in facilitating or restricting faunal and floral exchange; and the key concepts of vicariance and dispersal through which continental drift shapes biogeographic distribution patterns.

Series Learning Outcomes

Upon completing this Series, you should be able to:

- **SLO 1.1** describe Wegener continental drift hypothesis, the evidence supporting it, and plate tectonics as its mechanism,
- **SLO 1.2** describe Pangaea, Gondwanaland, and Laurasia and explain the biogeographic consequences of their breakup,
- **SLO 1.3** explain the theory of land bridges and describe the biogeographic effects of major historical land bridges, and
- **SLO 1.4** distinguish vicariance from dispersal and explain how continental drift generates disjunct distribution patterns

1.1 The Theory of Continental Drift

1.1.1 Wegener and the continental drift hypothesis

Alfred Wegener, a German meteorologist and geophysicist, proposed the continental drift hypothesis in 1912, suggesting that the continents were once joined in a single supercontinent he called Pangaea (meaning "all land") and have since moved apart to their current positions; Wegener was struck by the remarkable fit of the opposing coastlines of South America and Africa, which suggested they had once been joined, and he compiled evidence from geology, palaeontology, palaeoclimatology, and biology to support his hypothesis.

Although Wegener assembled a compelling body of evidence, his hypothesis was initially rejected by most geologists because he could not propose a plausible physical mechanism capable of moving entire continents through solid oceanic crust; the missing mechanism was supplied decades later by the theory of plate tectonics, which provided the physical framework of seafloor spreading and convection in the mantle that drives continental movement; Wegener is now recognised as a visionary whose hypothesis, though initially controversial, fundamentally transformed understanding of Earth history.

Fill in the blank: Alfred Wegener proposed that the continents were once joined in a single supercontinent called ________ , which has since broken apart and drifted to the current positions of the continents.

1.1.2 Evidence for continental drift

The evidence Wegener assembled in support of continental drift includes: geometric fit of continents (the matching outlines of opposing continental shelves, particularly South America and Africa, suggesting a former connection); geological evidence (matching rock types, ages, and structural features such as fold mountain belts across the Atlantic, consistent with the continuation of the same geological formations before separation); palaeoclimatic evidence (glacial deposits and striated bedrock indicating past glaciation in regions now near the equator, such as India and southern Africa, consistent with their former position near the South Pole).

Palaeontological evidence is among the most compelling: the freshwater reptile Mesosaurus, found only in South America and southern Africa, could not have crossed the open Atlantic Ocean, suggesting the two continents were once joined; the seed fern Glossopteris, a distinctive fossil plant found on all southern continents (South America, Africa, Antarctica, Australia, and India), demonstrates that these landmasses were once connected; similarly, the Lystrosaurus mammal-like reptile fossils found across Africa, Antarctica, and India support a common landmass.

Fill in the blank: The fossil seed fern ________ , found on all southern continents, provides compelling palaeontological evidence that these landmasses were once joined in a single supercontinent.

1.1.3 Plate tectonics as the mechanism

The theory of plate tectonics, developed in the 1960s, provided the physical mechanism that Wegener lacked; the Earth lithosphere (crust and upper mantle) is divided into a mosaic of rigid plates that move relative to one another, driven by convection currents in the underlying asthenosphere; at mid-ocean ridges (divergent plate boundaries), new oceanic crust is continuously created as magma rises and solidifies, pushing the plates apart in a process called seafloor spreading; at subduction zones (convergent boundaries), older oceanic crust is consumed back into the mantle.

Continental drift is therefore a consequence of plate movement: continents are embedded in and carried along with the lithospheric plates; the rate of plate movement is typically a few centimetres per year, similar to the rate at which fingernails grow, but over geological timescales of tens to hundreds of millions of years this produces the vast movements documented in the geological and palaeontological record; palaeomagnetic evidence (the alternating bands of normal and reversed magnetic polarity symmetrically distributed on either side of mid-ocean ridges) provided decisive proof of seafloor spreading.

Fill in the blank: Seafloor spreading at mid-ocean ________ creates new oceanic crust as magma rises and solidifies, pushing tectonic plates apart and driving continental drift.

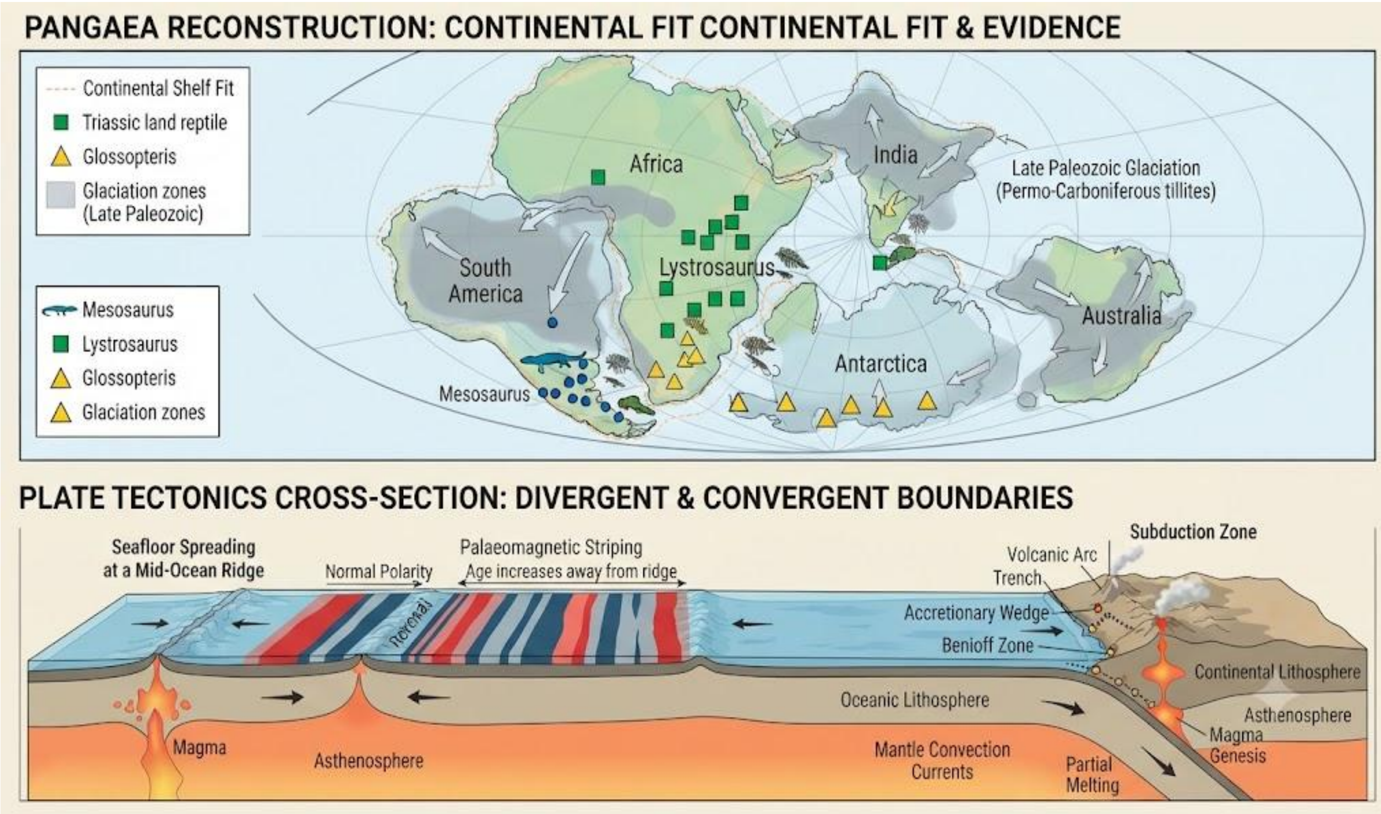

Figure 1.1: Continental drift theory and evidence

Pilot questions 1.1

1. State the name and year of Wegener continental drift hypothesis and the supercontinent he proposed.
2. Name four types of evidence Wegener used to support continental drift.
3. Explain why Wegener hypothesis was initially rejected.
4. Explain what plate tectonics is and how it provides the mechanism for continental drift.
5. Explain what seafloor spreading is and where it occurs.

1.2 Gondwanaland and Laurasia

1.2.1 Pangaea, Gondwanaland, and Laurasia

Approximately 335 to 175 million years ago, the Earth landmasses were assembled into a single supercontinent called Pangaea, which began to fragment during the Triassic and Jurassic periods; the initial fragmentation split Pangaea into two major landmasses: Laurasia in the north (comprising what are now North America, Europe, and most of Asia) and Gondwanaland (also called Gondwana) in the south (comprising what are now South America, Africa, Antarctica, Australia, and the Indian subcontinent).

The two landmasses were initially separated by the Tethys Sea, a warm shallow tropical ocean; Gondwanaland itself began to fragment further during the Jurassic and Cretaceous periods, with different landmass fragments separating at different times and rates; the Indian subcontinent broke from Antarctica and drifted northward to collide with Eurasia approximately 50 million years ago, forming the Himalayan mountain range; Africa separated from South America during the Cretaceous, opening the South Atlantic Ocean.

Fill in the blank: Pangaea first fragmented into ________ in the north (comprising North America, Europe, and Asia) and Gondwanaland in the south.

1.2.2 The breakup of Gondwanaland

The sequence and timing of Gondwanaland breakup is reconstructed from geological, palaeomagnetic, and palaeontological evidence: Africa began separating from South America approximately 130 to 135 million years ago (Early Cretaceous), with the South Atlantic Ocean progressively widening; India separated from Antarctica-Australia around 130 million years ago and drifted rapidly northward; Australia and Antarctica remained joined until approximately 35 to 45 million years ago, when Australia separated and drifted northward, and Antarctica became isolated over the South Pole.

The progressive isolation of each Gondwanaland fragment at a different time had profound biogeographic consequences: organisms present on the separating landmass were vicariated (split apart by the opening ocean), and each isolated fragment subsequently underwent independent evolutionary diversification; the biota of Australia, South America, and Africa all bear the legacy of their Gondwanaland origin, with shared ancient lineages (such as the ratite birds and southern beeches Nothofagus) distributed across fragments that were once joined.

Fill in the blank: Africa began separating from South America approximately ________ million years ago in the Early Cretaceous, progressively opening the South Atlantic Ocean.

1.2.3 Biogeographic consequences of Gondwanaland

The breakup of Gondwanaland explains several striking biogeographic patterns: the distribution of ratite birds (ostriches in Africa, rheas in South America, emus and cassowaries in Australia, kiwis in New Zealand, and the extinct moas in New Zealand and elephant birds in Madagascar) across southern continents reflects their shared Gondwanaland ancestry, with the flightless condition making overwater dispersal implausible; the distribution of the freshwater lungfishes (in Africa, South America, and Australia) and the Nothofagus beech trees across southern landmasses similarly reflects Gondwanaland vicariance.

Not all southern hemisphere disjunct distributions are explained by Gondwanaland: some taxa have dispersed across ocean gaps after the continents separated, and molecular clock analyses have shown that the divergence times of some "Gondwanaland relict" taxa postdate the continental separation, indicating dispersal rather than vicariance as the explanation; distinguishing true Gondwanaland relicts (organisms whose distributions reflect the ancient continental connections) from more recent dispersers requires integrating fossil evidence, molecular phylogenies, and divergence time estimation.

Fill in the blank: The distribution of ________ birds (including ostriches, rheas, emus, and kiwis) across southern continents is a classic example of a Gondwanaland biogeographic pattern reflecting their shared ancient ancestry.

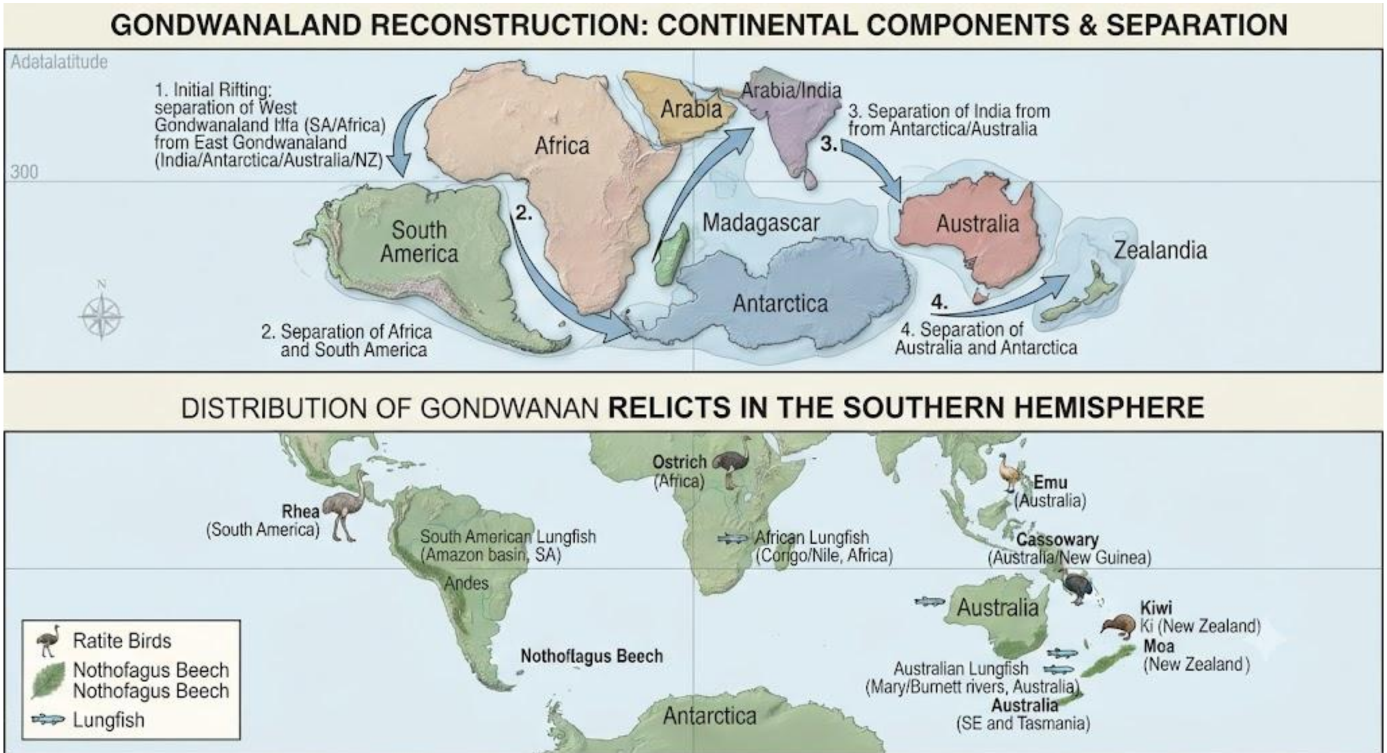

Figure 1.2: Gondwanaland and its breakup

Pilot questions 1.2

1. State the approximate time period during which Pangaea existed and when it began to fragment.
2. Name the two major landmasses that formed when Pangaea initially split.
3. Name the five landmasses that made up Gondwanaland.
4. State when Africa began to separate from South America and what ocean formed between them.
5. Give two examples of Gondwanaland biogeographic patterns.

1.3 Land Bridges

1.3.1 The theory of land bridges

The land bridge theory proposes that temporary or permanent connections between landmasses across what are now ocean barriers allowed the exchange of biota between regions that are currently separated by water; land bridges may form through tectonic uplift, volcanic island chains, or through the lowering of sea level during glacial periods (when large amounts of water are locked in ice sheets, exposing continental shelves); these connections can allow organisms that cannot disperse across open ocean to colonise new regions.

The recognition that sea level changes of over 100 metres occurred during Pleistocene glacial cycles was critical to understanding many faunal distributions, since such sea level drops would have exposed extensive areas of continental shelf and connected landmasses that are now separated by shallow seas; the land bridge concept was initially sometimes overused to explain all disjunct distributions before continental drift was accepted, but remains a valid and important biogeographic mechanism for explaining distributions where the geological evidence supports such connections.

Fill in the blank: During glacial periods, falling sea levels expose continental shelves and can create ________ bridges connecting landmasses that are currently separated by shallow ocean.

1.3.2 Major land bridges and their biogeographic effects

The Bering Land Bridge (Beringia), connecting Alaska and Siberia across what is now the Bering Strait, is one of the most biogeographically significant land bridges; it was exposed multiple times during Pleistocene glaciations when sea levels fell, allowing repeated faunal exchange between Asia and North America; this bridge facilitated the dispersal of mammoths, horses, bison, and other large mammals from Asia into North America, and the southward migration of humans into the Americas from Siberia approximately 15,000 to 20,000 years ago.

The Isthmus of Panama formed approximately 3 million years ago when the Caribbean and Pacific plates collided, creating a permanent land connection between North and South America and triggering the Great American Biotic Interchange (GABI); this event allowed the northward migration of South American taxa (such as armadillos, opossums, and ground sloths) into North America and the southward migration of North American taxa (such as horses, tapirs, deer, and large cats) into South America, dramatically changing the mammalian fauna of both continents.

Fill in the blank: The formation of the Isthmus of Panama approximately 3 million years ago triggered the Great American Biotic ________ , allowing the exchange of mammals between North and South America.

1.3.3 Land bridges versus rafting

Not all distributions across ocean barriers are explained by land bridges; organisms can also disperse across open water by rafting on floating vegetation mats, logs, or other debris carried by ocean currents; rafting is particularly plausible for small organisms (lizards, rodents, invertebrates, seeds, and spores) that can survive extended ocean crossings on such rafts; the colonisation of oceanic islands provides examples of successful overwater dispersal by rafting and other long-distance dispersal mechanisms.

Distinguishing between land bridge dispersal and rafting (or other overwater dispersal mechanisms) requires integrating the geological record (is there evidence for a land connection at the relevant time?), the fossil record (when do the organisms first appear in the relevant region?), and molecular phylogenetic data (what are the divergence times between populations or species on either side of the barrier?); the contrast between the mammalian fauna of Madagascar (largely absent of placental mammals, consistent with overwater dispersal of a limited number of lineages) versus Australia (rich marsupial fauna consistent with Gondwanaland vicariance) illustrates the need for case-by-case analysis.

Fill in the blank: ________ is a dispersal mechanism in which organisms cross ocean barriers on floating vegetation mats or debris, explaining some distributions where no land bridge existed.

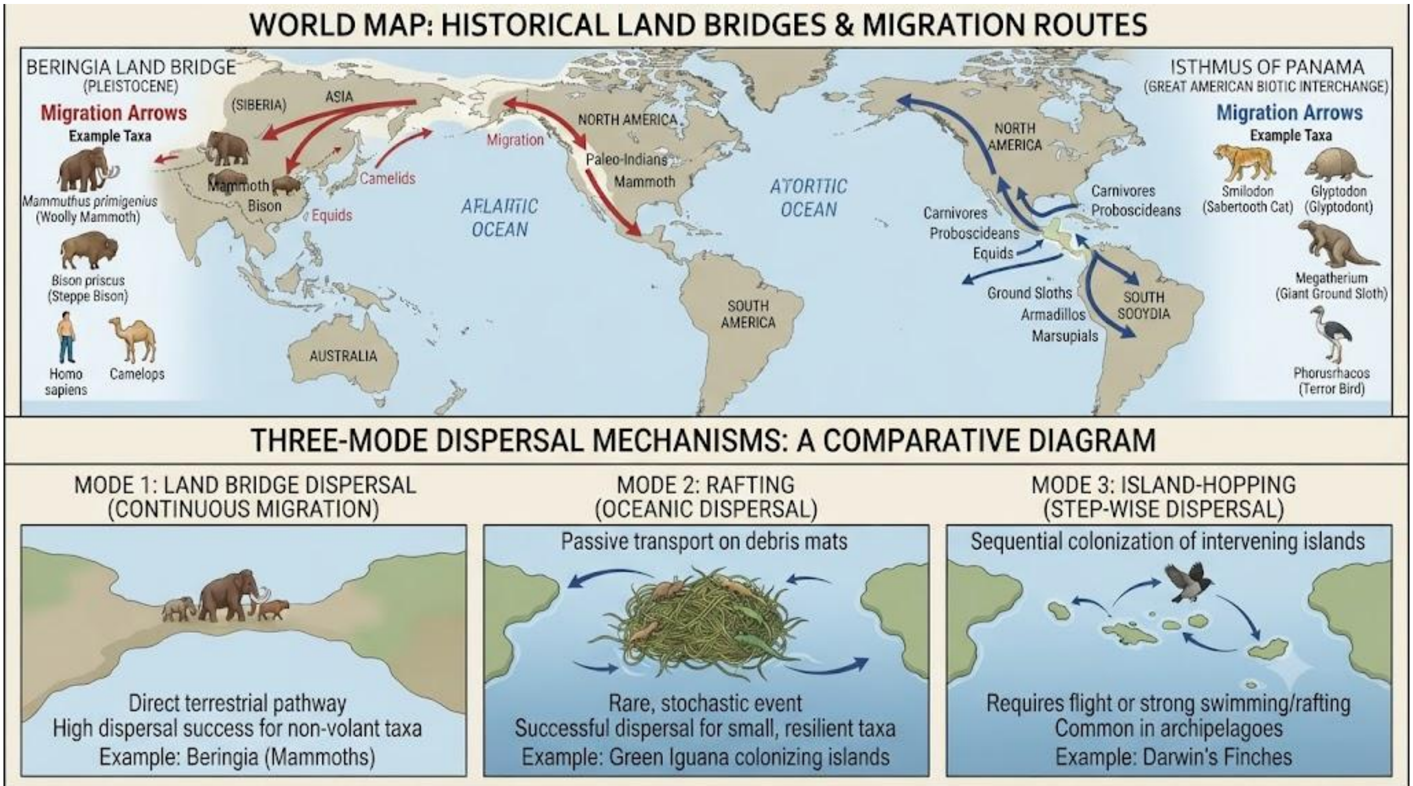

Figure 1.3: Land bridges and dispersal mechanisms

Pilot questions 1.3

1. Define land bridge and explain how glaciation can create one.
2. Describe the Bering Land Bridge and its biogeographic significance.
3. Describe the Great American Biotic Interchange and what caused it.
4. Name two South American taxa that dispersed into North America via the Isthmus of Panama.
5. Explain what rafting is and give an example of where it may explain a distribution.

1.4 Continental Drift and Biogeography

1.4.1 Vicariance and dispersal

Two fundamental processes generate disjunct distributions (the occurrence of related taxa in geographically separated areas): vicariance and dispersal; vicariance occurs when a previously continuous population or distribution is split by the appearance of a geographic barrier (such as an ocean opening, a mountain range rising, or a river changing course), isolating the resulting populations and allowing them to diverge independently; the timing of vicariance events should correspond to the geological history of the barrier concerned.

Dispersal (in the biogeographic sense) refers to the movement of organisms across a pre-existing barrier to colonise a new area; long-distance dispersal events are typically rare but, once successful, can explain distributions across major ocean barriers without requiring a land connection; vicariance biogeography and dispersal biogeography were historically competing schools of thought, but modern biogeography integrates both, recognising that different taxa and different distribution patterns may be better explained by one process or the other, requiring case-by-case analysis combining geological, fossil, and molecular evidence.

Fill in the blank: ________ occurs when a geographic barrier splits a previously continuous distribution, isolating populations that then diverge independently on each side of the barrier.

1.4.2 Continental drift and disjunct distributions

Disjunct distributions where related taxa occur on continents now separated by ocean are among the most striking patterns in biogeography, and continental drift provides the primary explanation for those involving ancient lineages; the southern beeches of the genus Nothofagus occur in South America, southern Australia, New Zealand, and as fossils in Antarctica, reflecting their Gondwanaland origin; Proteaceae (the protea family) are similarly distributed across southern Africa, Australia, and South America, reflecting ancient Gondwanaland connections.

The timing of the divergence between populations or species on separated landmasses can be estimated using molecular clocks (the rate at which DNA sequences accumulate mutations), and this estimated divergence time can be compared with the geological timing of the continental separation event; when divergence times match the geological ages of separation, vicariance is strongly supported; when divergence times are substantially younger than the continental separation, long-distance dispersal after separation is the more likely explanation.

Fill in the blank: Molecular ________ estimate divergence times between populations by measuring the rate at which DNA sequences accumulate mutations, allowing comparison with geological separation events.

1.4.3 Applying continental drift to interpreting distribution patterns

The practical application of continental drift theory in biogeography involves constructing area cladograms (diagrams showing the phylogenetic relationships among taxa mapped onto the geographic areas they inhabit) and comparing these with the geological history of the areas; if the phylogenetic pattern among taxa matches the sequence of geological splitting events (area cladogram congruent with the geological history), this is evidence for vicariance driven by those geological events; this method, called vicariance biogeography or cladistic biogeography, tests whether biological distributions are explained by geological history.

Continental drift also provides the temporal framework for interpreting when barriers formed and disappeared, which is essential for understanding both vicariance and dispersal events; the opening and closing of seaways (such as the closing of the Tethys Sea as Africa and Eurasia collided, and the opening of the Drake Passage as South America separated from Antarctica) created and removed barriers to dispersal, shaping the history of marine as well as terrestrial biota; biogeographers therefore work closely with geologists and palaeontologists to reconstruct the changing geography of the past.

Fill in the blank: An area ________ maps the phylogenetic relationships among taxa onto the geographic areas they inhabit, allowing comparison with the geological history of area separation.

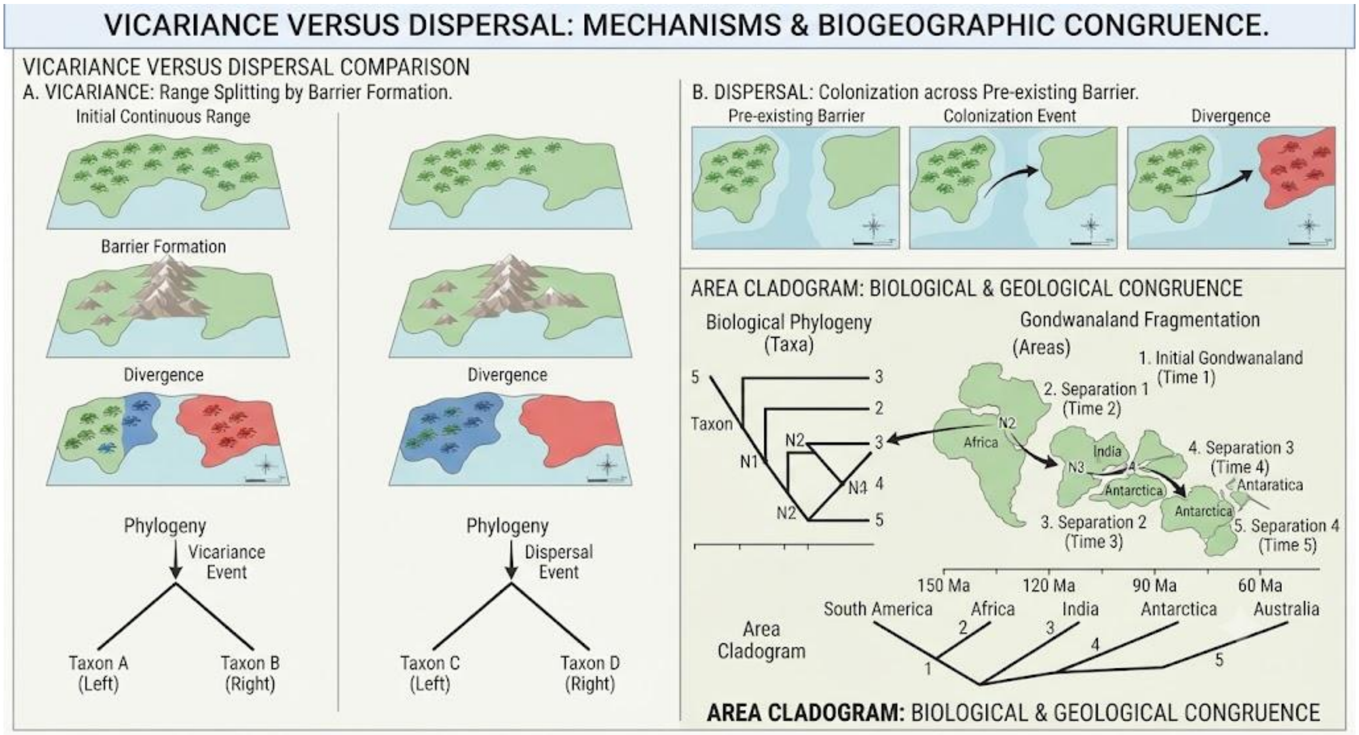

Figure 1.4: Vicariance, dispersal, and area cladograms

Pilot questions 1.4

1. Distinguish between vicariance and dispersal as explanations for disjunct distributions.
2. Give one example of a disjunct distribution explained by Gondwanaland vicariance.
3. Explain how molecular clocks are used in biogeography.
4. Explain what an area cladogram is and how it is used.
5. Give one example of a seaway opening or closing that shaped biogeographic patterns.

Series Summary

This Series introduced the geological foundations of biogeography, beginning with Alfred Wegener continental drift hypothesis and the evidence he assembled from fossil distributions, geological continuities, and palaeoclimatic data. Plate tectonics, developed in the 1960s, supplied the physical mechanism through seafloor spreading at mid-ocean ridges. Together, these insights explain how the supercontinent Pangaea fragmented into Gondwanaland and Laurasia, with each Gondwanaland landmass separating at a different time and leaving a distinctive biological legacy in the organisms that evolved in isolation on each fragment.

The Series also examined land bridges as a complementary mechanism, exploring how temporary connections such as Beringia and the Isthmus of Panama facilitated major faunal exchanges, and how rafting provides an alternative explanation where no land connection existed. The distinction between vicariance, where a barrier splits an existing distribution, and dispersal, where organisms actively cross a barrier, was established as the central conceptual framework for interpreting how continental drift and related geological events produced the distribution patterns studied throughout this course.

Glossary of Terms

- **Area cladogram:** a phylogenetic tree in which taxa are replaced by the geographic areas they inhabit, used to compare biological history with geological area history.
- **Continental drift:** the movement of Earth lithospheric plates and the continents embedded within them over geological time.
- **Disjunct distribution:** the occurrence of related taxa in geographically separated areas with no continuous range between them.
- **Gondwanaland:** the southern supercontinent comprising South America, Africa, Antarctica, Australia, and India, which fragmented from Pangaea during the Mesozoic.
- **Land bridge:** a terrestrial connection between otherwise separated landmasses, allowing exchange of biota between regions.

- **Vicariance:** the splitting of a previously continuous distribution by the formation of a geographic barrier.
- **Seafloor spreading:** the creation of new oceanic crust at mid-ocean ridges, which drives the movement of tectonic plates.

Concept Check Questions [Series 1]

Objective Questions

1. Alfred Wegener proposed that the continents were once joined in a single supercontinent called ________ . (Linked to SLO 1.1)
2. Pangaea first split into Laurasia in the north and ________ in the south. (Linked to SLO 1.2)
3. The formation of the Isthmus of Panama approximately 3 million years ago triggered the Great American Biotic ________ . (Linked to SLO 1.3)
4. ________ occurs when a geographic barrier splits a previously continuous distribution into isolated populations. (Linked to SLO 1.4)
5. New oceanic crust is created at mid-ocean ridges through ________ spreading. (Linked to SLO 1.1)

Short-Answer Questions

6. Name four types of evidence Wegener used for continental drift. (Linked to SLO 1.1)
7. Name the five landmasses that made up Gondwanaland. (Linked to SLO 1.2)
8. Describe the biogeographic significance of the Bering Land Bridge. (Linked to SLO 1.3)
9. Distinguish between vicariance and dispersal. (Linked to SLO 1.4)
10. Give two examples of Gondwanaland biogeographic patterns. (Linked to SLO 1.2)

Long-Answer Questions

11. Describe Wegener continental drift hypothesis and the plate tectonic mechanism that explains it. (Linked to SLO 1.1)
12. Describe Gondwanaland and the biogeographic consequences of its breakup. (Linked to SLO 1.2)
13. Explain land bridges and their biogeographic effects, and distinguish vicariance from dispersal. (Linked to SLOs 1.3, 1.4)

Answers to Concept Check Questions [Series 1]

Objective Questions

1. Pangaea.
2. Gondwanaland.
3. Interchange.
4. Vicariance.
5. Seafloor.

Short-Answer Questions

6. Geometric fit of continental coastlines, matching geological formations, palaeoclimatic evidence of past glaciation in tropical regions, and palaeontological evidence (Mesosaurus, Glossopteris).
7. South America, Africa, Antarctica, Australia, and India.
8. Beringia was a land bridge connecting Alaska and Siberia, exposed during Pleistocene glaciations, allowing mammals such as horses and mammoths to move from Asia to North America and humans to migrate into the Americas.
9. Vicariance splits an existing distribution by forming a barrier; dispersal involves organisms crossing a pre-existing barrier to colonise a new area.
10. The distribution of ratite birds across southern continents, and the distribution of Nothofagus beeches across South America, Australia, New Zealand, and Antarctica.

Long-Answer Questions

11. Wegener (1912) proposed that Pangaea fragmented and its pieces drifted apart, supported by the geometric fit of continents, matching fossils (Glossopteris, Mesosaurus), geological continuities, and past glaciation in now-tropical regions. Plate tectonics (1960s) provides the mechanism: lithospheric plates are driven apart by seafloor spreading at mid-ocean ridges and consumed at subduction zones.
12. Gondwanaland comprised South America, Africa, Antarctica, Australia, and India. It fragmented sequentially from the Jurassic onwards. Each separating fragment carried its biota into isolation,

producing the southern hemisphere distributions of ratite birds, Nothofagus, Proteaceae, and freshwater lungfishes that are classic examples of Gondwanaland vicariance.

13. Land bridges are terrestrial connections between separated landmasses, formed by tectonic activity or glacial sea level fall. Beringia allowed Asian-North American faunal exchange; the Isthmus of Panama triggered the Great American Biotic Interchange. Rafting explains some distributions lacking a land connection. Vicariance is passive splitting by a barrier; dispersal is active crossing of a barrier.

Answers to Pilot Questions [Series 1]

Part 1.1

1. Alfred Wegener proposed the continental drift hypothesis in 1912; he called the original supercontinent Pangaea.
2. Geometric fit of coastlines, matching geological formations across continents, palaeoclimatic evidence, and palaeontological evidence (fossil distributions).
3. Wegener could not propose a plausible physical mechanism to move continents through solid oceanic crust.
4. Plate tectonics divides the lithosphere into rigid plates driven by convection in the mantle; continents are carried on these plates.
5. Seafloor spreading is the creation of new oceanic crust as magma rises at mid-ocean ridges and solidifies, pushing plates apart; it occurs at divergent plate boundaries such as the Mid-Atlantic Ridge.

Part 1.2

1. Pangaea existed approximately 335 to 175 million years ago and began fragmenting in the Triassic and Jurassic.
2. Laurasia (north) and Gondwanaland (south).
3. South America, Africa, Antarctica, Australia, and India.

4. Africa began separating from South America approximately 130 to 135 million years ago (Early Cretaceous), forming the South Atlantic Ocean.
5. The distribution of ratite birds across southern continents; the distribution of Nothofagus beeches across South America, Australia, New Zealand, and Antarctica.

Part 1.3

1. A land bridge is a terrestrial connection between separated landmasses; glaciation lowers sea level by locking water in ice sheets, exposing continental shelves and connecting shallow-sea-separated landmasses.
2. Beringia connected Alaska and Siberia across the Bering Strait during Pleistocene glaciations, allowing mammals (mammoths, horses, bison) to move between Asia and North America, and humans to migrate into the Americas.
3. The Isthmus of Panama formed approximately 3 million years ago, connecting North and South America and triggering the Great American Biotic Interchange, a massive two-way exchange of mammalian fauna.
4. Armadillos and opossums (northward into North America).
5. Rafting is the passive dispersal of organisms across open ocean on floating debris; it may explain the presence of lizards on oceanic islands or the colonisation of Madagascar by lemur ancestors.

Part 1.4

1. Vicariance splits an existing continuous distribution by forming a barrier; dispersal involves an organism crossing a pre-existing barrier to reach a new area.
2. The distribution of Nothofagus beeches across South America, southern Australia, New Zealand, and Antarctica (as fossils) reflects Gondwanaland vicariance.
3. Molecular clocks estimate divergence times between lineages by measuring accumulated mutations in DNA, allowing the timing of the split to be compared with the geological age of the separating barrier.

4. An area cladogram replaces taxa in a phylogenetic tree with the geographic areas they inhabit; congruence between the area cladogram and the geological history of area separation supports vicariance.
5. The closing of the Tethys Sea as Africa collided with Eurasia created a land connection that shaped Eurasian and African faunal distributions; the opening of the Drake Passage isolated Antarctica.

References and Attribution

Textual References (Books and External Sources)

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- National Open University of Nigeria (NOUN). (2023). Biogeography and soil biology course material. NOUN Press.

Figures, Plates, Tables, and Boxes

- Figure 1.1: Continental drift theory and evidence Attribution: AI generated. Suggested OER search string: "continental drift Wegener evidence Mesosaurus Glossopteris plate tectonics seafloor spreading biogeography diagram OER".
- Figure 1.2: Gondwanaland and its breakup Attribution: AI generated. Suggested OER search string: "Gondwanaland breakup Laurasia ratite birds Nothofagus biogeographic relict vicariance southern hemisphere OER".

- Figure 1.3: Land bridges and dispersal mechanisms Attribution: AI generated. Suggested OER search string: "land bridge Beringia Isthmus Panama Great American Biotic Interchange rafting dispersal biogeography OER".
- Figure 1.4: Vicariance, dispersal, and area cladograms Attribution: AI generated. Suggested OER search string: "vicariance dispersal area cladogram biogeography continental drift disjunct distribution Gondwanaland OER".

Course code: BIO 303

Course title: Biogeography and Soil Biology

Course credit load: 2 Units

Series 2: Global Flora and Fauna Distribution

- **Part 2.1: Phytogeographical Regions of the World**
    - Sub Part 2.1.1: Principles of phytogeography
    - Sub Part 2.1.2: Major floristic kingdoms
    - Sub Part 2.1.3: Factors controlling plant distribution
- **Part 2.2: Zoogeographical Regions of the World**
    - Sub Part 2.2.1: Principles of zoogeography
    - Sub Part 2.2.2: Wallace faunal regions
    - Sub Part 2.2.3: Factors controlling animal distribution
- **Part 2.3: Relationships Between Plant and Animal Distributions**
    - Sub Part 2.3.1: Plant-animal coevolution and interdependence
    - Sub Part 2.3.2: Local examples of plant-animal distribution relationships
    - Sub Part 2.3.3: Human influence on flora and fauna distribution
- **Part 2.4: Factors Affecting Distribution**
    - Sub Part 2.4.1: Climate and latitude
    - Sub Part 2.4.2: Physical barriers and corridors
    - Sub Part 2.4.3: Biotic interactions

Introduction

The living world is not distributed uniformly across the Earth: different regions support characteristically different assemblages of plants and animals, shaped by climate, geological history, barriers to dispersal, and the evolutionary history of the organisms themselves. Phytogeography and zoogeography are the subdisciplines of biogeography that describe and explain the global distribution of plants and animals respectively, identifying the major regions of the world and the forces that produced them.

This Series examines the major phytogeographical and zoogeographical regions of the world, the factors controlling plant and animal distributions, and the intimate relationships between plant and animal distributions that arise through coevolution and ecological interdependence. It also considers the growing influence of humans in modifying natural distribution patterns, and synthesises the physical, biological, and historical factors that together determine which organisms occur where on Earth.

Series Learning Outcomes

Upon completing this Series, you should be able to:

- **SLO 2.1** describe the major phytogeographical regions of the world and the factors controlling plant distribution,
- **SLO 2.2** describe the major zoogeographical regions of the world and the factors controlling animal distribution,
- **SLO 2.3** explain the relationships between plant and animal distributions, including coevolution and human influence, and
- **SLO 2.4** explain how climate, physical barriers, and biotic interactions affect the distribution of organisms.

2.1 Phytogeographical Regions of the World

2.1.1 Principles of phytogeography

Phytogeography (plant geography) is the study of the geographic distribution of plants and the factors responsible for those distributions; it operates at multiple scales, from the global distribution of biomes (broad vegetation types such as tropical rainforest, savanna, and tundra, determined primarily by climate) to the regional distribution of floristic kingdoms and provinces (defined by the taxonomic composition of their flora, including the presence of endemic families or genera), to the local distribution of plant communities determined by microclimate, soil, and competition.

The floristic kingdom concept, developed by botanists including Engler and Good, divides the world into major phytogeographical units based on the composition and affinities of their native floras; kingdoms are defined by having a significant proportion of endemic plant families or genera (taxa found nowhere else), reflecting a long history of isolation or independent evolution; the boundaries between kingdoms are never sharp but reflect gradients in floristic composition, and they do not correspond precisely to the continental boundaries or faunal regions.

Fill in the blank: Phytogeography operates at multiple scales, from the global distribution of ________ (broad vegetation types determined by climate) to the regional composition of floristic kingdoms.

2.1.2 Major floristic kingdoms

The most widely recognised classification divides the world into six floristic kingdoms: the Holarctic Kingdom (the largest, covering most of the Northern Hemisphere including North America, Europe, and Asia north of the tropics, sharing many plant families due to past land connections and similar climates); the Neotropical Kingdom (Central and South America, extraordinarily rich in endemic families including bromeliads, cacti, and a vast diversity of orchids and palms); the Palaeotropical Kingdom (tropical Africa, Asia, and Pacific islands, rich in palms, dipterocarp forests in Southeast Asia, and African endemic families); and the Cape

Kingdom (the smallest, covering only the southwestern tip of South Africa, with the highest plant species density per unit area on Earth, dominated by the fynbos biome).

The remaining two kingdoms are the Australian Kingdom (Australia, with a flora of extraordinary endemism including Eucalyptus, Acacia, Proteaceae, and many other endemic families reflecting its long isolation since Gondwanaland breakup) and the Antarctic Kingdom (the southern tip of South America, New Zealand, and sub-Antarctic islands, sharing Gondwanaland floristic elements including Nothofagus and Proteaceae); the extraordinarily high endemism of the Australian and Cape kingdoms reflects prolonged geographical isolation combined with diverse soils and climates, which together promoted rapid diversification.

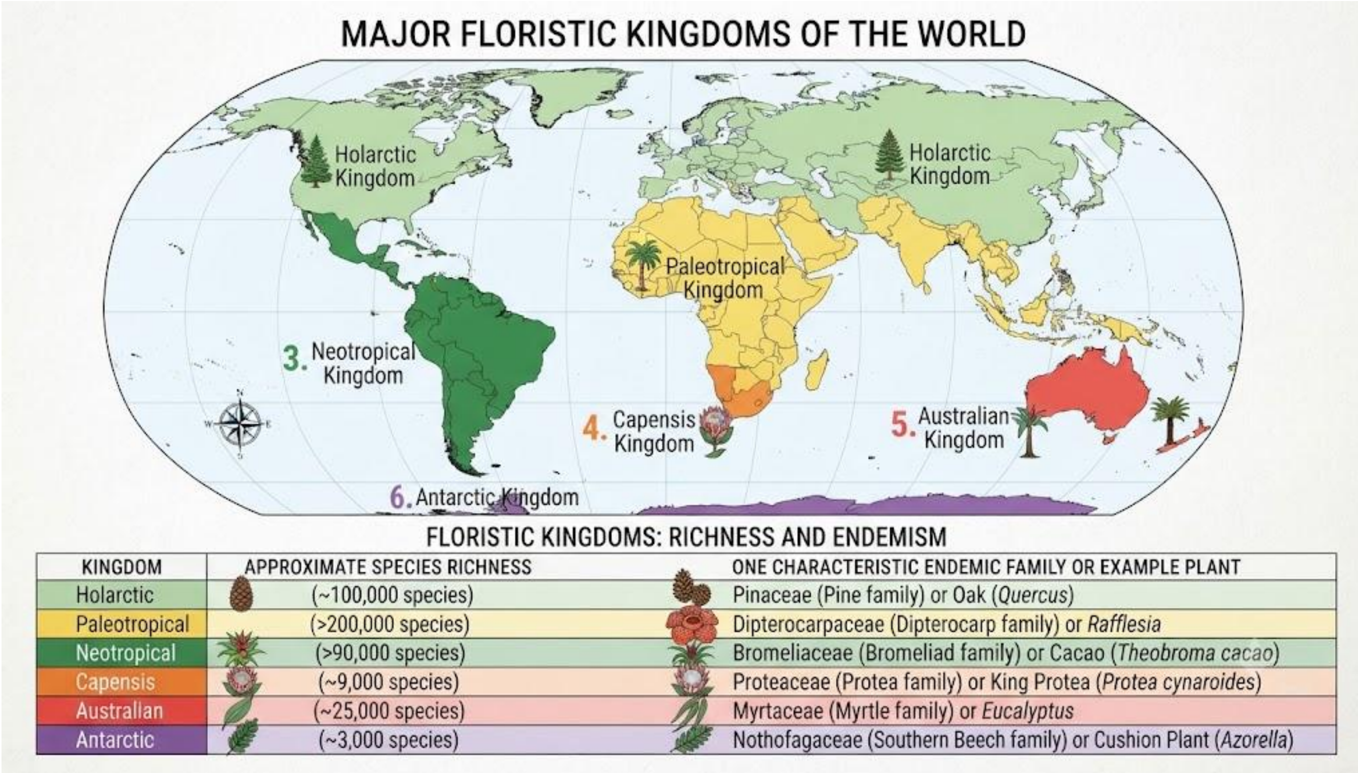
Fill in the blank: The ________ Kingdom, covering southwestern South Africa, has the highest plant species density per unit area on Earth, dominated by the fynbos biome.

2.1.3 Factors controlling plant distribution

Climate is the dominant control on large-scale plant distribution: temperature sets the thermal limits within which different plant functional types can survive and reproduce (determining the transition from tropical to temperate to boreal to arctic vegetation), while precipitation and its seasonality determine the transition from rainforest to seasonal forest to savanna to desert along moisture gradients; the combination of temperature and moisture is captured in bioclimatic indices that predict the broad vegetation type a given location can support.

Soil type, topography, and disturbance history also exert strong influences at finer scales: certain plant families or genera are restricted to specific soil chemistries (such as the highly specialised flora of serpentine soils, poor in nutrients but rich in heavy metals, which supports a distinctive assemblage of metal-tolerant plants), while geological history and barriers to dispersal determine which species are available to colonise a suitable site; the interaction of all these factors produces the actual plant distribution observed at any given location.

Fill in the blank: ________ is the dominant control on large-scale plant distribution, with temperature setting thermal limits and precipitation determining the transition from rainforest to desert.



KINGDOM	APPROXIMATE SPECIES RICHNESS	ONE CHARACTERISTIC ENDEMIC FAMILY OR EXAMPLE PLANT
Holarctic	(~100,000 species)	Pinaceae (Pine family) or Oak (*Quercus*)
Paleotropical	(>200,000 species)	Dipterocarpaceae (Dipterocarp family) or *Rafflesia*
Neotropical	(>90,000 species)	Bromeliaceae (Bromeliad family) or Cacao (*Theobroma cacao*)
Capensis	(~9,000 species)	Proteaceae (Protea family) or King Protea (*Protea cynaroides*)
Australian	(~25,000 species)	Myrtaceae (Myrtle family) or *Eucalyptus*
Antarctic	(~3,000 species)	Nothofagaceae (Southern Beech family) or Cushion Plant (*Azorella*)

Figure 2.1: World phytogeographical regions

Pilot questions 2.1

1. Define phytogeography and explain what a floristic kingdom is.
2. Name the six major floristic kingdoms.
3. Which floristic kingdom has the highest plant species density per unit area?
4. Name two characteristic plant groups of the Australian Kingdom.
5. Name two climatic factors that control large-scale plant distribution.

2.2 Zoogeographical Regions of the World

2.2.1 Principles of zoogeography

Zoogeography is the study of the geographic distribution of animals and the historical, ecological, and evolutionary processes that produced those distributions; like phytogeography, it recognises that the composition of animal faunas differs systematically between major geographic regions, reflecting the combined influence of geological history (which landmasses were connected when, determining which animals could reach which regions), climate (which sets the environmental limits for survival and reproduction), and evolutionary history (which groups originated where and diversified over time).

The foundations of modern zoogeography were laid by Philip Sclater, who in 1858 proposed a division of the world into six major faunal regions based on the distribution of birds, and by Alfred Russel Wallace, who extended and refined this scheme to encompass all animals; Wallace travelled extensively in South America and Southeast Asia, and the boundary he identified between the Oriental and Australian faunal regions in the Indonesian archipelago (now called the Wallace Line) remains one of the most famous and sharply defined biogeographic boundaries in the world.

Fill in the blank: The ________ Line, identified by Alfred Russel Wallace in the Indonesian archipelago, marks one of the sharpest biogeographic boundaries in the world, separating the Oriental and Australian faunal regions.

2.2.2 Wallace faunal regions

The six major zoogeographical regions, with their characteristic faunas, are: the Palaearctic region (Europe, Asia north of the tropics, and North Africa; diverse temperate mammals including deer, bears, wolves, and migratory birds); the Nearctic region (North America north of Mexico; bison, pronghorn antelope, wolverine, and many shared taxa with the Palaearctic due to Beringian connections); the Neotropical region (Central and South America; extraordinarily diverse, with unique taxa including sloths, anteaters, tapirs, rheas, toucans, and the greatest diversity of freshwater fish and tropical birds).

The Ethiopian (Afrotropical) region (Africa south of the Sahara; lions, elephants, giraffes, hippopotamuses, gorillas, and a rich endemic bird fauna); the Oriental region (tropical Asia including India, Southeast Asia, and the major Asian islands; tigers, orangutans, gibbons, Asian elephants, and peacocks); and the Australian region (Australia, New Guinea, and New Zealand; dominated by marsupials and monotremes, with the most distinctive mammalian fauna on Earth including kangaroos, wallabies, koalas, wombats, and the platypus and echidna, plus a highly endemic bird fauna including kiwis, lyrebirds, and birds-of-paradise).

Fill in the blank: The ________ region encompasses Africa south of the Sahara and includes lions, elephants, giraffes, hippopotamuses, and gorillas among its characteristic large mammals.

2.2.3 Factors controlling animal distribution

Animal distributions are influenced by many of the same physical factors as plant distributions (climate, topography, and barriers) but are additionally shaped by the distribution of their food resources; herbivores are constrained by the distribution of their host plants, carnivores by the distribution of their prey, and specialised feeders (such as nectar-feeders and fruit specialists) by the phenology and distribution of their food sources; this means that changes in plant distribution (whether caused by climate change, habitat loss, or plant invasion) cascade through to affect animal distributions.

Dispersal ability strongly influences animal distributions: highly mobile animals such as birds and bats can cross ocean barriers and colonise remote islands, producing more cosmopolitan distributions than poorly dispersing terrestrial mammals; the low dispersal ability of freshwater fish (restricted to connected drainage systems) and land snails makes them particularly informative indicators of past land connections and geological history; the degree to which an animal group can cross barriers is therefore a key variable in explaining its current distribution pattern.

Fill in the blank: Animal dispersal ability strongly influences distribution patterns; highly mobile animals such as ________ and bats produce more cosmopolitan distributions than poorly dispersing terrestrial mammals.

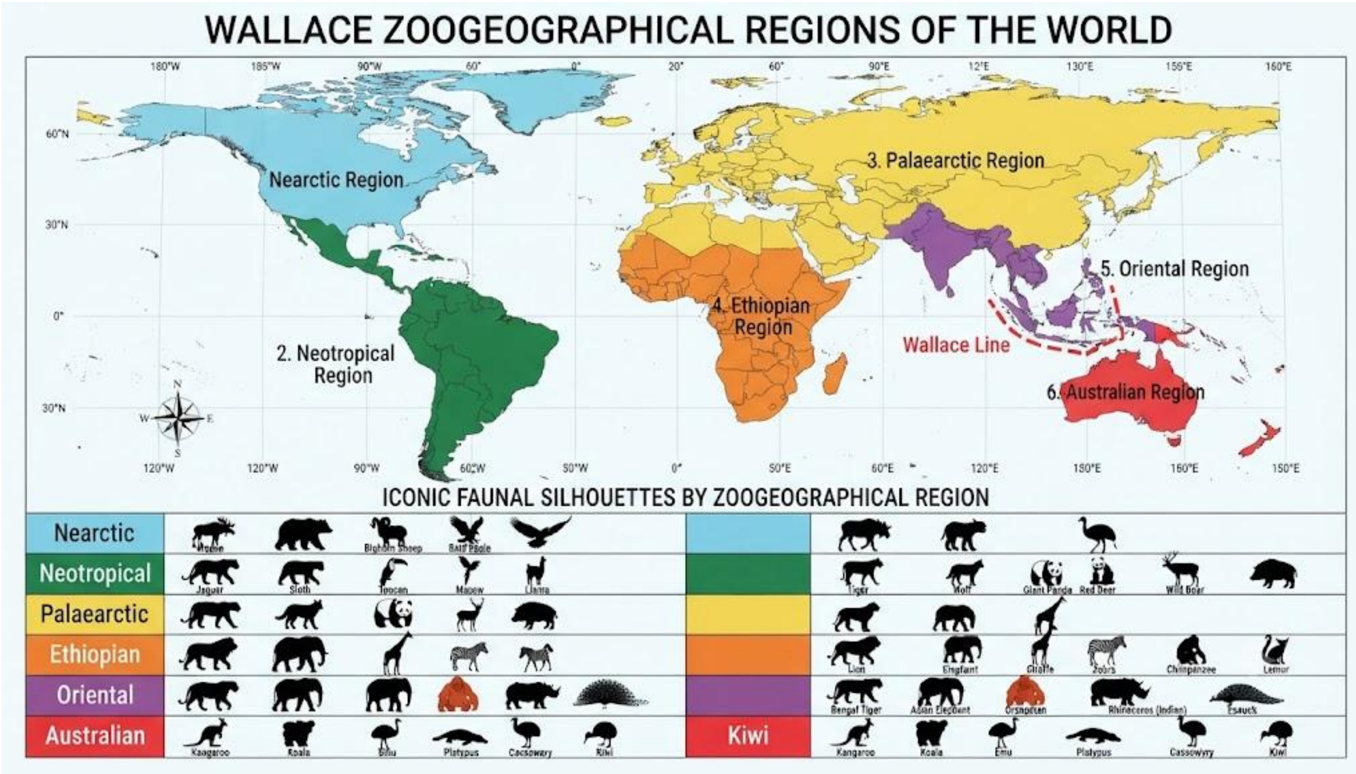


Figure 2.2: Wallace zoogeographical regions

Pilot questions 2.2

1. Name the six zoogeographical regions proposed by Wallace.
2. What is the Wallace Line and where is it located?
3. Name three characteristic large mammals of the Ethiopian region.
4. Explain why the Australian region has such a distinctive mammalian fauna.
5. Explain how dispersal ability influences an animal group distribution pattern.

2.3 Relationships Between Plant and Animal Distributions

2.3.1 Plant-animal coevolution and interdependence

Plants and animals have profoundly shaped each other distribution patterns through coevolution, the reciprocal evolutionary influence of interacting species on one another; pollination mutualisms (between flowering plants and their pollinators, including bees, butterflies, moths, hummingbirds, and bats) have driven the diversification of both groups, with many plant species depending on a specific pollinator and that pollinator depending on the plant for nectar or pollen; the coincident distributions of such mutualistic partners are therefore closely linked.

Seed dispersal by animals (frugivory and scatter-hoarding) links the distributions of fruit-bearing plants to those of their dispersers; in tropical forests, where the majority of tree species produce fleshy fruits consumed by birds and mammals, the loss of large frugivores through hunting or habitat loss can reduce seed dispersal away from parent trees, affecting forest regeneration and plant distribution at the landscape scale; the fig-fig wasp mutualism, one of the most specialised plant-animal interactions, illustrates how tightly the distribution of one species can be tied to that of another.

Fill in the blank: ________ (the reciprocal evolutionary influence of interacting species) has driven close relationships between flowering plants and their pollinators, linking their distributions.

2.3.2 Local examples of plant-animal distribution relationships

In the African savanna, the distribution of large grazing mammals (wildebeest, zebra, buffalo) is closely linked to the distribution of grass-dominated vegetation, and the grazing activity of these herbivores in turn maintains the grassland by suppressing woody plant establishment; the distribution of elephants in African forests and savannas influences the distribution of many plant species through bark-stripping, uprooting trees, and dispersing large seeds that no other extant animal can disperse; such keystone species effects mean that the loss of a single large animal can cascade through the plant community.

In Nigeria and West Africa, the distribution of frugivorous birds such as hornbills is closely linked to the distribution of large-seeded forest trees whose seeds they disperse; the forest fig trees support a diverse community of frugivores including primates, birds, and bats, and their fruiting events are critical food resources linking the spatial distributions of many animal species to those of the fig trees; recognising these linkages is essential for conservation planning, since protecting the plants without their animal mutualists, or vice versa, may be insufficient to maintain either.

Fill in the blank: In African savannas, large grazing mammals such as wildebeest and zebra maintain grassland by suppressing woody plant establishment, illustrating how ________ distributions are intimately linked to plant community structure.

2.3.3 Human influence on flora and fauna distribution

Human activity has become the dominant contemporary driver of changes in flora and fauna distribution, operating through habitat destruction (converting natural ecosystems to agriculture and urban land, fragmenting and reducing the ranges of native species), introduction of invasive alien species (which can outcompete, prey upon, or hybridise with native species, causing range contractions or extinctions), overexploitation (hunting, fishing, and collecting reducing population sizes), and climate change (shifting the thermal and precipitation envelopes that determine species ranges).

Introductions of alien species have fundamentally altered distribution patterns worldwide: the introduction of European rabbits to Australia, Nile perch to Lake Victoria, and invasive plant species such as water hyacinth throughout tropical Africa and Asia illustrate how human-mediated range expansions can catastrophically alter native communities; conversely, human-assisted range extensions of crop plants and domesticated animals have produced global distributions for species such as maize, cassava, cattle, and goats that far exceed their natural ranges, reshaping ecosystems and human food systems alike.

Fill in the blank: ________ alien species introduced by humans can outcompete, prey upon, or hybridise with native species, causing range contractions or local extinctions of native flora and fauna.

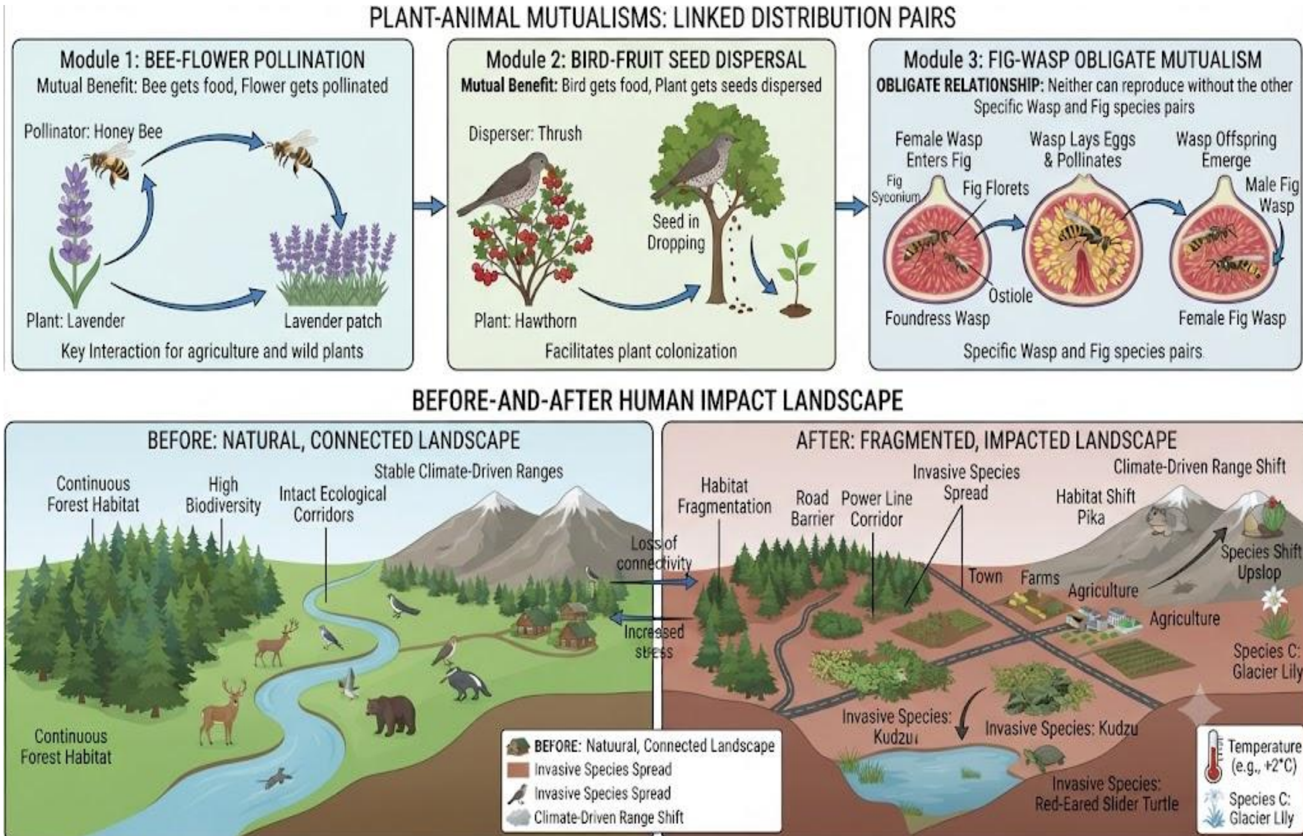


Figure 2.3: Plant-animal distribution relationships

Pilot questions 2.3

1. Explain what coevolution is and give one example involving a plant and an animal.
2. Explain how the loss of large frugivores can affect plant distribution.
3. Give one local African example of a plant-animal distribution relationship.
4. Name three ways in which human activity alters flora and fauna distribution.
5. Give one example of an invasive alien species introduction and its effect on native biota.

2.4 Factors Affecting Distribution

2.4.1 Climate and latitude

Climate is the primary determinant of large-scale distribution patterns for both plants and animals; temperature and precipitation, and their seasonality, define the envelope within which a species can survive, reproduce, and maintain viable populations; latitudinal gradients in temperature and seasonality produce the well-known pattern of declining species richness from the tropics toward the poles (the latitudinal diversity gradient), which holds for most taxonomic groups and has been attributed to the greater energy availability, climatic stability, and longer evolutionary history of tropical regions.

Altitudinal gradients in temperature mirror latitudinal gradients, producing zonation of vegetation types on mountains that mimics the latitudinal sequence from tropical to polar vegetation; each 1,000 metre increase in elevation corresponds approximately to a 6.5 degree Celsius decrease in temperature, equivalent to moving approximately 900 km toward the nearest pole; this parallelism between altitudinal and latitudinal zones is exploited by organisms that track suitable climatic conditions by migrating seasonally between altitudes rather than latitudes.

Fill in the blank: Species richness generally ________ from the tropics toward the poles, a pattern known as the latitudinal diversity gradient, attributed to greater energy availability and climatic stability in tropical regions.

2.4.2 Physical barriers and corridors

Physical barriers such as mountain ranges, deserts, rivers, and oceans restrict the movement of organisms between areas, limiting dispersal and promoting geographic isolation; the degree to which a barrier is effective depends on the dispersal ability of the organism concerned: a large river that is an absolute barrier for a terrestrial rodent may be easily crossed by a bird or a bat; mountain ranges such as the Himalayas, the Andes, and the African Rift act as significant barriers for lowland species while simultaneously providing corridors for montane species along their length.

Corridors are linear landscape features that connect otherwise isolated habitat patches or regions, facilitating the movement of organisms between them; natural corridors include river valleys, mountain chains, and coastal strips; the Central American isthmus served as a biological corridor (as well as the land bridge discussed in the previous Series) allowing the exchange of North and South American taxa after its formation; in conservation biology, the design of habitat corridors to connect fragmented reserves is an important strategy for maintaining the dispersal and gene flow needed to sustain viable populations of wide-ranging species.

Fill in the blank: Physical ________ such as mountain ranges, deserts, and oceans restrict organism movement and promote geographic isolation, while corridors facilitate dispersal between separated areas.

2.4.3 Biotic interactions

The distribution of a species is determined not only by the physical environment but also by its interactions with other organisms: competition can exclude a species from areas where a superior competitor is present even if the physical conditions are otherwise suitable; predation can prevent a species from establishing in areas where it would otherwise thrive; and mutualistic relationships (such as those with mycorrhizal fungi or specific pollinators) can restrict a species to areas where its mutualist is also present; the distinction between the fundamental niche (the full range of conditions a species can tolerate in the absence of biotic interactions) and the realised niche (the actual conditions it occupies in the presence of competitors and predators) captures this contrast.

Disease and parasitism also influence distributions: the restriction of many large wild ungulates in Africa to areas outside the range of the tsetse fly (which transmits trypanosomiasis, or sleeping sickness) illustrates how a parasitic organism can define the boundary of an otherwise suitable range; the chytrid fungus Batrachochytrium dendrobatidis has caused the collapse of amphibian populations across multiple continents, dramatically reducing the realised distributions of many frog species; these biotic controls on distribution are increasingly important as climate change and human activity shift the ranges of parasites, predators, and competitors.

Fill in the blank: The ________ niche is the full range of conditions a species can tolerate in the absence of biotic interactions, while the realised niche reflects the conditions actually occupied in the presence of competitors and predators.

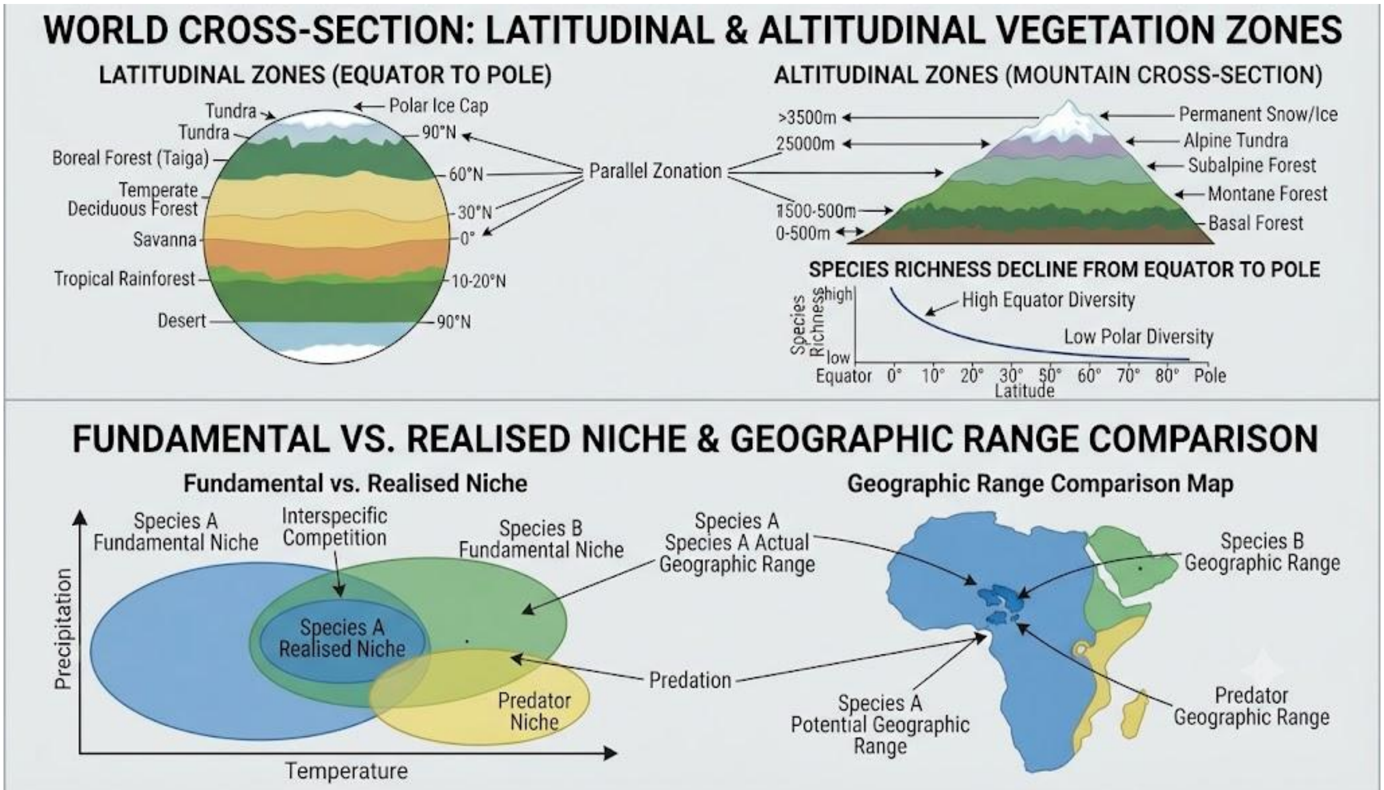


Figure 2.4: Factors affecting distribution

Pilot questions 2.4

1. Define the latitudinal diversity gradient and give one explanation for it.
2. Explain how altitudinal and latitudinal gradients in vegetation are similar.
3. Define physical barrier and give two examples.
4. Distinguish between the fundamental niche and the realised niche.
5. Give one example of a biotic interaction that restricts a species distribution.

Series Summary

This Series explored the patterns and causes of global flora and fauna distribution. The world is divided into six major floristic kingdoms, each characterised by a distinctive endemic plant flora shaped by geological history and climate, with the Australian and Cape kingdoms standing out for their extraordinary levels of endemism. The six Wallace zoogeographical regions reflect similar patterns for animals, with the Australian region unique in its marsupial-dominated fauna and the Wallace Line marking a sharp faunal boundary through the Indonesian archipelago.

Underpinning all these patterns are the interacting forces of climate and latitude, physical barriers and corridors, and biotic interactions including competition, predation, and mutualism. The close links between plant and animal distributions through coevolution, pollination, and seed dispersal mean that changes to one group ripple through to the other. Human activity through habitat destruction, invasive species introductions, overexploitation, and climate change is now reshaping distribution patterns at a pace and scale with no natural equivalent, making the understanding of natural distribution a foundation for conservation action.

Glossary of Terms

- **Biome:** a broad vegetation type defined primarily by climate, such as tropical rainforest, savanna, or tundra, occurring wherever the relevant climatic conditions prevail.
- **Coevolution:** the reciprocal evolutionary influence of two or more interacting species on one another, producing closely linked adaptations and often tightly coupled distributions.
- **Endemic:** restricted to a particular geographic area and found nowhere else in the world.
- **Floristic kingdom:** a major phytogeographical region defined by a distinctive flora with a significant proportion of endemic plant families or genera.
- **Fundamental niche:** the full range of environmental conditions a species can tolerate and utilise in the absence of biotic interactions such as competition and predation.

- **Latitudinal diversity gradient:** the general pattern of declining species richness from the species-rich tropics toward the species-poor polar regions.
- **Realised niche:** the actual environmental conditions a species occupies in nature, typically smaller than the fundamental niche due to competition, predation, and other biotic constraints.
- **Wallace Line:** the biogeographic boundary through the Indonesian archipelago separating the Oriental faunal region from the Australian faunal region, identified by Alfred Russel Wallace.
- **Zoogeographical region:** a major division of the world defined by the composition of its native animal fauna, reflecting geological history, climate, and dispersal history.

Concept Check Questions [Series 2]

Objective Questions

1. The ________ Kingdom in southwestern South Africa has the highest plant species density per unit area on Earth. (Linked to SLO 2.1)
2. The Wallace ________ marks the boundary between the Oriental and Australian faunal regions in the Indonesian archipelago. (Linked to SLO 2.2)
3. ________ (the reciprocal evolutionary influence of interacting species) drives close links between flowering plants and their pollinators. (Linked to SLO 2.3)
4. Species richness generally ________ from the tropics toward the poles, a pattern known as the latitudinal diversity gradient. (Linked to SLO 2.4)
5. The ________ niche is the full range of conditions a species can tolerate in the absence of biotic interactions. (Linked to SLO 2.4)

Short-Answer Questions

1. Name the six major floristic kingdoms. (Linked to SLO 2.1)
2. Name the six Wallace zoogeographical regions. (Linked to SLO 2.2)
3. Explain how the loss of large frugivores can affect plant distribution. (Linked to SLO 2.3)
4. Distinguish between the fundamental niche and the realised niche. (Linked to SLO 2.4)
5. Name three ways in which human activity alters flora and fauna distribution. (Linked to SLO 2.3)

Long-Answer Questions

1. Describe the major floristic kingdoms and the factors controlling plant distribution. (Linked to SLO 2.1)
2. Describe the major zoogeographical regions and the factors controlling animal distribution. (Linked to SLO 2.2)
3. Explain the relationships between plant and animal distributions and how climate, barriers, and biotic interactions affect distribution. (Linked to SLOs 2.3, 2.4)

Answers to Concept Check Questions [Series 2]

Objective Questions

1. Cape.
2. Line.
3. Coevolution.
4. Decreases.
5. Fundamental.

Short-Answer Questions

1. Holarctic, Neotropical, Palaeotropical, Cape, Australian, and Antarctic.
2. Palaearctic, Nearctic, Neotropical, Ethiopian (Afrotropical), Oriental, and Australian.
3. Large frugivores disperse seeds away from parent trees; their loss reduces seed dispersal distances, limiting plant recruitment to areas near parent trees and altering forest composition and distribution over time.
4. The fundamental niche is the full range of conditions tolerable in the absence of biotic interactions; the realised niche is the actual conditions occupied in the presence of competitors and predators, typically a subset of the fundamental niche.
5. Habitat destruction, introduction of invasive alien species, and overexploitation (or climate change).

Long-Answer Questions

1. The six floristic kingdoms (Holarctic, Neotropical, Palaeotropical, Cape, Australian, Antarctic) are defined by endemic plant families and genera. The Cape and Australian kingdoms have the highest endemism due to prolonged isolation. Climate (temperature and precipitation) is the dominant large-scale control on plant distribution; soil type, topography, and dispersal history operate at finer scales.
2. The six Wallace zoogeographical regions (Palaearctic, Nearctic, Neotropical, Ethiopian, Oriental, Australian) reflect geological history and climate. The Australian region is unique in its marsupial fauna due to Gondwanaland isolation. The Wallace Line marks the sharp Oriental-Australian boundary. Dispersal ability, food resource distribution, and climate all control animal distributions.
3. Coevolution links plant and animal distributions through pollination and seed dispersal mutualisms; losing frugivores cascades into plant distribution changes. Human activity

through habitat destruction, invasive species, and overexploitation reshapes distributions. Climate determines large-scale patterns; barriers restrict movement while corridors facilitate it; competition, predation, and mutualism define the realised niche within physically suitable areas.

Answers to Pilot Questions [Series 2]

Part 2.1

1. Phytogeography is the study of plant geographic distribution; a floristic kingdom is a major phytogeographical unit defined by a distinctive flora with a significant proportion of endemic families or genera.
2. Holarctic, Neotropical, Palaeotropical, Cape, Australian, and Antarctic.
3. The Cape Kingdom in southwestern South Africa.
4. Eucalyptus and Acacia (or Proteaceae).
5. Temperature and precipitation (and their seasonality).

Part 2.2

1. Palaearctic, Nearctic, Neotropical, Ethiopian (Afrotropical), Oriental, and Australian.
2. The Wallace Line is a biogeographic boundary through the Indonesian archipelago between Bali and Lombok and between Borneo and Sulawesi, separating the Oriental and Australian faunal regions.
3. Lions, elephants, and giraffes (or hippopotamuses, gorillas).
4. Australia has been isolated since the Gondwanaland breakup, allowing marsupials and monotremes to diversify without competition from placental mammals, producing an extraordinarily distinctive fauna.
5. Highly mobile animals such as birds can cross ocean barriers and colonise remote areas, producing cosmopolitan distributions; poorly dispersing animals such as land snails are restricted by barriers and have more localised distributions reflecting past land connections.

Part 2.3

1. Coevolution is the reciprocal evolutionary influence of interacting species; example: flowering plants and their bee pollinators, where floral shape, colour, and nectar reward have co-evolved with bee foraging behaviour.
2. Large frugivores disperse seeds; without them, seeds fall near parent trees, reducing dispersal distance, changing forest structure and plant species distribution over time.
3. The distribution of hornbills linked to large-seeded forest trees in West Africa; the distribution of elephants shaping plant communities through seed dispersal and tree modification.
4. Habitat destruction, introduction of invasive alien species, and overexploitation through hunting or collecting.
5. The introduction of Nile perch into Lake Victoria led to the extinction of many endemic cichlid fish species through predation and competition.

Part 2.4

1. The latitudinal diversity gradient is the pattern of higher species richness in the tropics declining toward the poles; it is attributed to greater solar energy input, climatic stability, and longer evolutionary history in tropical regions.
2. Both show a sequence from warm/productive vegetation types at low elevation or latitude through to cold/sparse vegetation at high elevation or high latitude; each 1,000 m rise in altitude approximates the effect of moving about 900 km poleward.
3. A physical barrier is a geographic feature that restricts the movement of organisms; examples include mountain ranges (Himalayas, Andes) and oceans.
4. The fundamental niche is all conditions tolerable in the absence of biotic interactions; the realised niche is the subset of conditions actually occupied when competitors and predators are present.
5. The tsetse fly restricts large ungulate distribution in Africa by transmitting trypanosomiasis; any area within the tsetse range is effectively excluded from the realised niche of susceptible ungulate species.

References and Attribution

Textual References (Books and External Sources)

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Figures, Plates, Tables, and Boxes

- Figure 2.1: World phytogeographical regions Attribution: AI generated. Suggested OER search string: "floristic kingdoms phytogeography world plant distribution Holarctic Neotropical Cape Australian biogeography map OER".
- Figure 2.2: Wallace zoogeographical regions Attribution: AI generated. Suggested OER search string: "zoogeographical regions Wallace Line biogeography world fauna distribution Palaearctic Neotropical Ethiopian map OER".
- Figure 2.3: Plant-animal distribution relationships Attribution: AI generated. Suggested OER search string: "plant animal coevolution pollination seed dispersal mutualism invasive species habitat fragmentation biogeography OER".
- Figure 2.4: Factors affecting distribution Attribution: AI generated. Suggested OER search string: "latitudinal diversity gradient altitudinal zonation fundamental realised niche biotic interactions barriers corridors biogeography OER".

Course code: BIO 303

Course title: Biogeography and Soil Biology

Course credit load: 2 Units

Series 3: Succession, Colonisation and Dispersal

- ## Part 3.1: Ecological Succession
  - Sub Part 3.1.1: Primary and secondary succession
  - Sub Part 3.1.2: Mechanisms and models of succession
  - Sub Part 3.1.3: Climax communities
- ## Part 3.2: Colonisation
  - Sub Part 3.2.1: Colonisation of bare substrates
  - Sub Part 3.2.2: Colonisation of new land and volcanic islands
  - Sub Part 3.2.3: Factors affecting colonisation success
- ## Part 3.3: Dispersal
  - Sub Part 3.3.1: Mechanisms of plant dispersal
  - Sub Part 3.3.2: Mechanisms of animal dispersal
  - Sub Part 3.3.3: Barriers and filters to dispersal
- ## Part 3.4: Succession, Colonisation and Dispersal in Context
  - Sub Part 3.4.1: Succession after disturbance
  - Sub Part 3.4.2: Dispersal and range expansion
  - Sub Part 3.4.3: Conservation implications

Introduction

Ecosystems are not static: they change through time as species arrive, establish, and replace one another in a process called succession. The ability of organisms to reach new or disturbed sites through dispersal is the engine that drives colonisation and succession, and understanding how organisms move through landscapes and across barriers is therefore central to understanding how communities assemble and how species ranges expand or contract over time.

This Series covers the processes of ecological succession from bare substrates through pioneer communities to climax vegetation; the colonisation of bare ground, new land, and oceanic islands; the mechanisms by which plants and animals disperse across landscapes and over barriers; and the applied significance of these processes for interpreting range expansions, managing habitat restoration, and understanding the community-level consequences of dispersal limitation and habitat fragmentation.

Series Learning Outcomes

Upon completing this Series, you should be able to:

- **SLO 3.1** distinguish primary from secondary succession and describe the mechanisms and models of succession, including climax communities,
- **SLO 3.2** describe colonisation of bare substrates and new land, and explain the factors affecting colonisation success,
- **SLO 3.3** describe the mechanisms of plant and animal dispersal and explain how barriers and filters limit dispersal, and
- **SLO 3.4** explain the significance of succession, colonisation, and dispersal for disturbance recovery, range expansion, and conservation.

3.1 Ecological Succession

3.1.1 Primary and secondary succession

Ecological succession is the directional, predictable change in community composition over time at a given location, as species colonise, establish, and are replaced by subsequent species; primary succession begins on substrates that have never supported life before, or from which all life and soil has been completely removed, such as bare rock exposed by glacial retreat, newly solidified lava flows, or sand dunes; because no soil, seed bank, or residual organic matter is present, primary succession starts from absolute zero and is typically a slow process spanning centuries.

Secondary succession begins on a substrate that previously supported a community and retains soil, a seed bank, and residual nutrients from the previous community, even though the vegetation has been removed by disturbance (such as fire, flood, agricultural abandonment, or logging); because the substrate is biologically and chemically pre-conditioned by the previous community, secondary succession is generally much faster than primary succession, with vegetation often recovering within decades; old-field succession (on abandoned agricultural land) is one of the most studied examples.

Fill in the blank: ________ succession begins on bare substrates with no previous life or soil, while secondary succession occurs on disturbed substrates that retain soil and a seed bank from the previous community.

3.1.2 Mechanisms and models of succession

Three main mechanisms drive successional change: facilitation (early-arriving pioneer species modify the environment in ways that make it more suitable for later species but less suitable for themselves, so pioneers are eventually replaced by the species they have facilitated; for example, nitrogen-fixing pioneer plants enrich soil nitrogen, enabling colonisation by later non-fixing species that can outcompete the pioneers); tolerance (species at all successional stages can establish from the beginning, but later species simply grow more slowly and eventually overtop and shade out the earlier, faster-growing species); and inhibition (early colonisers inhibit the establishment of later species, and succession only proceeds when the early colonisers die or are removed by disturbance).

The Clements model of succession (monoclimax theory) proposed that succession follows a deterministic, predictable pathway converging on a single climax community determined solely by regional climate; Gleason individualistic model proposed instead that each species responds independently to environmental gradients, and succession is less deterministic and more variable than Clement proposed; current understanding integrates both views, recognising that succession is broadly directional but influenced by chance colonisation events, the history of the site, and local environmental variation.

Fill in the blank: In the ________ mechanism of succession, pioneer species modify the environment in ways that benefit later species but reduce their own competitive advantage, causing gradual replacement.

3.1.3 Climax communities

A climax community is the relatively stable, self-perpetuating community that develops at the end of a successional sequence under a given set of climatic conditions; the Clementsian view treated the climax as a single, determinate endpoint (the monoclimax) for each climatic region; in practice, many apparently stable mature communities do exist (mature oak-hickory forest in temperate eastern North America, tropical rainforest in equatorial regions), but they are not permanently static and can be shifted by sufficiently large disturbances, shifting climates, or the arrival of new species.

The concept of a polyclimax (multiple possible stable endpoints depending on soil type, topography, local climate, and disturbance history, even within a single climatic region) better captures the observed diversity of mature community types; for example, on the same landscape in West Africa, soil and drainage differences support closed-canopy forest, derived savanna, and gallery forest as locally stable endpoints; the distinction between true climax communities maintained by climate and edaphic climaxes or plagioclimaxes maintained by soil or human disturbance is important for interpreting vegetation patterns.

Fill in the blank: A ________ climax refers to multiple possible stable endpoints within a single climatic region, depending on soil type, topography, and local disturbance history.

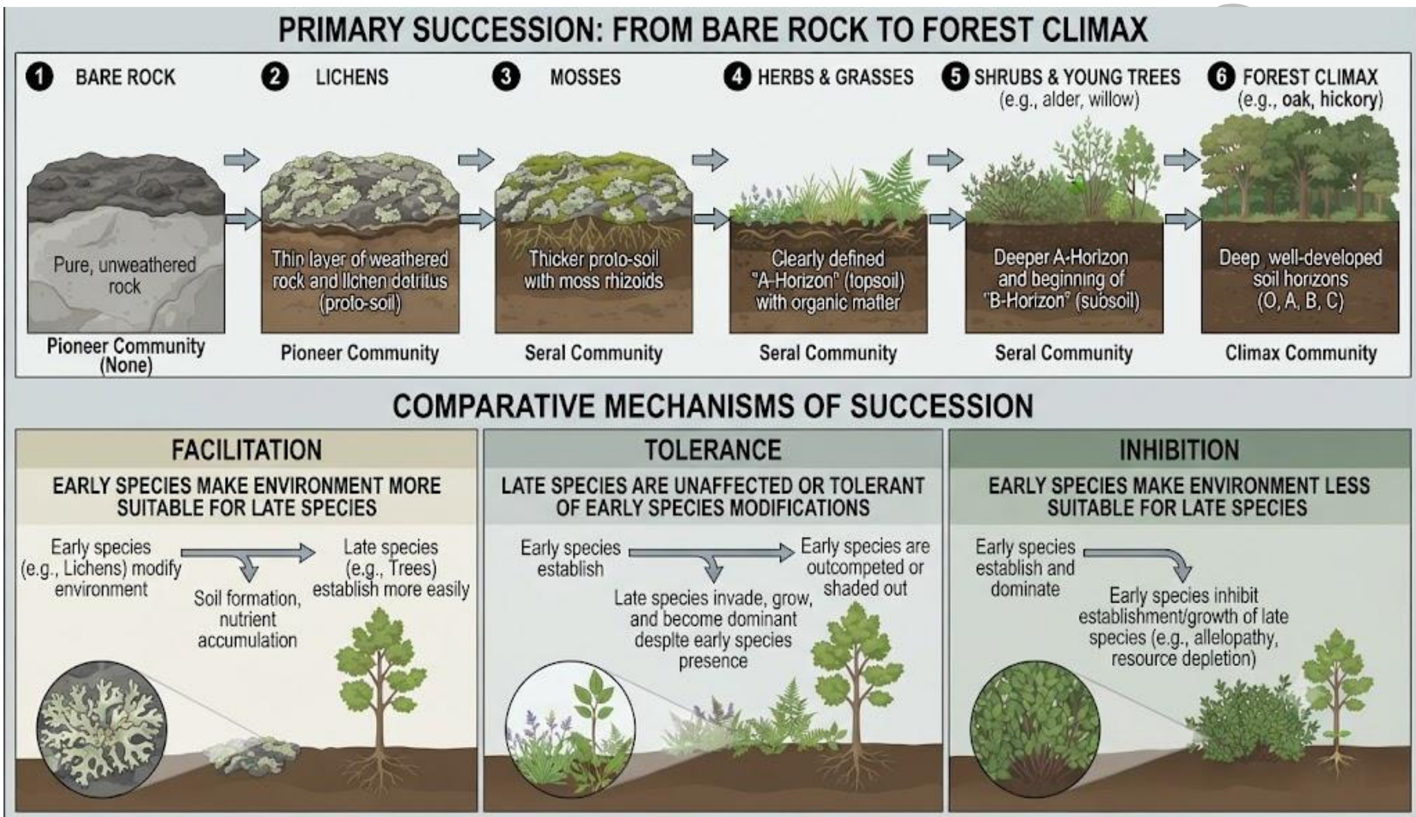

Figure 3.1: Ecological succession

Pilot questions 3.1

1. Distinguish between primary and secondary succession.
2. Give one example each of a habitat where primary and secondary succession would occur.
3. Describe the facilitation mechanism of succession.
4. Distinguish between the monoclimax and polyclimax concepts.
5. Define a plagioclimax and give one example.

3.2 Colonisation

3.2.1 Colonisation of bare substrates

Colonisation is the establishment of organisms in a previously unoccupied or newly available site; on bare mineral substrates such as rock, sand, or freshly deposited alluvium, the first colonisers (pioneer species) must be able to tolerate extreme physical conditions including intense solar radiation, extreme temperature fluctuations, desiccation, nutrient poverty, and lack of shelter; pioneer species typically have efficient dispersal mechanisms (producing large quantities of small, wind-dispersed propagules), rapid growth rates, high tolerance of physiological stress, and the ability to fix atmospheric nitrogen or exploit minimal nutrients.

Cryptogams (lichens, mosses, and cyanobacteria) are the most successful colonisers of bare rock because they can survive severe desiccation, resume growth rapidly after rewetting, and are capable of weathering the mineral substrate and accumulating organic matter; lichens in particular dissolve minerals through the organic acids they secrete, contributing to physical and chemical weathering that gradually builds a thin substrate capable of supporting other organisms; over time, the accumulating organic matter and weathered mineral particles form the precursor of true soil.

Fill in the blank: ________ such as lichens, mosses, and cyanobacteria are the most successful colonisers of bare rock due to their ability to tolerate desiccation and weather mineral substrates.

3.2.2 Colonisation of new land and volcanic islands

The colonisation of newly formed volcanic islands provides a natural experiment in community assembly from scratch; the Surtsey volcanic island, which emerged from the sea off Iceland in 1963, has been extensively studied as organisms arrived from the Icelandic mainland by wind, sea, and birds over the subsequent decades; the sequence of colonisation was strongly influenced by distance from source areas, the prevailing wind direction, and the presence of seabirds whose nesting activity introduced nutrients and propagules from their bodies and guano.

The 1883 eruption of Krakatau in Indonesia, which destroyed all life on the island, allowed the recolonisation process to be followed over more than a century; the initial colonisers were wind-dispersed ferns and grasses, followed by bird-dispersed seeds brought by fruit-eating birds from the neighbouring islands of Java and Sumatra; within decades, a forest community had established, demonstrating the importance of the surrounding species pool and dispersal mechanisms in determining the rate and trajectory of colonisation on newly available land.

Fill in the blank: The recolonisation of ________ after the 1883 eruption provided a long-term natural experiment in island colonisation, demonstrating the importance of the surrounding species pool and dispersal vectors.

3.2.3 Factors affecting colonisation success

Colonisation success is determined by several interacting factors: propagule pressure (the number and frequency of dispersal events delivering propagules to the site; high propagule pressure increases the probability of successful establishment); the match between the physiological tolerances of the arriving species and the environmental conditions at the site; the presence or absence of competitors, predators, or mutualists at the site (biotic resistance); and the availability of suitable microsites (physical locations within the site that provide shelter, moisture, or nutrients sufficient for germination and establishment).

Priority effects (the influence of early-arriving species on the establishment success of later arrivals, either through facilitation or inhibition) mean that the identity and order of colonists can influence the trajectory of community development; stochastic (chance) events in colonisation, such as which propagule arrives first or which microsite it lands on, can therefore produce different community compositions at similar sites even when the regional species pool and physical environment are the same; this contingency in community assembly has important implications for predicting and managing ecosystem restoration.

Fill in the blank: ________ effects describe how early-arriving species influence the establishment success of later arrivals, either facilitating or inhibiting their colonisation.

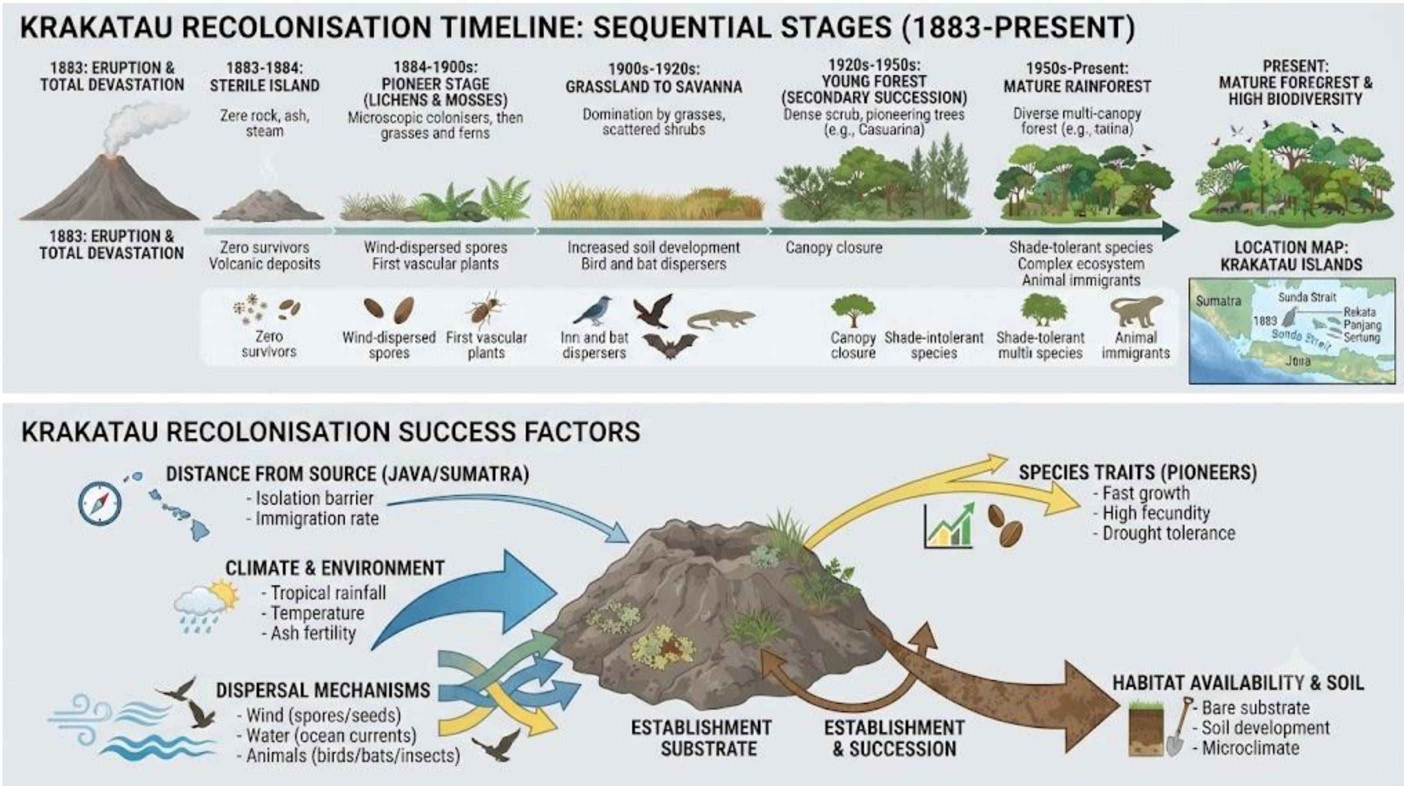

Figure 3.2: Colonisation of new substrates

Pilot questions 3.2

1. Define colonisation and name two characteristics of pioneer species.
2. Explain why cryptogams are particularly successful colonisers of bare rock.
3. Describe what happened at Krakatau in 1883 and why it is biogeographically significant.
4. Define propagule pressure and explain its importance for colonisation.
5. Explain what priority effects are and why they matter for community assembly.

3.3 Dispersal

3.3.1 Mechanisms of plant dispersal

Plant dispersal (the movement of seeds, spores, or vegetative propagules away from the parent plant) occurs through several principal mechanisms: anemochory (wind dispersal, including plumed or winged seeds such as those of dandelion, cotton, and maple, and dust-like spores of ferns and mosses that can travel thousands of kilometres); hydrochory (water dispersal, including seeds floating in rivers to new riverine habitats, or oceanic dispersal of coconuts and mangrove propagules); zoochory (animal dispersal, subdivided into endozoochory where seeds pass through the gut after ingestion of fleshy fruits, and epizoochory where seeds or fruits with hooks or sticky surfaces attach to animal fur or feathers).

Autochory (self-dispersal) includes ballistic dispersal by plants that explosively eject seeds (such as Impatiens touch-me-not and Hura the sandbox tree), and barochory (gravity dispersal) where heavy fruits simply fall; each dispersal mechanism has characteristic dispersal distances, with wind and animal gut-passage typically producing long-distance dispersal events while gravity produces very short distances; the dispersal syndrome (the combination of morphological traits associated with a particular dispersal mechanism) is an important tool for predicting how a plant will disperse and therefore how quickly it can colonise new sites.

Fill in the blank: ________ is the mechanism of plant dispersal by animals, and includes endozoochory (seeds ingested and passed through the gut) and epizoochory (seeds attached to fur or feathers).

3.3.2 Mechanisms of animal dispersal

Animals disperse by active movement (walking, flying, or swimming) or passively (rafting, being carried by wind or water, or hitchhiking on other organisms or human transport); natal dispersal (the movement of young animals away from their birth site to establish a new territory or home range) is a fundamental behavioural event in the life of most vertebrates and many invertebrates, and its distance and direction largely determine gene flow between populations and the rate at which a species can expand its range into new areas.

Long-distance dispersal events, though rare for any individual, are disproportionately important in biogeography because they determine whether organisms can cross barriers and colonise remote areas; the colonisation of oceanic islands by terrestrial birds, bats, and lizards despite separation by hundreds or thousands of kilometres of ocean requires occasional long-distance dispersal events, sometimes aided by storms; migratory birds and marine mammals that move between continents act as dispersal vectors for parasites, pathogens, and smaller organisms (such as seeds in gut contents or invertebrates attached to feathers).

Fill in the blank: ________ dispersal is the movement of young animals away from their birth site to establish in a new area, and largely determines gene flow between populations and the rate of range expansion.

3.3.3 Barriers and filters to dispersal

A dispersal barrier is any feature of the landscape that prevents or greatly reduces the movement of organisms across it; barriers are not absolute for all species but are selective, acting as filters that allow some species through while blocking others; a sea channel is an absolute barrier for a terrestrial rodent but no barrier at all for a seabird; a mountain range is a barrier for lowland forest species but a corridor for montane species; the distinction between sweepstake routes (barriers that allow very occasional crossings by almost any group, such as transoceanic dispersal) and filter bridges (connections that allow crossing by some but not all groups) is important in historical biogeography.

Human modification of landscapes creates new barriers (roads, urban areas, agricultural land, and reservoirs that fragment natural habitats and reduce the permeability of the landscape to dispersing organisms) and removes natural barriers (transport pathways and introduced propagule pressure that allow alien species to bypass barriers they could never cross naturally); the net effect of human landscape modification is typically to reduce dispersal of native species while facilitating the spread of alien invasive species, with serious consequences for biodiversity and ecosystem function.

Fill in the blank: A ________ route is a dispersal pathway across a major barrier that allows very occasional crossings by almost any taxonomic group, such as transoceanic dispersal to remote islands.

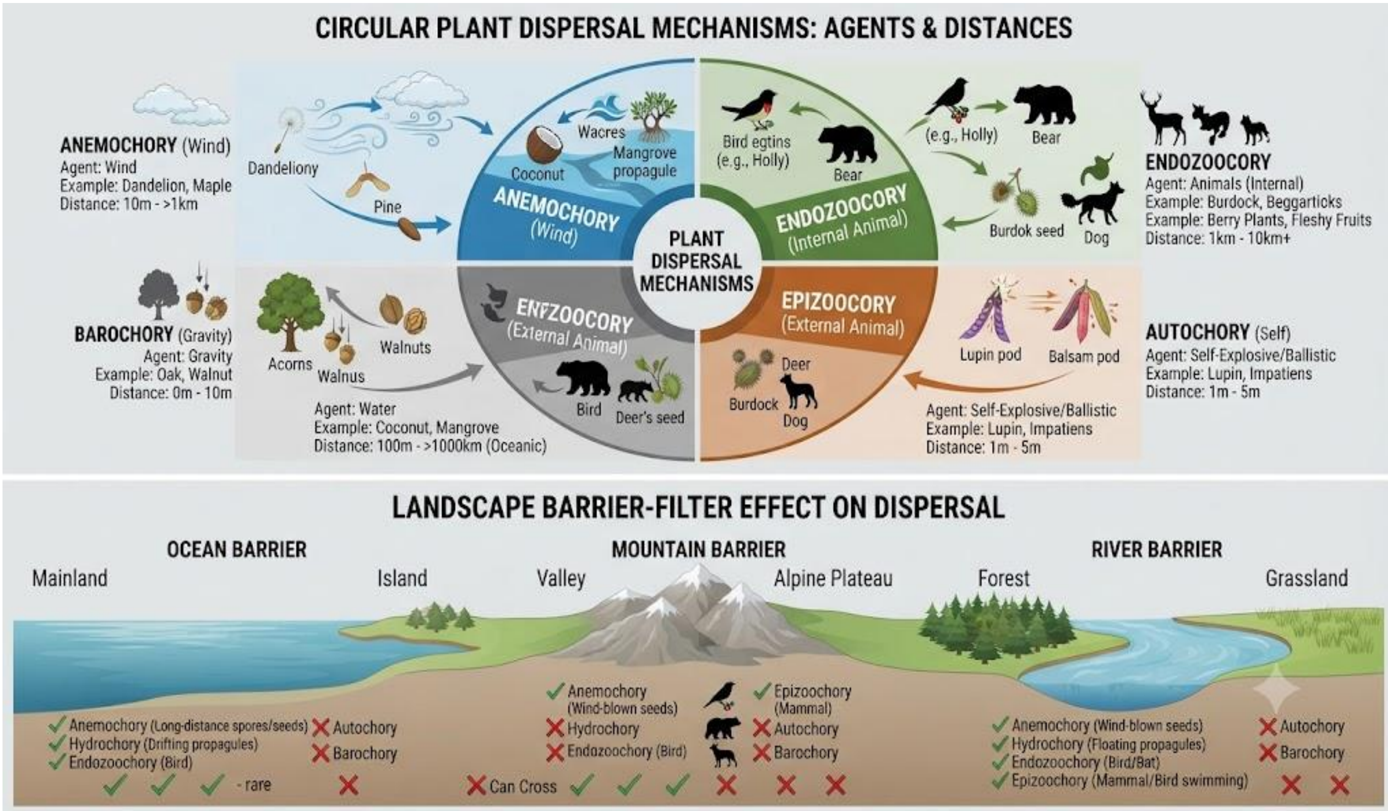

Figure 3.3: Plant and animal dispersal mechanisms

Pilot questions 3.3

1. Name and briefly describe four mechanisms of plant seed dispersal.
2. Distinguish between endozoochory and epizoochory.
3. Define natal dispersal and explain its biogeographic significance.
4. Explain what a dispersal barrier is and give two examples.
5. Distinguish between a sweepstake route and a filter bridge.

3.4 Succession, Colonisation and Dispersal in Context

3.4.1 Succession after disturbance

Disturbance (any event that removes or damages organisms and creates openings for colonisation) is a normal and important component of most ecosystems, maintaining species diversity by preventing competitive exclusion by dominant species (the intermediate disturbance hypothesis proposes that species diversity is highest at intermediate levels of disturbance frequency and intensity, where neither early-successional specialists nor late-successional dominants can monopolise the community); fires, floods, windthrow, herbivory, and human clearance all function as disturbances that reset succession to earlier stages.

The resilience and trajectory of post-disturbance succession depends on the nature and severity of the disturbance, the composition of the surrounding species pool, the dispersal distances of key species, and the condition of the seed bank and soil; in tropical forests, selective logging that retains the seed bank and surrounding forest cover allows rapid secondary succession, while complete forest clearance followed by agricultural use degrades the seed bank, reduces the local species pool, and can deflect succession toward persistent grass-dominated states rather than recovering forest.

Fill in the blank: The intermediate ________ hypothesis proposes that species diversity is highest at intermediate levels of disturbance, where neither early- nor late-successional species can monopolise the community.

3.4.2 Dispersal and range expansion

Species ranges expand when individuals successfully disperse beyond the existing range boundary, establish viable populations, and those populations in turn produce dispersing offspring that continue the expansion; the rate of range expansion depends on the dispersal distance per generation, the intrinsic growth rate of the population, and the suitability of the landscape beyond the current range boundary; rapid range expansions are documented for many invasive alien species, which often lack the natural enemies that limit their populations in their native range, and for native species tracking climate-driven shifts in their suitable habitat.

Range expansions are not always continuous: species can undergo long-distance jump dispersal events that establish outlier populations well beyond the main range boundary, and these outlier populations can then serve as bridgeheads for further expansion; the collared dove (Streptopelia decaocto) expanded its range across Europe from its original range in Turkey and the Balkans over just a few decades in the mid-twentieth century, demonstrating how rapid range expansion can be when a species encounters a landscape of suitable but previously unoccupied habitat.

Fill in the blank: ________ dispersal events establish outlier populations well beyond the main range boundary and can accelerate overall range expansion by acting as bridgeheads for further spread.

3.4.3 Conservation implications

Understanding succession, colonisation, and dispersal is essential for conservation biology and ecological restoration: the rate and trajectory of succession after disturbance determines how quickly degraded habitats can recover, and whether active intervention (planting, seeding, or controlling invasive species) is needed to overcome dispersal limitation or competitive inhibition that would otherwise deflect succession away from the desired endpoint; passive restoration (removing the disturbance pressure and allowing succession to proceed naturally) is most effective where the surrounding landscape provides a diverse propagule source and where the seed bank is largely intact.

Habitat fragmentation reduces the permeability of landscapes to dispersing organisms, isolating populations in habitat patches and reducing the gene flow and recolonisation that maintain genetic diversity and rescue declining populations; designing landscape-scale conservation networks with sufficient connectivity (via habitat corridors and stepping-stone patches) to maintain dispersal is a central goal of conservation planning; understanding which species are most dispersal-limited and most vulnerable to fragmentation allows prioritisation of connectivity interventions for the species most at risk.

Fill in the blank: ________ restoration relies on removing disturbance pressure and allowing natural succession to proceed, and is most effective where the surrounding landscape provides a diverse propagule source.

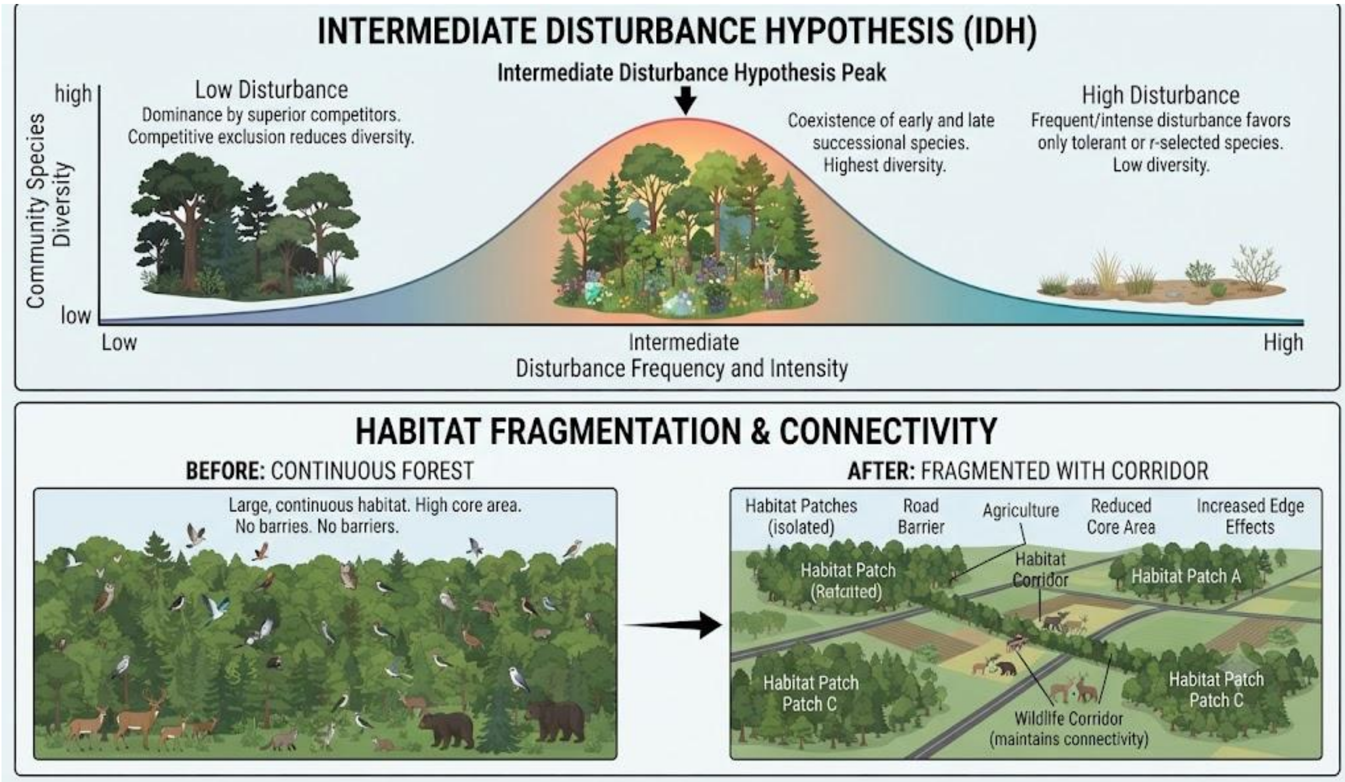

Figure 3.4: Succession and dispersal in applied context

Pilot questions 3.4

1. State the intermediate disturbance hypothesis.
2. Name three types of disturbance that reset succession to earlier stages.
3. Explain what determines the rate of a species range expansion.
4. Explain what jump dispersal is and give one example.
5. Explain why passive restoration may be insufficient in heavily fragmented landscapes.

Series Summary

This Series examined the dynamic processes through which communities assemble, develop, and change over time. Ecological succession progresses from bare substrates through pioneer communities to more complex mature assemblages, driven by facilitation, tolerance, or inhibition mechanisms, with primary succession beginning on lifeless substrates and secondary succession rebuilding on previously occupied ground. The concept of the climax community captures the relatively stable endpoint of succession, though both monoclimax and polyclimax views recognise that multiple stable states can exist depending on local environmental conditions and disturbance history.

Colonisation and dispersal are the engines of succession and range change. Pioneer species must overcome extreme physical conditions to establish on bare ground, as illustrated by the recolonisation of Krakatau. Dispersal mechanisms ranging from wind and water to animal vectors determine which species reach new sites and how quickly ranges expand, while barriers and filters shape the biogeographic patterns that result. Applied understanding of these processes informs habitat restoration, the management of invasive species, and the design of landscape connectivity networks to support dispersal in fragmented environments.

Glossary of Terms

- **Anemochory:** dispersal of seeds or spores by wind, characteristic of plants producing light, plumed, or winged propagules such as dandelions and maples.
- **Climax community:** the relatively stable, self-perpetuating plant community that develops at the end of a successional sequence under a given set of environmental conditions.
- **Cryptogams:** non-flowering plants and plant-like organisms including lichens, mosses, and algae, which are typically the first colonisers of bare mineral substrates.
- **Dispersal:** the movement of individuals or propagules away from their origin, enabling colonisation of new sites and gene flow between populations.

- **Facilitation:** a successional mechanism in which pioneer species modify the environment in ways that benefit later-arriving species but reduce their own competitive advantage.
- **Intermediate disturbance hypothesis:** the proposal that species diversity is highest at intermediate levels of disturbance frequency and intensity.
- **Natal dispersal:** the movement of a young animal away from its birth site to establish a new home range or territory.
- **Pioneer species:** the first organisms to colonise a bare or disturbed substrate, typically tolerant of extreme physical conditions and capable of efficient dispersal.
- **Primary succession:** succession beginning on substrates that have never previously supported life or from which all life and soil have been completely removed.
- **Secondary succession:** succession on a previously occupied substrate that retains soil, a seed bank, and residual nutrients from the prior community.

Concept Check Questions [Series 3]

Objective Questions

1. ________ succession begins on substrates with no previous life or soil, while secondary succession occurs on disturbed substrates retaining a seed bank. (Linked to SLO 3.1)
2. In the facilitation mechanism, pioneer species modify the environment to benefit ________ species, eventually causing their own replacement. (Linked to SLO 3.1)
3. ________ such as lichens, mosses, and cyanobacteria are the most successful colonisers of bare rock. (Linked to SLO 3.2)
4. ________ is the dispersal of plant propagules by animals through ingestion and gut passage. (Linked to SLO 3.3)
5. The intermediate ________ hypothesis proposes that species diversity is highest at intermediate levels of disturbance. (Linked to SLO 3.4)

Short-Answer Questions

1. Distinguish between primary and secondary succession. (Linked to SLO 3.1)
2. Describe the facilitation mechanism of succession. (Linked to SLO 3.1)
3. Explain why cryptogams are successful early colonisers. (Linked to SLO 3.2)
4. Name and describe four mechanisms of plant seed dispersal. (Linked to SLO 3.3)
5. Explain why passive restoration may be insufficient in highly fragmented landscapes. (Linked to SLO 3.4)

Long-Answer Questions

1. Describe primary and secondary succession, the mechanisms driving succession, and the climax community concept. (Linked to SLO 3.1)
2. Describe colonisation of bare substrates and explain the factors affecting colonisation success. (Linked to SLO 3.2)
3. Describe the mechanisms of plant and animal dispersal, and explain barriers and filters to dispersal. (Linked to SLO 3.3)

Answers to Concept Check Questions [Series 3]

Objective Questions

1. Primary.
2. Later.
3. Cryptogams.
4. Endozoochory.
5. Disturbance.

Short-Answer Questions

1. Primary succession starts on lifeless substrates with no soil; secondary succession occurs on disturbed substrates that retain soil, a seed bank, and residual nutrients.
2. Pioneer species modify the environment (e.g. enriching soil nitrogen) making it suitable for later species that can outcompete the pioneers, leading to gradual replacement of the pioneers.
3. Cryptogams tolerate extreme desiccation and temperature fluctuations, can weather mineral substrates through organic acid secretion, and accumulate organic matter, building a substrate for later colonisers.
4. Anemochory (wind), hydrochory (water), zoochory (animals, including endozoochory and epizoochory), and autochory (self-dispersal by explosive or gravity mechanisms).
5. In heavily fragmented landscapes, few propagules from surrounding habitat can reach isolated patches; the local seed bank may be depleted; competitive or invasive species may inhibit succession; active intervention such as planting or seeding may be needed to overcome dispersal limitation.

Long-Answer Questions

1. Primary succession begins on bare substrates (rock, lava, sand) with no soil; secondary succession rebuilds on previously occupied ground retaining soil and seed bank. Facilitation: pioneers improve conditions for later species. Tolerance: all establish early but slow-growing late species eventually dominate. Inhibition: pioneers block later species until they die or are disturbed. Climax community is the stable endpoint; monoclimax (one climatic endpoint) versus polyclimax (multiple endpoints depending on soil, topography) are contrasting views.
2. Colonisation of bare substrates requires extreme stress tolerance; pioneer species have efficient dispersal, rapid growth, and ability to exploit minimal nutrients. Cryptogams colonise bare rock by tolerating desiccation and weathering minerals. Volcanic islands (Krakatau, Surtsey) illustrate natural colonisation experiments. Colonisation success depends

on propagule pressure, environmental match, biotic resistance, microsite availability, and priority effects.

3. Plant dispersal: anemochory (wind), hydrochory (water), endozoochory (seed ingested and passed in gut), epizoochory (attached to fur/feathers), autochory (self-dispersal). Animal dispersal: active movement (natal dispersal) and passive (rafting, storm-aided). Barriers are landscape features restricting movement (oceans, mountains); sweepstake routes allow rare crossings; filter bridges allow some but not all groups. Human fragmentation creates new barriers for native species while facilitating invasive species spread.

Answers to Pilot Questions [Series 3]

Part 3.1

1. Primary succession begins on bare substrates with no soil or seed bank; secondary succession occurs on substrates previously supporting life, retaining soil and seed bank.
2. Primary: bare lava flow or glacially scoured rock. Secondary: abandoned agricultural field or logged forest.
3. Pioneer species modify the environment (e.g. fixing nitrogen or building organic matter) making conditions better for later species; those later species outcompete and eventually replace the pioneers.
4. Monoclimax: one stable climax determined by regional climate. Polyclimax: multiple stable endpoints within a region, varying with soil, topography, and local disturbance history.
5. A plagioclimax is a community maintained in an artificially early successional state by ongoing human disturbance (e.g. grazing or burning); example: West African derived savanna maintained by repeated burning of forest.

Part 3.2

1. Colonisation is the establishment of organisms in a previously unoccupied site; pioneer species characteristics include efficient dispersal, stress tolerance, rapid growth, and ability to fix nitrogen or exploit minimal nutrients.

2. Cryptogams tolerate extreme desiccation, resume growth rapidly after rewetting, and can weather mineral substrates through organic acid secretion, gradually building organic matter that supports further colonisation.
3. Krakatau erupted in 1883, destroying all life on the island; subsequent recolonisation by wind-dispersed and bird-dispersed species has been studied for over a century, making it a classic natural experiment in island colonisation.
4. Propagule pressure is the number and frequency of dispersal events delivering propagules to a site; high propagule pressure increases the probability that at least some arrivals will successfully establish.
5. Priority effects occur when early-arriving species influence the success of later colonisers through facilitation or inhibition; they mean that colonisation history can determine community composition even when sites are physically identical.

Part 3.3

1. Anemochory (wind, e.g. dandelion), hydrochory (water, e.g. coconut), endozoochory (ingested by animals, e.g. fleshy berries), epizoochory (attached to fur, e.g. burdock hooks).
2. Endozoochory: seeds are ingested in fleshy fruits and passed through the gut of an animal, often with enhanced germination. Epizoochory: seeds or fruits with hooks, barbs, or sticky coatings attach to the external surface of animals.
3. Natal dispersal is the movement of young animals from their birth site to establish elsewhere; it determines gene flow between populations and the rate at which a species can expand its range into new areas.
4. A dispersal barrier is any landscape feature restricting organism movement; examples: ocean (absolute barrier for terrestrial rodents), mountain range (barrier for lowland species).
5. A sweepstake route is a barrier that allows very occasional crossings by almost any group; a filter bridge allows crossing by some but not all groups, selectively filtering which taxa can disperse across it.

Part 3.4

1. The intermediate disturbance hypothesis proposes that species diversity is highest at intermediate levels of disturbance frequency and intensity, where neither early-successional pioneers nor late-successional dominants can monopolise the community.
2. Fire, flood, and windthrow (or herbivory, selective logging).

3. The rate of range expansion depends on dispersal distance per generation, the intrinsic population growth rate, and the suitability and permeability of the landscape beyond the current range boundary.
4. Jump dispersal is a long-distance colonisation event that establishes a population well beyond the main range boundary; example: the establishment of a collared dove population far ahead of the main expanding front in Europe.
5. In fragmented landscapes, few propagules from surrounding habitat reach isolated patches; the seed bank may be depleted; without sufficient connectivity, natural recolonisation is too slow and active restoration through planting or seeding is needed.

References and Attribution

Textual References (Books and External Sources)

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Figures, Plates, Tables, and Boxes

- Figure 3.1: Ecological succession Attribution: AI generated. Suggested OER search string: "ecological succession primary secondary climax facilitation tolerance inhibition pioneer community diagram biogeography OER".
- Figure 3.2: Colonisation of new substrates Attribution: AI generated. Suggested OER search string: "colonisation bare substrate Krakatau Surtsey volcanic island pioneer species propagule pressure priority effects OER".
- Figure 3.3: Plant and animal dispersal mechanisms Attribution: AI generated. Suggested OER search string: "plant dispersal mechanisms anemochory zoochory hydrochory animal dispersal barriers filters sweepstake routes biogeography OER".
- Figure 3.4: Succession and dispersal in applied context Attribution: AI generated. Suggested OER search string: "intermediate disturbance hypothesis succession range expansion habitat fragmentation connectivity corridor conservation restoration biogeography OER".

Course code: BIO 303

Course title: Biogeography and Soil Biology

Course credit load: 2 Units

Series 4: Endemicity, Refugia and Island Biogeography

- **Part 4.1: Endemicity**
  - Sub Part 4.1.1: Definition and types of endemism
  - Sub Part 4.1.2: Centres of endemism
  - Sub Part 4.1.3: Causes of endemism
- **Part 4.2: Refugia**
  - Sub Part 4.2.1: The concept of refugia
  - Sub Part 4.2.2: Pleistocene refugia in Africa
  - Sub Part 4.2.3: Refugia and biodiversity hotspots
- **Part 4.3: Island Biogeography**
  - Sub Part 4.3.1: The theory of island biogeography
  - Sub Part 4.3.2: Species-area relationships
  - Sub Part 4.3.3: Turnover and equilibrium
- **Part 4.4: Applications of Island Biogeography and Endemicity**
  - Sub Part 4.4.1: Island biogeography and conservation biology
  - Sub Part 4.4.2: Endemicity and conservation priorities
  - Sub Part 4.4.3: Climate change and endemic species

Introduction

Some of the most striking features of biogeographic patterns are the extraordinary concentrations of unique species found in particular places. Endemism, the restriction of a species to a defined geographic area, is not distributed randomly across the Earth but is concentrated in regions with long histories of isolation, climatic stability, or exceptional environmental diversity. Understanding where endemic species are concentrated and why they occur there is central to biogeography and to conservation.

This Series covers endemism and its causes; the concept of refugia as areas where species survived past climatic extremes and from which they subsequently recolonised surrounding areas; the equilibrium theory of island biogeography and the species-area relationship; and the practical applications of these concepts to conservation biology, the designation of protected areas, and the identification of species most vulnerable to ongoing climate change.

Series Learning Outcomes

Upon completing this Series, you should be able to:

- **SLO 4.1** define endemism, distinguish its types, describe centres of endemism, and explain the causes of endemism,
- **SLO 4.2** explain the concept of refugia and describe the role of Pleistocene refugia in generating current biodiversity patterns in Africa,
- **SLO 4.3** describe the equilibrium theory of island biogeography, the species-area relationship, and species turnover, and
- **SLO 4.4** explain the conservation applications of island biogeography and endemicity, and the vulnerability of endemic species to climate change.

4.1 Endemicity

4.1.1 Definition and types of endemism

Endemism refers to the restriction of a taxon (species, genus, or family) to a defined geographic area; a species is said to be endemic to a region if it occurs naturally there and nowhere else in the world; the scale of the area used to define endemism is variable and context-dependent, ranging from a single mountain, lake, or island at the finest scale, through national endemics (species restricted to a single country), to regional endemics (restricted to a biogeographic region such as West Africa or the Mediterranean basin).

Palaeoendemics (relict endemics) are species that were once more widely distributed but have become restricted to a small area as their former range contracted due to climate change, habitat loss, or competitive exclusion; they are often taxonomically isolated, representing ancient lineages with few close relatives; neoendemics (young endemics) are recently evolved species that have not yet had time to spread beyond their area of origin; distinguishing palaeoendemics from neoendemics requires integrating phylogenetic, fossil, and molecular clock evidence.

Fill in the blank: ________ are endemic species that were once more widely distributed but have contracted to a small area, while neoendemics are recently evolved species that have not yet spread beyond their origin.

4.1.2 Centres of endemism

Centres of endemism (also called areas of endemism or endemic bird areas) are geographic areas with an unusually high concentration of endemic species relative to their area; well-known centres of endemism include the Cape Floristic Region of southwestern South Africa (with over 8,500 plant species, approximately 70 percent endemic), the Hawaiian Islands (with extraordinarily high endemism in birds, plants, and invertebrates reflecting long isolation and adaptive radiation), Madagascar (highly endemic mammals, birds, reptiles, and plants including the lemurs, whose entire diversity is endemic to the island), and the Albertine Rift of East and Central Africa.

The identification of centres of endemism is a key step in systematic conservation planning, since these areas contain irreplaceable biodiversity (species found nowhere else) that cannot be substituted by protecting other areas; the overlap of multiple centres of endemism with high species richness, high threat from habitat loss, and small remaining natural habitat defines biodiversity hotspots (a concept developed by Norman Myers and subsequently formalised by Conservation International), which have become the focus of major international conservation investment.

Fill in the blank: ________ hotspots are regions with exceptional concentrations of endemic species, high overall species richness, and severe habitat loss, prioritised for international conservation investment.

4.1.3 Causes of endemism

Endemism is generated by any process that restricts a taxon to a limited area: geographic isolation (islands, mountain tops, isolated lakes, and caves cut off from similar habitats generate endemism through restricted gene flow and independent evolution); climatic or ecological specialisation (species adapted to highly specific soil types, microhabitats, or climatic conditions that occur only in a limited area); long evolutionary history in isolation (taxa with ancient lineages that evolved in a region over tens of millions of years accumulate endemic diversity through in-situ diversification, as in Australia and Madagascar).

Endemism is typically higher in regions with complex topography (where mountains create many isolated valleys and elevational gradients supporting diverse communities), diverse soils, long geological stability, and low extinction rates; islands are inherently strong generators of endemism because their isolation filters which colonists arrive and prevents subsequent gene flow with the mainland, allowing the colonists to diverge independently; the extraordinary endemism of oceanic islands such as Hawaii and the Galapagos reflects the combination of isolation, diverse habitats, and adaptive radiation from a small number of ancestral colonists.

Fill in the blank: Islands generate high endemism because their ________ from mainland areas prevents gene flow, allowing colonist lineages to diverge independently and undergo adaptive radiation.

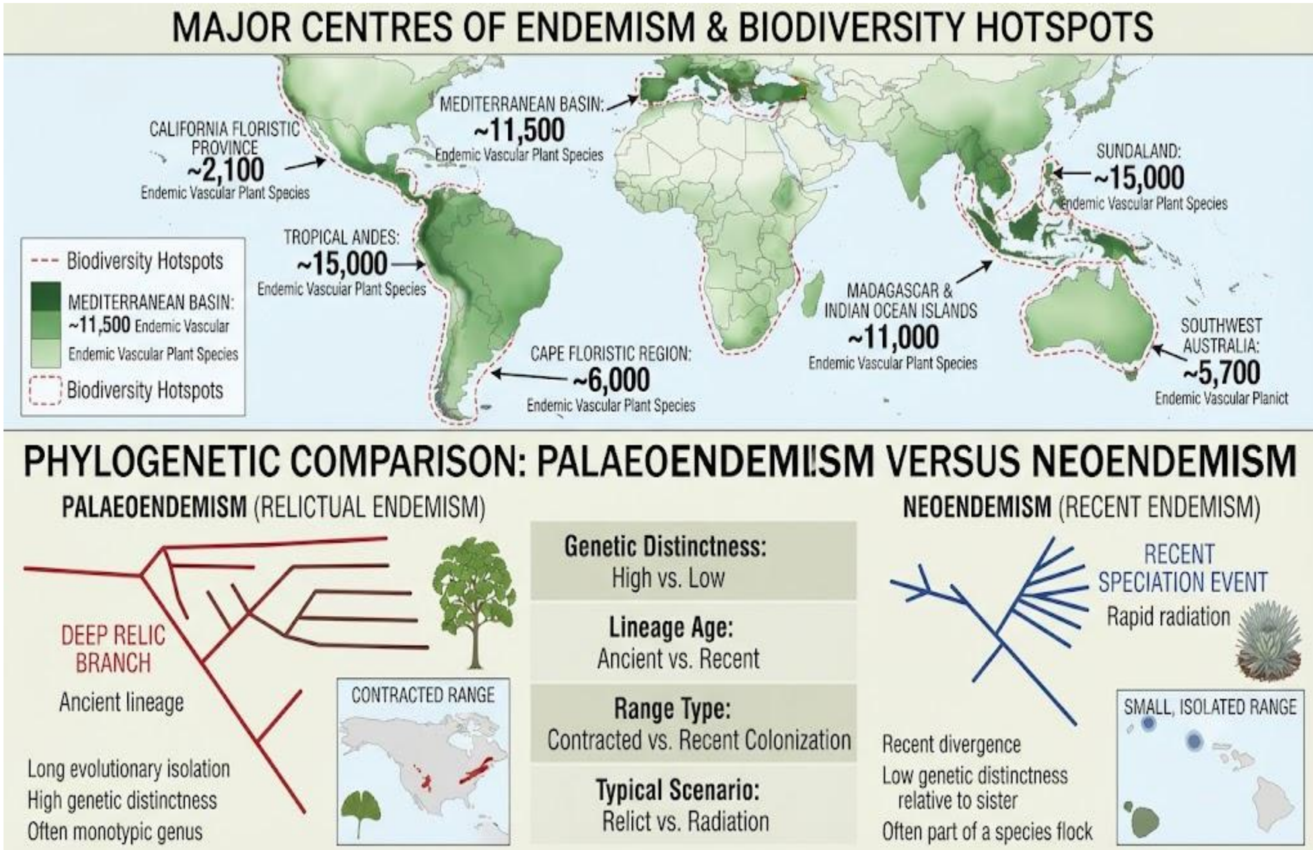

Figure 4.1: Endemicity and centres of endemism

Pilot questions 4.1

1. Define endemism and explain how the scale of the defined area affects the designation.
2. Distinguish between palaeoendemics and neoendemics.
3. Name three centres of endemism and state one characteristic endemic taxon for each.
4. Explain what a biodiversity hotspot is.
5. Give three causes of high endemism in a region.

4.2 Refugia

4.2.1 The concept of refugia

A refugium (plural refugia) is an area where a population of organisms survived a period of unfavourable environmental conditions (such as glaciation, aridification, or sea level change) that eliminated populations from surrounding areas; populations confined to refugia during an adverse period survived in relatively stable local conditions, and after conditions improved they expanded back out from the refugium into surrounding areas, recolonising the previously inhospitable terrain; this pattern of contraction into refugia followed by expansion produces genetic signatures that can be detected in molecular phylogeographic analyses.

The refugium concept was developed initially in the context of Pleistocene glacial cycles in the northern hemisphere, where ice sheets forced plant and animal communities southward into refugia in southern Europe, the Iberian peninsula, the Balkans, and Italy; after each glacial retreat, recolonisation of northern Europe proceeded from these southern refugia, producing a characteristic pattern of declining genetic diversity from south to north (reflecting the accumulated genetic drift in small refugial populations) and distinct genetic lineages reflecting the different refugial populations.

Fill in the blank: A ________ is an area where populations survived an adverse environmental period while surrounding areas became uninhabitable, subsequently providing the source for recolonisation of the wider region.

4.2.2 Pleistocene refugia in Africa

In Africa, the Pleistocene was characterised not by glaciation at the landscape scale (except at high elevations) but by alternating periods of greater and lesser aridity; during arid phases, forests contracted to refugia in areas with reliable rainfall (particularly along the west African coast, in the Congo Basin, and in the East African mountains), while savanna and desert expanded; the theory of Pleistocene forest refugia in Africa, developed by Jurgen Haffer from analysis of bird distributions, proposed that the fragmentation of forest into isolated refugia promoted speciation by isolating populations.

Evidence for Pleistocene forest refugia in Africa comes from the distribution of forest-restricted species (with many showing disjunct distributions or centres of diversity corresponding to proposed refugia), pollen records showing past vegetation changes, and molecular phylogeographic studies revealing deep genetic divergences between populations in different refugial areas; the Upper Guinea forests of West Africa (including those of Nigeria), the Congo Basin, and the East African montane forests are the main proposed African refugia, and their boundaries correspond to centres of high endemism and species richness in many plant, bird, and invertebrate groups.

Fill in the blank: The theory of Pleistocene forest ________ in Africa proposes that forest contracted into isolated pockets during arid phases, promoting speciation by separating previously continuous populations.

4.2.3 Refugia and biodiversity hotspots

There is a strong correspondence between the locations of proposed Pleistocene refugia and present-day biodiversity hotspots and centres of endemism, supporting the refugial hypothesis as a major mechanism generating the current pattern of tropical biodiversity; regions that served as refugia during past unfavourable periods accumulated unique endemic species through in-refugium speciation, and retained higher overall diversity because they acted as persistent source areas from which surrounding regions were colonised and recolonised through repeated cycles of contraction and expansion.

However, the relationship between refugia and hotspots is not universal: not all hotspots coincide with proposed refugia, and some refugia may not have high current diversity if subsequent colonisation has been limited; the refugial hypothesis complements rather than replaces other explanations for biodiversity hotspots, including the effects of contemporary climate stability, topographic complexity, and habitat diversity; integrating all these mechanisms is necessary for a complete understanding of why biodiversity is distributed unevenly across tropical Africa and the world.

Fill in the blank: The strong correspondence between proposed Pleistocene ________ locations and present-day biodiversity hotspots supports the idea that refugia generated endemism through in-refugium speciation and acted as source areas for recolonisation.

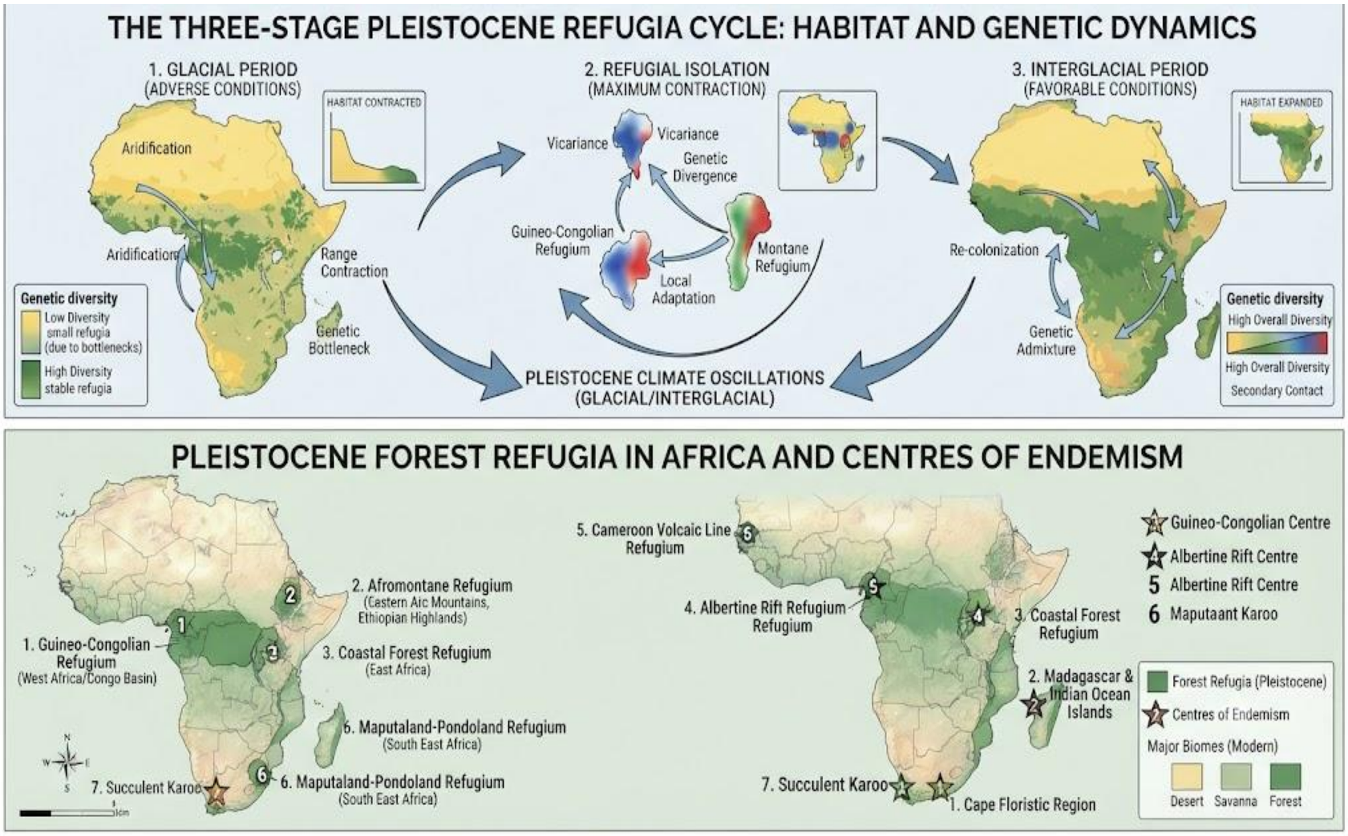

Figure 4.2: Refugia and Pleistocene forest refugia in Africa

Pilot questions 4.2

1. Define refugium and explain the biogeographic significance of refugia.
2. Explain the difference between Pleistocene refugia in Europe and in Africa.
3. Name the three main proposed Pleistocene forest refugia in Africa.
4. Explain what evidence supports the existence of Pleistocene forest refugia in Africa.
5. Explain the relationship between refugia and biodiversity hotspots.

4.3 Island Biogeography

4.3.1 The theory of island biogeography

The equilibrium theory of island biogeography, proposed by Robert MacArthur and Edward O. Wilson in 1967, provides a dynamic model for predicting the number of species on an island as a function of two opposing processes: immigration (the arrival of new species from the mainland source pool, which is highest on islands close to the mainland and declines as species already present on the island reduce the number of new species that can arrive and establish) and extinction (the local disappearance of species from the island, which increases as more species accumulate because populations are small and prone to stochastic extinction).

At equilibrium, the immigration rate of new species equals the extinction rate of resident species, producing a characteristic equilibrium species number that is predicted to be higher on larger islands (where populations are larger and extinction rates lower) and on islands closer to the mainland source pool (where immigration rates are higher); the theory was tested and supported by Wilson and Simberloff famous defaunation experiment, in which small mangrove islands in Florida were fumigated to remove all arthropods and the subsequent recolonisation was monitored, with species numbers returning to pre-defaunation equilibrium levels.

Fill in the blank: In the equilibrium theory of island biogeography, the equilibrium species number is reached when the rate of ________ of new species equals the rate of extinction of resident species.

4.3.2 Species-area relationships

The species-area relationship (SAR) is one of the most robust patterns in ecology and biogeography: larger areas consistently contain more species than smaller areas, following a power law relationship S = cA^z, where S is the number of species, A is the area, c is a constant reflecting the richness of the biota, and z is the slope of the relationship on a log-log plot (typically between 0.15 and 0.35 for archipelagos, and steeper for true islands than for habitat islands); larger islands have more species because they support larger populations (lower extinction rates), greater habitat diversity, and higher immigration rates.

The species-area relationship has important practical implications: it predicts that reducing the area of a habitat (through deforestation, drainage, or other human land conversion) will result in the loss of a predictable proportion of species; using typical z values, reducing habitat area by 90 percent would be expected to result in the eventual loss of approximately 50 percent of species in the long run; this extinction debt (the species that are committed to extinction by current habitat loss but have not yet disappeared because populations are declining toward zero) is a major conservation concern.

Fill in the blank: The species-area relationship predicts that reducing habitat area by 90 percent would be expected to result in the eventual loss of approximately ________ percent of species, a phenomenon called extinction debt.

4.3.3 Turnover and equilibrium

The equilibrium theory predicts that even when total species number is at equilibrium, the composition of the community is not static; species continuously go locally extinct and are replaced by colonisers, producing a turnover of species identity even as the total count remains approximately constant; the rate of this turnover is higher on small islands near the mainland (high extinction and high immigration) and lower on large remote islands (low extinction and low immigration); turnover can be measured by monitoring which species are present at successive intervals and calculating the proportion that have changed.

Empirical tests of the equilibrium theory have generally supported its broad predictions, particularly the positive relationship between island size and species number and the negative relationship between island isolation and species number; however, the theory has been criticised for treating all species as equivalent colonists and extinction risks (ignoring the biological characteristics of individual species), and for not fully accounting for the role of within-island speciation (which is particularly important on large, old, isolated islands such as Hawaii where in-situ diversification contributes substantially to species richness).

Fill in the blank: Species ________ is the continuous replacement of locally extinct species by new colonists, which occurs even when total island species number is at equilibrium.

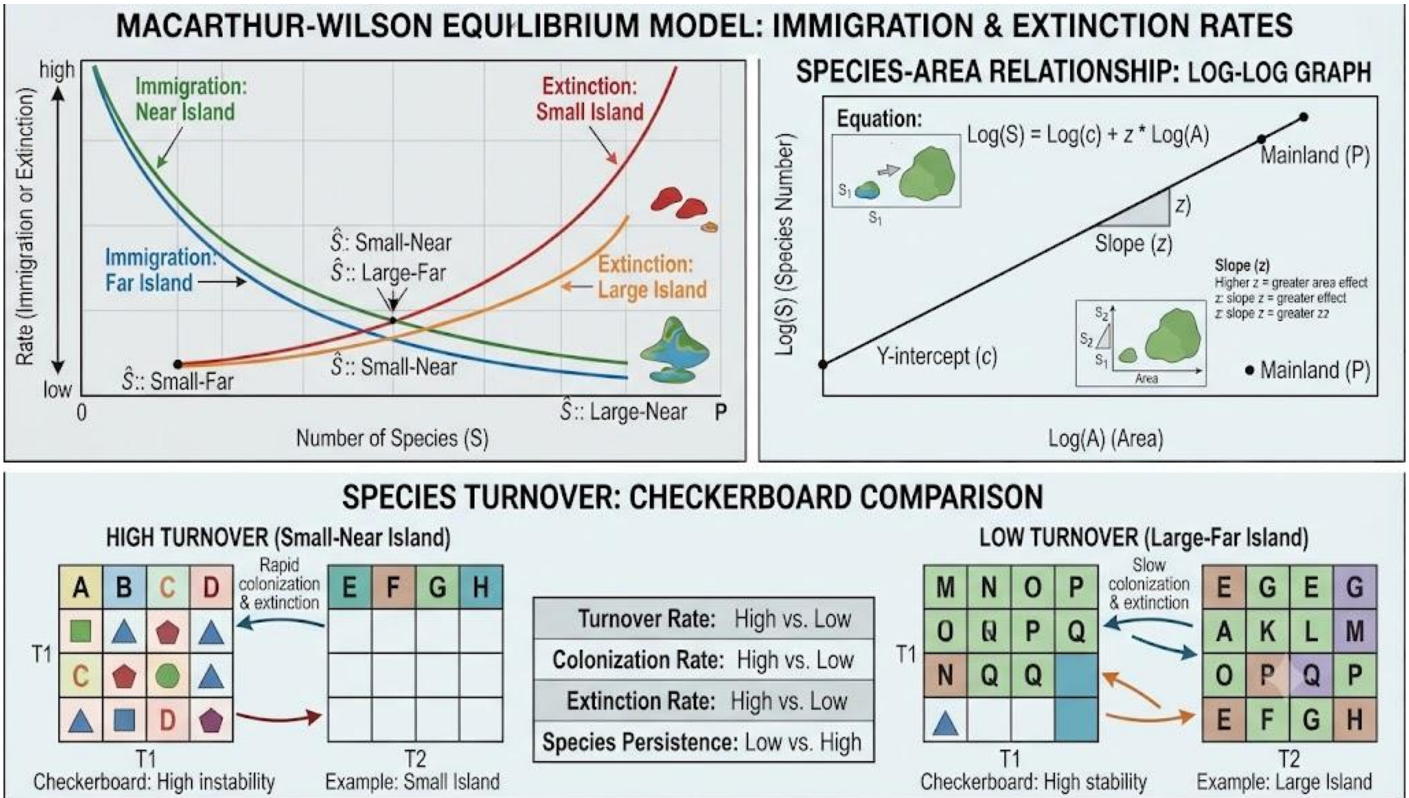

Figure 4.3: Island biogeography theory

Pilot questions 4.3

1. State the equilibrium theory of island biogeography and name its two founders.
2. Explain how island size and distance from mainland affect equilibrium species number.
3. State the species-area relationship equation and explain what each term represents.
4. Explain what extinction debt means in the context of the species-area relationship.
5. Explain what species turnover is and on which type of island it is fastest.

4.4 Applications of Island Biogeography and Endemicity

4.4.1 Island biogeography and conservation biology

The principles of island biogeography have been directly applied to conservation biology through the recognition that habitat fragments in a degraded landscape function as habitat islands surrounded by a sea of unsuitable land; the species-area relationship predicts that smaller and more isolated fragments will support fewer species and suffer higher extinction rates; the design of nature reserves and protected area networks has been substantially influenced by island biogeography theory, particularly through debates about whether a single large reserve (SLOSS) or several small reserves of equivalent total area better protect biodiversity.

Current consensus favours large reserves to support larger populations and more habitat diversity, with corridors connecting patches to facilitate dispersal and recolonisation; the minimum viable population concept (the smallest population likely to persist for a defined period) and metapopulation theory (the dynamics of networks of populations connected by dispersal) complement island biogeography as frameworks for designing reserves that maintain long-term viable populations; the lesson from island biogeography that isolation increases extinction risk is a powerful argument for maintaining landscape connectivity in conservation planning.

Fill in the blank: The ________ debate in conservation biology asks whether a single large reserve or several small reserves better protect biodiversity, directly applying the principles of island biogeography.

4.4.2 Endemicity and conservation priorities

Endemic species have restricted ranges by definition, making them inherently more vulnerable to extinction from habitat loss, invasive species, or climate change than widespread species; because endemic species cannot colonise new areas if their current range is destroyed, protecting existing habitat in centres of endemism is the only conservation option; the identification and protection of centres of endemism and biodiversity hotspots has therefore become a primary focus of global conservation strategy, with organisations such as the IUCN and Conservation International directing resources toward these irreplaceable areas.

The Key Biodiversity Areas (KBA) framework identifies sites of global significance for biodiversity conservation based on criteria including the presence of threatened endemic species; globally threatened endemic species that are restricted to a single site create high-priority KBAs where site protection is essential to prevent extinction; for island endemics, where entire species may occur on a single small island, the vulnerabilty is extreme and even small disturbances such as the introduction of a predator or disease can cause rapid extinction, as illustrated by the catastrophic bird extinctions on Pacific islands following the introduction of rats and snakes.

Fill in the blank: Endemic species are inherently more vulnerable to extinction than widespread species because they cannot ________ new areas if their restricted range is destroyed.

4.4.3 Climate change and endemic species

Climate change poses a particularly acute threat to endemic species, especially those restricted to narrow climatic envelopes (such as montane endemics dependent on cool high-elevation conditions) that will shift or disappear as temperatures rise; species can potentially track shifting climatic conditions by moving to higher elevations or latitudes, but endemic species with very small ranges may find that their entire climatic envelope disappears or shifts beyond their dispersal capacity, leaving them without suitable habitat anywhere within reach.

Species distribution models (SDMs, also called climate envelope models) project how the geographic range of a species will change under future climate scenarios by mapping the current climatic conditions within which the species is found and then projecting where those conditions will occur in the future; for many endemic species in tropical mountains, the Cape Floristic Region, and Mediterranean-climate shrublands, SDMs project severe range contractions or complete loss of suitable climate space under moderate to high warming scenarios, identifying these species as priorities for urgent conservation intervention and, in some cases, for assisted migration to new sites with suitable future climates.

Fill in the blank: Species ________ models project future ranges by mapping the climatic conditions currently occupied by a species and projecting where those conditions will be found under future climate scenarios.

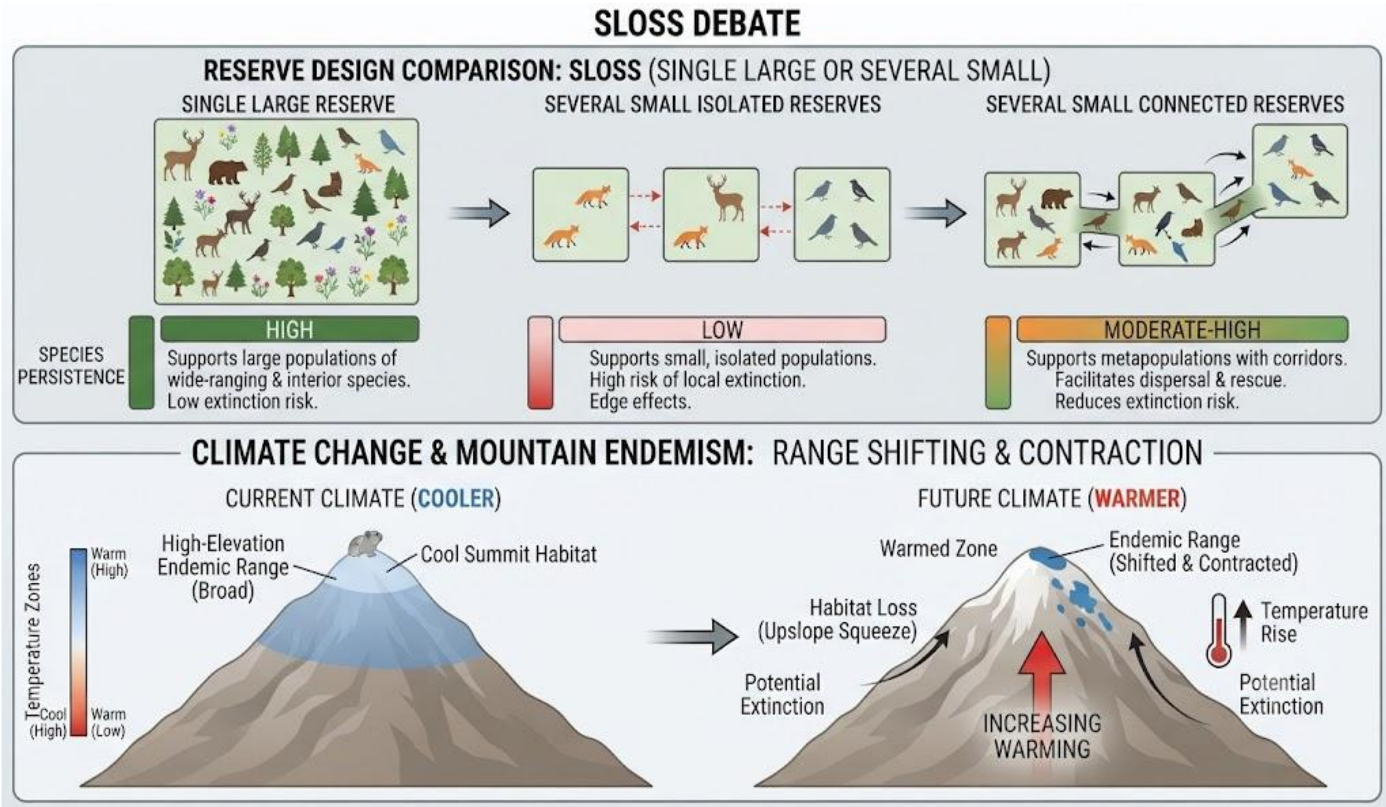

Figure 4.4: Applications of island biogeography and endemic species conservation

Pilot questions 4.4

1. Explain how island biogeography principles apply to conservation of fragmented habitats.
2. Explain what the SLOSS debate is and what current conservation consensus recommends.
3. Explain why endemic species are inherently more vulnerable to extinction than widespread species.
4. Describe what a species distribution model is and how it is used.
5. Explain why montane endemic species are particularly vulnerable to climate change.

Series Summary

This Series explored three deeply connected biogeographic concepts. Endemism, the restriction of species to defined areas, is unevenly distributed across the Earth, concentrated in regions with long isolation, topographic complexity, or stable climates. Centres of endemism and biodiversity hotspots identify the most irreplaceable areas for conservation. The concept of refugia explains how populations survived past climatic extremes in sheltered pockets, and the Pleistocene forest refugia hypothesis accounts for the high endemism and species richness observed in the Upper Guinea forests, the Congo Basin, and the East African highlands.

The equilibrium theory of island biogeography, formulated by MacArthur and Wilson, established a quantitative framework for understanding species number on islands as the balance between immigration and extinction, with the species-area relationship providing a predictive tool for habitat loss consequences. These principles translate directly into conservation: fragmented habitat patches function as islands, reserve design should prioritise size and connectivity, and endemic species with restricted ranges face the greatest risk from both habitat loss and climate change. Together, these concepts form an essential toolkit for understanding and protecting biodiversity.

Glossary of Terms

- **Biodiversity hotspot:** a region with exceptional concentrations of endemic species, high total species richness, and severe loss of original natural habitat, prioritised for international conservation.
- **Endemic species:** a species that occurs naturally only within a defined geographic area and nowhere else in the world.
- **Extinction debt:** the number of species committed to eventual extinction by current habitat loss, though not yet disappeared because populations are still declining toward zero.
- **Neoendemic:** a recently evolved endemic species that has not yet had time to disperse beyond its area of origin.

- **Palaeoendemicspecies:** a once-widespread species that has contracted to a restricted range, typically representing an ancient isolated lineage.
- **Refugium (pl. refugia):** an area where populations survived an unfavourable climatic period while surrounding areas became uninhabitable.
- **SLOSS debate:** the conservation debate about whether a single large reserve or several small reserves of equivalent total area better protects biodiversity.
- **Species-area relationship:** the empirical pattern that larger areas contain more species, described by the equation S = cA^z.
- **Species distribution model:** a model that projects the geographic range of a species under current or future climate conditions by mapping its climatic envelope.
- **Turnover:** the replacement of locally extinct species by new colonists, occurring even when total island species number is at equilibrium.

Concept Check Questions [Series 4]

Objective Questions

1. ________ are endemic species that were once widespread but have contracted to a small area. (Linked to SLO 4.1)
2. A ________ is an area where populations survived an unfavourable climatic period that made surrounding areas uninhabitable. (Linked to SLO 4.2)
3. In the equilibrium theory of island biogeography, equilibrium species number is where immigration rate equals ________ rate. (Linked to SLO 4.3)
4. The species committed to eventual extinction by habitat loss but not yet disappeared represent the extinction ________ . (Linked to SLO 4.3)
5. Endemic species are particularly vulnerable because they cannot ________ new areas if their range is destroyed. (Linked to SLO 4.4)

Short-Answer Questions

1. Distinguish between palaeoendemics and neoendemics. (Linked to SLO 4.1)
2. Name three proposed Pleistocene forest refugia in Africa. (Linked to SLO 4.2)
3. Explain how island size and distance affect equilibrium species number. (Linked to SLO 4.3)
4. Explain what extinction debt means. (Linked to SLO 4.3)
5. Explain why montane endemic species are particularly vulnerable to climate change. (Linked to SLO 4.4)

Long-Answer Questions

1. Describe endemism, its types, centres of endemism, and causes. (Linked to SLO 4.1)
2. Explain the concept of refugia and describe Pleistocene forest refugia in Africa. (Linked to SLO 4.2)
3. Describe the equilibrium theory of island biogeography and its conservation applications. (Linked to SLOs 4.3, 4.4)

Answers to Concept Check Questions [Series 4]

Objective Questions

1. Palaeoendemics.
2. Refugium.
3. Extinction.
4. Debt.
5. Colonise.

Short-Answer Questions

1. Palaeoendemics were once widespread but have contracted to a small area, representing ancient isolated lineages; neoendemics are recently evolved species that have not yet dispersed beyond their area of origin.
2. Upper Guinea coastal forests (West Africa), Congo Basin, and East African montane forests.
3. Larger islands have lower extinction rates (larger populations) and support higher equilibrium species numbers; islands closer to the mainland have higher immigration rates and also higher equilibrium species numbers.
4. Extinction debt is the number of species committed to eventual extinction by current habitat loss but not yet disappeared because populations are still slowly declining toward zero.
5. Montane endemics depend on cool high-elevation conditions that will shift upward or disappear as temperatures rise; they cannot disperse to new suitable areas if their entire climatic envelope contracts or moves beyond the mountaintop.

Long-Answer Questions

1. Endemism is restriction of a species to a defined area. Palaeoendemics are ancient contracted-range species; neoendemics are recently evolved. Centres of endemism include the Cape Floristic Region, Madagascar, Hawaii, and the Albertine Rift. Endemism is caused by geographic isolation, ecological specialisation, long evolutionary history, topographic complexity, and adaptive radiation on islands.
2. A refugium is an area where populations survived adverse climatic conditions. In Africa, Pleistocene arid phases contracted forests to Upper Guinea, Congo Basin, and East African refugia; humid phases allowed expansion. Evidence includes disjunct species distributions,

pollen records, and molecular phylogeographic studies. Refugia correspond to present-day centres of endemism and biodiversity hotspots.

3. MacArthur and Wilson equilibrium theory: species number balances immigration and extinction; larger, nearer islands have more species. Species-area relationship: $S = cA^z$; reducing area by 90% causes ~50% species loss (extinction debt). Conservation applications: habitat fragments function as islands; SLOSS debate favours large connected reserves; endemic species in centres of endemism need priority protection; SDMs identify climate change vulnerability.

Answers to Pilot Questions [Series 4]

Part 4.1

1. Endemism is restriction of a taxon to a defined geographic area; the scale of the area matters because a species endemic to a mountain may not be endemic to a country or continent, so endemism designation depends on the scale of reference used.
2. Palaeoendemics were once widespread but have contracted to a small area and often represent ancient isolated lineages; neoendemics are recently evolved species that have not yet spread from their area of origin.
3. Cape Floristic Region (fynbos plants), Madagascar (lemurs), Hawaiian Islands (honeycreeper birds).
4. A biodiversity hotspot is a region with exceptional concentrations of endemic species, high species richness, and severe loss of natural habitat, prioritised for international conservation investment.
5. Geographic isolation, ecological specialisation to unique soils or habitats, and long evolutionary history in isolation.

Part 4.2

1. A refugium is an area where populations survived an adverse climatic period; their biogeographic significance is that they served as source areas for recolonisation of surrounding regions after conditions improved, and accumulated endemic species through in-refugium speciation.

2. European Pleistocene refugia were caused by glaciation, forcing communities southward into southern European refugia; African Pleistocene refugia resulted from aridification contracting forest to moist coastal and basin areas, not from glaciation.
3. Upper Guinea coastal forests (West Africa), Congo Basin core, and East African montane forests.
4. Disjunct distributions of forest-restricted species centred on proposed refugia, pollen records showing past vegetation contraction, and molecular phylogeographic studies revealing deep genetic divergences between populations in different refugia.
5. Refugia and hotspots strongly overlap because refugia accumulated endemic species through in-refugium speciation during repeated contractions, and acted as persistent sources of diversity from which surrounding areas were repeatedly recolonised.

Part 4.3

1. The equilibrium theory of island biogeography (MacArthur and Wilson, 1967) proposes that species number on an island is determined by the balance between immigration of new species from the mainland and local extinction of resident species.
2. Larger islands have lower extinction rates (larger populations) and support more habitat diversity, giving higher equilibrium species numbers; nearer islands have higher immigration rates, also giving higher equilibrium species numbers.
3. $S = cA^z$; S is species number, A is area, c is a biota richness constant, z is the slope of the log-log species-area line (typically 0.15 to 0.35).
4. Extinction debt is the number of species that are committed to eventual extinction by current habitat loss but have not yet disappeared because their populations are still slowly declining toward zero.
5. Species turnover is the continuous replacement of locally extinct species by new colonists even when total species number is at equilibrium; it is fastest on small islands near the mainland, which have both high extinction and high immigration rates.

Part 4.4

1. Habitat fragments in degraded landscapes function as habitat islands; the species-area relationship predicts that smaller, more isolated fragments support fewer species and suffer higher extinction rates; reserve design and corridor provision follow from these principles.

2. The SLOSS debate asks whether a single large or several small reserves better protect biodiversity; current consensus favours large reserves with corridors, as these support larger populations, more habitat diversity, and maintain dispersal between patches.
3. Endemic species have restricted ranges and cannot colonise new areas if their current range is destroyed; if their only habitat is lost, extinction is inevitable.
4. A species distribution model maps the climatic conditions currently occupied by a species and projects where those conditions will occur under future climate scenarios, showing how the species range will expand, contract, or shift.
5. Montane endemics depend on cool conditions that exist only at high elevations; as temperatures rise, suitable conditions move upward and eventually disappear off the mountaintop, leaving no suitable habitat within the species dispersal range.

References and Attribution

Textual References (Books and External Sources)

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Figures, Plates, Tables, and Boxes

- Figure 4.1: Endemicity and centres of endemism Attribution: AI generated. Suggested OER search string: "endemism centres endemism biodiversity hotspots Cape Floristic Madagascar Hawaii palaeoendemism neodendemism biogeography OER".
- Figure 4.2: Refugia and Pleistocene forest refugia in Africa Attribution: AI generated. Suggested OER search string: "refugia Pleistocene forest refugia Africa biodiversity hotspots genetic diversity contraction expansion biogeography OER".
- Figure 4.3: Island biogeography theory Attribution: AI generated. Suggested OER search string: "island biogeography MacArthur Wilson equilibrium species area relationship turnover immigration extinction diagram OER".
- Figure 4.4: Applications of island biogeography and endemic species conservation Attribution: AI generated. Suggested OER search string: "island biogeography reserve design SLOSS conservation endemic species climate change species distribution model mountain OER".

Course code: BIO 303

Course title: Biogeography and Soil Biology

Course credit load: 2 Units

Series 5: Soil Biology and Environmental Processes

- **Part 5.1: Physical and Chemical Nature of Soil**
    - Sub Part 5.1.1: Soil composition and texture
    - Sub Part 5.1.2: Soil structure and profile
    - Sub Part 5.1.3: Soil chemistry and pH
- **Part 5.2: Soil Organisms and Detritus**
    - Sub Part 5.2.1: Detritus organisms and soil fauna
    - Sub Part 5.2.2: Soil microorganisms
    - Sub Part 5.2.3: Soil food web
- **Part 5.3: Nutrient Cycling and Mineral Pools**
    - Sub Part 5.3.1: The carbon cycle in soil
    - Sub Part 5.3.2: The nitrogen cycle in soil
    - Sub Part 5.3.3: Other nutrient cycles and mineral pools
- **Part 5.4: Soil-Water-Plant Relationships and Soil Erosion**
    - Sub Part 5.4.1: Plant and animal soil-water relationships
    - Sub Part 5.4.2: Soil sampling techniques
    - Sub Part 5.4.3: Causes of soil erosion and alleviation methods

Introduction

Soil is far more than a passive substrate for plant growth: it is a complex, living system in which physical, chemical, and biological processes interact to regulate the availability of water and nutrients, decompose organic matter, store carbon, and support an extraordinary diversity of organisms from bacteria and fungi to earthworms and insects. Understanding soil biology and the processes it drives is essential for agriculture, ecology, and environmental management.

This Series covers the physical and chemical properties of soil that determine its character and fertility; the organisms that inhabit soil and form the detrital food web that drives decomposition and nutrient release; the cycling of carbon, nitrogen, and other nutrients through soil; the relationships between soil, water, plants, and animals; and the causes and alleviation of soil erosion, one of the most significant environmental problems affecting agricultural land in Nigeria and worldwide.

Series Learning Outcomes

Upon completing this Series, you should be able to:

- **SLO 5.1** describe the physical and chemical properties of soil, including texture, structure, profile, and pH,
- **SLO 5.2** describe the major groups of soil organisms and the structure of the soil food web,
- **SLO 5.3** explain the cycling of carbon and nitrogen through soil and describe other nutrient pools, and
- **SLO 5.4** explain plant and animal soil-water relationships, describe soil sampling techniques, and explain the causes and alleviation of soil erosion.

5.1 Physical and Chemical Nature of Soil

5.1.1 Soil composition and texture

Soil is a mixture of four major components: mineral particles (derived from the weathering of parent rock material), organic matter (in various stages of decomposition, from fresh plant litter to fully humified humus), water (occupying pores between particles and carrying dissolved nutrients), and air (also occupying pores, providing oxygen for root and microbial respiration); the relative proportions of these components and the sizes of the mineral particles largely determine the physical properties of the soil and its suitability for plant growth.

Soil texture is defined by the relative proportions of three mineral particle size classes: sand (particles 0.05 to 2 mm, coarse, visible to the naked eye, providing large pores for drainage and aeration but little surface area for nutrient retention), silt (particles 0.002 to 0.05 mm, intermediate), and clay (particles less than 0.002 mm, very fine, providing large surface area for nutrient adsorption but small pores that restrict drainage and aeration); soil texture is determined by the feel test or by laboratory mechanical analysis and expressed on a soil texture triangle as loam, sandy loam, clay loam, and other textural classes.

Fill in the blank: Soil texture is defined by the relative proportions of ________ , silt, and clay particle size classes, which together determine drainage, aeration, and nutrient retention properties.

5.1.2 Soil structure and profile

Soil structure refers to the arrangement of mineral particles and organic matter into aggregates (peds) of various shapes and sizes; good soil structure (well-aggregated soil) creates a porous network that balances water retention and drainage, facilitates root penetration, and supports abundant microbial activity; soil aggregates are stabilised by organic matter, fungal hyphae (particularly mycorrhizal hyphae), and microbial polysaccharides, explaining why soils with high organic matter content typically have better structure than those with low organic matter.

A soil profile is the vertical sequence of layers (horizons) visible in a soil pit, each with characteristic colour, texture, structure, and organic matter content reflecting the processes that formed it; a typical temperate or tropical forest soil profile includes the O horizon (organic layer of litter and humus at the surface), the A horizon (topsoil, rich in organic matter and biological activity), the B horizon (subsoil, where minerals leached from above may accumulate), the C horizon (weathered parent material), and the R horizon (unweathered bedrock); the depth and character of each horizon vary greatly with climate, vegetation, and time since soil formation.

Fill in the blank: The ________ horizon is the topsoil layer rich in organic matter and biological activity, overlying the B horizon where leached minerals may accumulate.

5.1.3 Soil chemistry and pH

Soil pH (the acidity or alkalinity of the soil solution) profoundly influences plant growth and nutrient availability: most nutrients (including nitrogen, phosphorus, potassium, calcium, and magnesium) are most available to plants at near-neutral pH (6 to 7), while strongly acid soils (pH below 5) often have high concentrations of soluble aluminium and manganese that are toxic to many plants, and strongly alkaline soils (pH above 8) often cause deficiencies of iron, manganese, and other micronutrients through precipitation; most crop plants grow best between pH 5.5 and 7.0.

Cation exchange capacity (CEC) is a key measure of soil chemical fertility, reflecting the ability of the soil to hold positively charged nutrient ions (cations such as Ca2+, Mg2+, K+, and NH4+) on negatively charged clay and humus surfaces, preventing their loss by leaching while keeping them available for root uptake; soils with high clay and organic matter content have high CEC and are generally more fertile than sandy soils with low CEC; liming (adding calcium carbonate) is a common agricultural practice in acid soils that both raises pH and increases CEC.

Fill in the blank: ________ exchange capacity (CEC) measures the ability of soil to hold positively charged nutrient ions on clay and humus surfaces, preventing leaching and maintaining fertility.

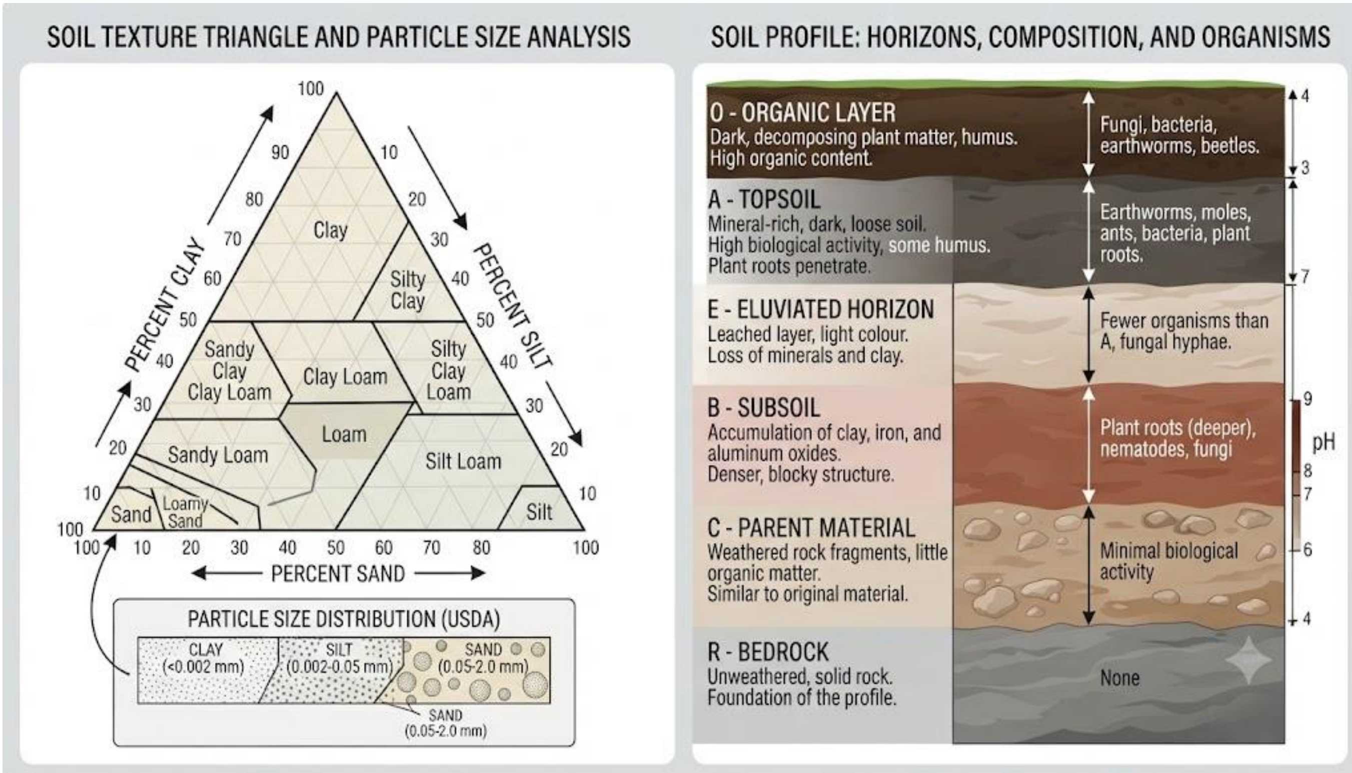

Figure 5.1: Soil composition, texture, and profile

Pilot questions 5.1

1. Name the four major components of soil.
2. Define soil texture and name the three particle size classes.
3. Describe the O and A horizons of a typical soil profile.
4. Explain how soil pH affects plant nutrient availability.
5. Define cation exchange capacity and explain its importance for soil fertility.

5.2 Soil Organisms and Detritus

5.2.1 Detritus organisms and soil fauna

Detritus organisms are those that obtain their energy from dead organic matter (detritus) rather than from living organisms or photosynthesis; in soil, the major groups of detritivore animals include earthworms (which ingest soil and organic matter, mixing and aerate the soil, producing casts rich in nutrients and microbial activity), millipedes and isopods (which fragment leaf litter, increasing the surface area available for microbial attack), termites (which break down wood and grass in tropical and subtropical soils, constructing mounds that alter soil structure over large areas), and nematodes (microscopic roundworms that are among the most abundant soil animals, feeding on bacteria, fungi, plant roots, and other nematodes).

Enchytraeids (potworms, small oligochaete worms related to earthworms), collembolans (springtails, small hexapods feeding on fungi, algae, and organic matter), and mites (abundant soil arthropods feeding on fungi, bacteria, and other micro-arthropods) complete the major soil macrofauna and mesofauna groups; the abundance and diversity of soil fauna is a useful indicator of soil health, since degraded or polluted soils support fewer and less diverse communities; earthworm density in particular is widely used as an indicator of soil biological activity and fertility.

Fill in the blank: ________ ingest soil and organic matter, mixing and aerating the soil while producing casts rich in nutrients, making them among the most ecologically important soil animals.

5.2.2 Soil microorganisms

Bacteria are the most numerically abundant soil organisms, with populations of tens of millions to billions of cells per gram of soil, carrying out a vast range of biochemical transformations including decomposition of organic matter, nitrification (conversion of ammonium to nitrate), denitrification (conversion of nitrate to nitrogen gas), nitrogen fixation, and dissolution of mineral nutrients; the bacterial community in soil is highly diverse and responds rapidly to changes in substrate availability, moisture, and temperature.

Fungi (particularly saprotrophic fungi that decompose organic matter and mycorrhizal fungi that form symbiotic associations with plant roots) are another dominant microbial group, contributing substantially to soil organic matter decomposition (especially of lignin, which few bacteria can efficiently degrade) and to the transfer of nutrients from soil to plant roots; actinomycetes (filamentous bacteria that produce the characteristic earthy smell of healthy soil) are important decomposers of recalcitrant organic compounds; algae and cyanobacteria contribute to soil surface crusts and are important in fixing nitrogen in waterlogged or exposed tropical soils.

Fill in the blank: ________ are the most numerically abundant soil organisms, carrying out decomposition, nitrification, denitrification, and nitrogen fixation among many other biochemical transformations.

5.2.3 Soil food web

The soil food web describes the network of feeding relationships among soil organisms, through which energy and nutrients flow from organic matter inputs at the base through successive trophic levels; at the base are the primary decomposers (bacteria and fungi) that break down dead organic matter and release its nutrients; these are consumed by primary consumers (bacterivorous and fungivorous nematodes, protozoa, collembolans, and mites); which in turn are consumed by secondary consumers (predatory nematodes, predatory mites, centipedes, and ground beetles); and at the top, larger predators such as moles, shrews, and ground-nesting birds.

The soil food web has two main energy channels: the bacterial channel (dominated by bacteria and their consumers, typically faster-cycling and associated with wetter, more nutrient-rich soils) and the fungal channel (dominated by fungi and their consumers, typically slower-cycling and associated with drier, more organic or acidic soils such as forest floors); the relative dominance of the bacterial versus fungal channel has important implications for nutrient cycling rates, carbon storage, and the response of the soil system to disturbance.

Fill in the blank: The soil food web has two main energy channels: the ________ channel (fast cycling, wetter soils) and the fungal channel (slower cycling, forest or acidic soils).

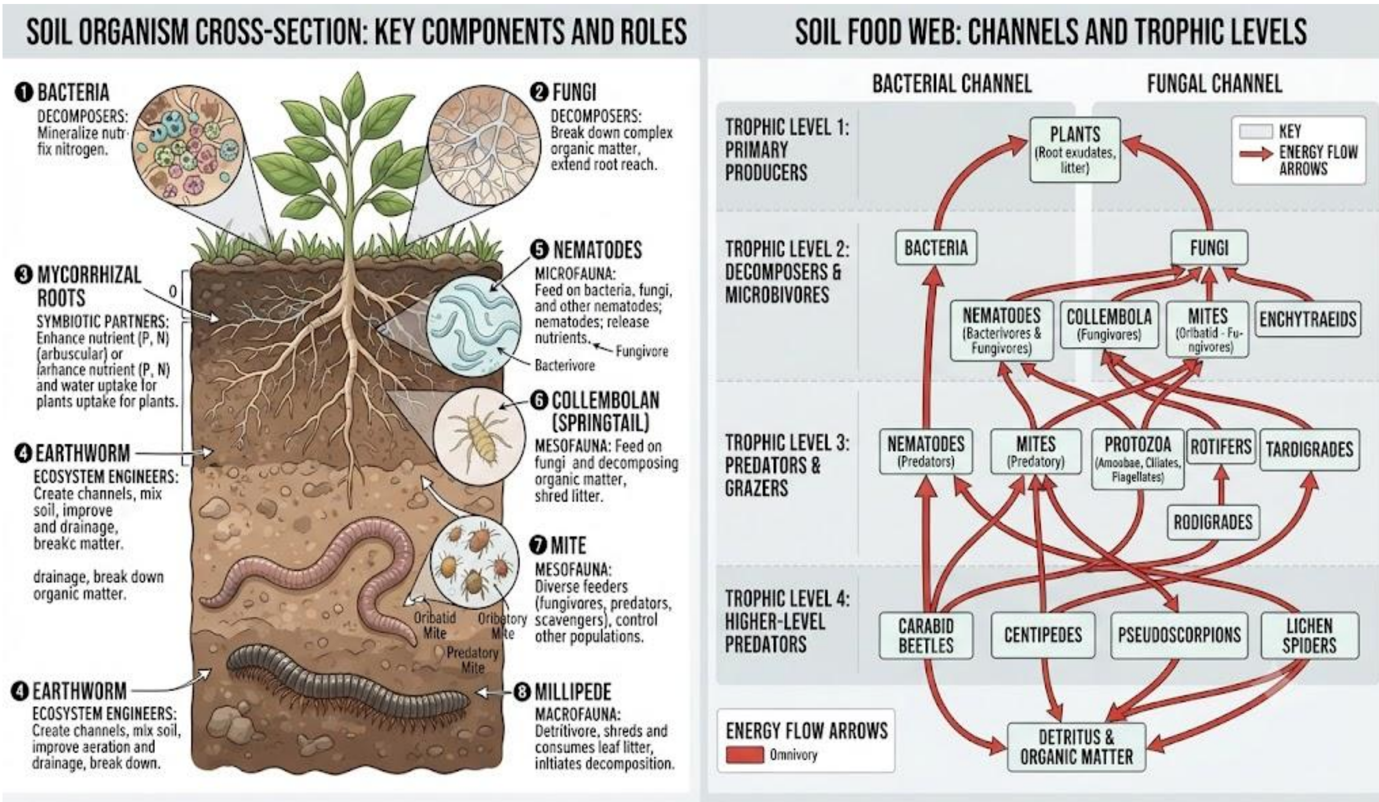

Figure 5.2: Soil organisms and food web

Pilot questions 5.2

1. Define detritus organisms and name four groups of soil fauna.
2. Explain why earthworms are considered important indicators of soil health.
3. Name four types of bacteria-mediated transformation in soil.
4. Explain the role of fungi in soil organic matter decomposition.
5. Distinguish between the bacterial channel and the fungal channel of the soil food web.

5.3 Nutrient Cycling and Mineral Pools

5.3.1 The carbon cycle in soil

The soil carbon cycle begins with the input of organic carbon to soil through plant litter fall (dead leaves, branches, and roots), root exudates (organic compounds released by living roots into the rhizosphere), and the death of soil organisms; this organic carbon is progressively decomposed by soil organisms, initially by macrofauna fragmenting litter, then by bacteria and fungi mineralising the organic compounds to carbon dioxide (released through soil respiration), water, and inorganic nutrients; a fraction of the carbon is incorporated into microbial biomass and, through successive microbial processing, into stable humus compounds that can persist in soil for decades to millennia.

Soil carbon storage (soil organic carbon, SOC) is of major global importance because soils contain more carbon than the atmosphere and all living vegetation combined; the balance between carbon inputs (from plant productivity) and outputs (through decomposition and soil respiration) determines whether a soil is a carbon sink (sequestering carbon) or a carbon source (releasing carbon to the atmosphere); land use change (particularly the conversion of forests or peatlands to agriculture) typically converts soils from sinks to sources, releasing large quantities of stored carbon as carbon dioxide and contributing to climate change.

Fill in the blank: Soils contain more carbon than the atmosphere and all living vegetation combined, making soil ________ carbon storage of major importance for global climate regulation.

5.3.2 The nitrogen cycle in soil

The nitrogen cycle in soil involves several linked microbially mediated transformations: nitrogen fixation (conversion of atmospheric N2 to ammonium by free-living bacteria such as Azotobacter and Clostridium in soil, and by symbiotic Rhizobium bacteria in root nodules of legumes); ammonification (decomposition of organic nitrogen compounds in dead organic matter to ammonium by soil bacteria and fungi); nitrification (conversion of ammonium to nitrite then to nitrate by nitrifying bacteria such as Nitrosomonas and Nitrobacter, producing the nitrate form readily taken up by most plants); and denitrification (conversion of nitrate to N2 or N2O gases by denitrifying bacteria under anaerobic conditions, returning nitrogen to the atmosphere and causing nitrogen loss from soil).

Plant uptake of mineral nitrogen (as nitrate or ammonium from the soil solution) removes nitrogen from the inorganic pool and incorporates it into plant biomass; when that biomass dies or is eaten and excreted, the nitrogen re-enters the soil organic nitrogen pool for decomposition; the nitrogen cycle is therefore a closed loop within the ecosystem, though gains occur through biological and atmospheric fixation and losses through denitrification, leaching of nitrate below the root zone, and volatilisation of ammonia; agricultural systems typically have large nitrogen losses through leaching and denitrification that must be replaced by fertiliser additions.

Fill in the blank: ________ is the conversion of nitrate to gaseous N2 or N2O by bacteria under anaerobic conditions, representing a loss of nitrogen from the soil back to the atmosphere.

5.3.3 Other nutrient cycles and mineral pools

Phosphorus cycling in soil differs from carbon and nitrogen cycling in that there is no significant atmospheric reservoir: phosphorus enters the ecosystem from the weathering of phosphate-bearing minerals, cycles through the biota via plant uptake, herbivory, decomposition, and microbial mineralisation, and is progressively lost through leaching and erosion; phosphorus availability is strongly influenced by soil pH (it is most available at pH 6 to 7), and phosphorus fixation by iron and aluminium oxides in acid tropical soils frequently makes phosphorus the most limiting nutrient for plant growth in these systems.

Sulphur, potassium, calcium, and magnesium also cycle through soil, each with a characteristic balance between inputs from weathering and atmospheric deposition, biological cycling through the soil food web, and losses through leaching and plant removal; the concept of nutrient pools (the quantities of a nutrient held in different forms: in living organisms, in dead organic matter, in inorganic soil solution, adsorbed on soil particles, or locked in unavailable mineral forms) and nutrient fluxes (the rates of transfer between pools) provides a quantitative framework for understanding soil fertility and the effects of management on nutrient availability.

Fill in the blank: Phosphorus availability in soil is most limited in acid tropical soils due to ________ by iron and aluminium oxides, making phosphorus the most limiting nutrient for plant growth in many tropical systems.

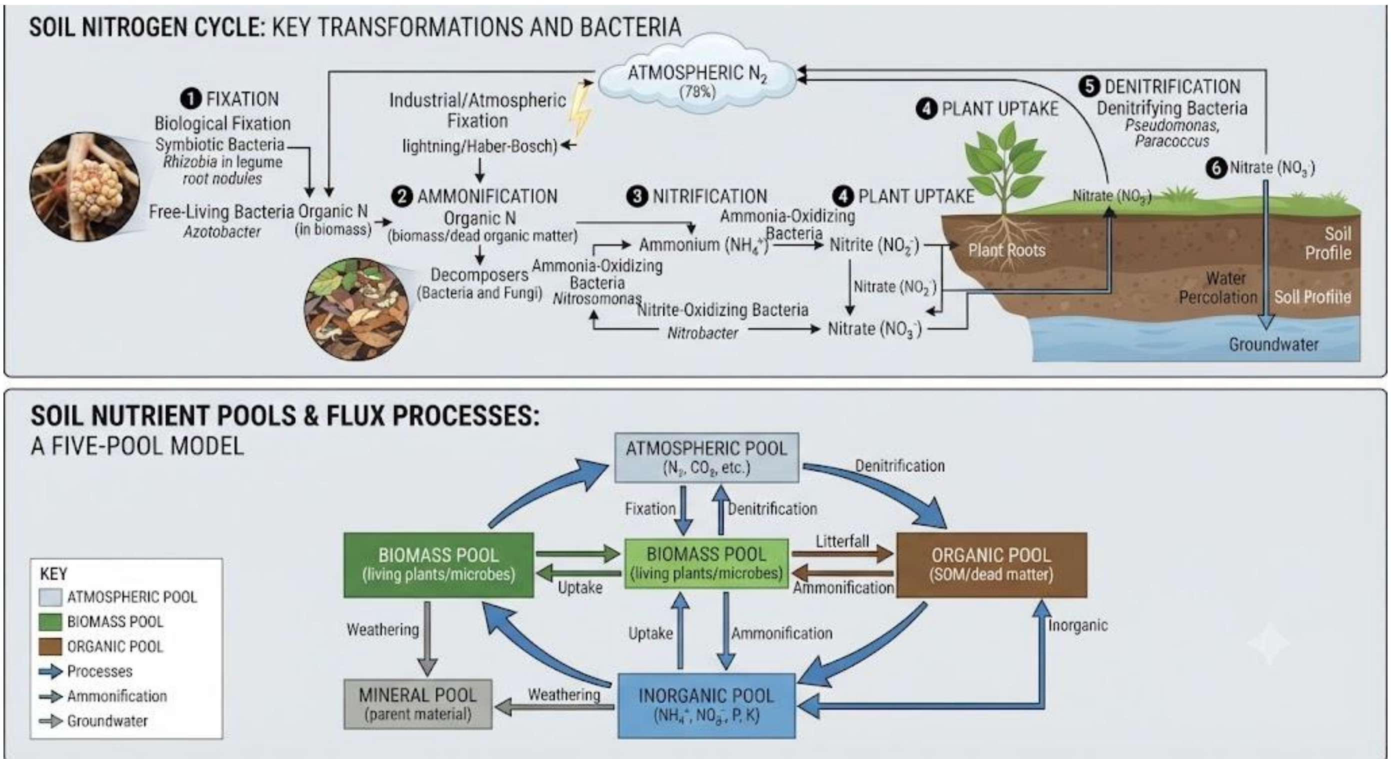

Figure 5.3: Soil nutrient cycling

Pilot questions 5.3

1. Describe the pathway of carbon from plant litter to stable soil humus.
2. Explain why soil carbon storage is globally significant.
3. Name the four major transformations in the soil nitrogen cycle and the bacteria involved in each.
4. Explain why phosphorus is often the most limiting nutrient in acid tropical soils.
5. Distinguish between a nutrient pool and a nutrient flux.

5.4 Soil-Water-Plant Relationships and Soil Erosion

5.4.1 Plant and animal soil-water relationships

Water in soil occupies the pore spaces between particles and is held by adhesion to particle surfaces and by surface tension; plant available water is the fraction of soil water that can be taken up by plant roots, defined as the water held between field capacity (the water remaining after free drainage has ceased, typically at soil water potential of about -0.03 MPa) and permanent wilting point (the water content at which soil holds water too tightly for roots to extract it, approximately -1.5 MPa); soils with high clay and organic matter content typically have higher total water-holding capacity and higher plant available water than sandy soils.

Soil animals depend on soil moisture for osmoregulation, respiration, and movement: earthworms must keep their skin moist for cutaneous gas exchange and are rapidly killed by desiccation, so their distribution and activity is strongly correlated with soil moisture; termites in dry regions construct elaborate nest structures that maintain high internal humidity; soil moisture also strongly influences the composition and activity of the microbial community, since most bacteria and fungi require liquid water films around soil particles for growth; drought and flooding both reduce microbial activity and nutrient cycling rates through different mechanisms.

Fill in the blank: Plant available water is the fraction of soil water held between ________ capacity and permanent wilting point, within which plant roots can extract water from the soil.

5.4.2 Soil sampling techniques

Soil sampling is the collection of representative soil samples for physical, chemical, or biological analysis; for chemical and physical analyses, samples are typically taken with a soil auger or core sampler to a specified depth (usually 0 to 15 cm for the topsoil and 15 to 30 cm for the subsoil), and multiple cores from across the sampling area are composited to reduce the effect of spatial variability; samples are air-dried, sieved, and analysed for pH, texture, organic matter content, and available nutrient concentrations by standard laboratory methods.

For soil biological sampling, different methods are used depending on the organism group: soil cores or monolith samples extracted and hand-sorted under a microscope for macrofauna such as earthworms and beetle larvae; Berlese-Tullgren funnels (which drive small arthropods out of soil samples by heating from above) for mesofauna such as mites and collembolans; dilution plate methods or DNA-based methods for bacteria and fungi; and nematode extraction by flotation or Baermann funnel methods; the choice of sampling depth, timing, and extraction method must be matched to the biology of the target organism group to obtain meaningful results.

Fill in the blank: ________ -Tullgren funnels drive small soil arthropods such as mites and collembolans out of soil samples by applying heat from above, collecting them for enumeration and identification.

5.4.3 Causes of soil erosion and alleviation methods

Soil erosion is the detachment and transport of soil particles by water (water erosion, the most common form in humid and sub-humid tropics including Nigeria) or wind (wind erosion, important in arid and semi-arid regions); water erosion occurs through raindrop impact (which dislodges particles from the soil surface), surface runoff (which carries suspended particles downslope), and rill and gully formation (where concentrated flow carves channels through the soil); the rate of erosion depends on rainfall intensity, slope gradient and length, soil erodibility (related to texture, organic matter, and aggregate stability), and vegetation cover.

Effective alleviation methods for soil erosion include: maintaining or restoring vegetation cover (the most effective erosion control, since roots bind soil, canopies intercept rainfall, and litter slows surface runoff); contour farming (ploughing and planting along contour lines rather than up and down slopes, reducing runoff velocity); terracing (constructing level platforms on slopes to reduce slope length and runoff velocity); mulching (covering the soil surface with organic material to intercept rain drops and reduce evaporation); grass strips and windbreaks (reducing runoff velocity and wind speed at the surface); and agroforestry systems (integrating trees with crops to provide surface cover and improve soil structure).

Fill in the blank: ________ farming, the practice of ploughing and planting along contour lines on slopes rather than up and down, reduces runoff velocity and is one of the most effective erosion control methods.

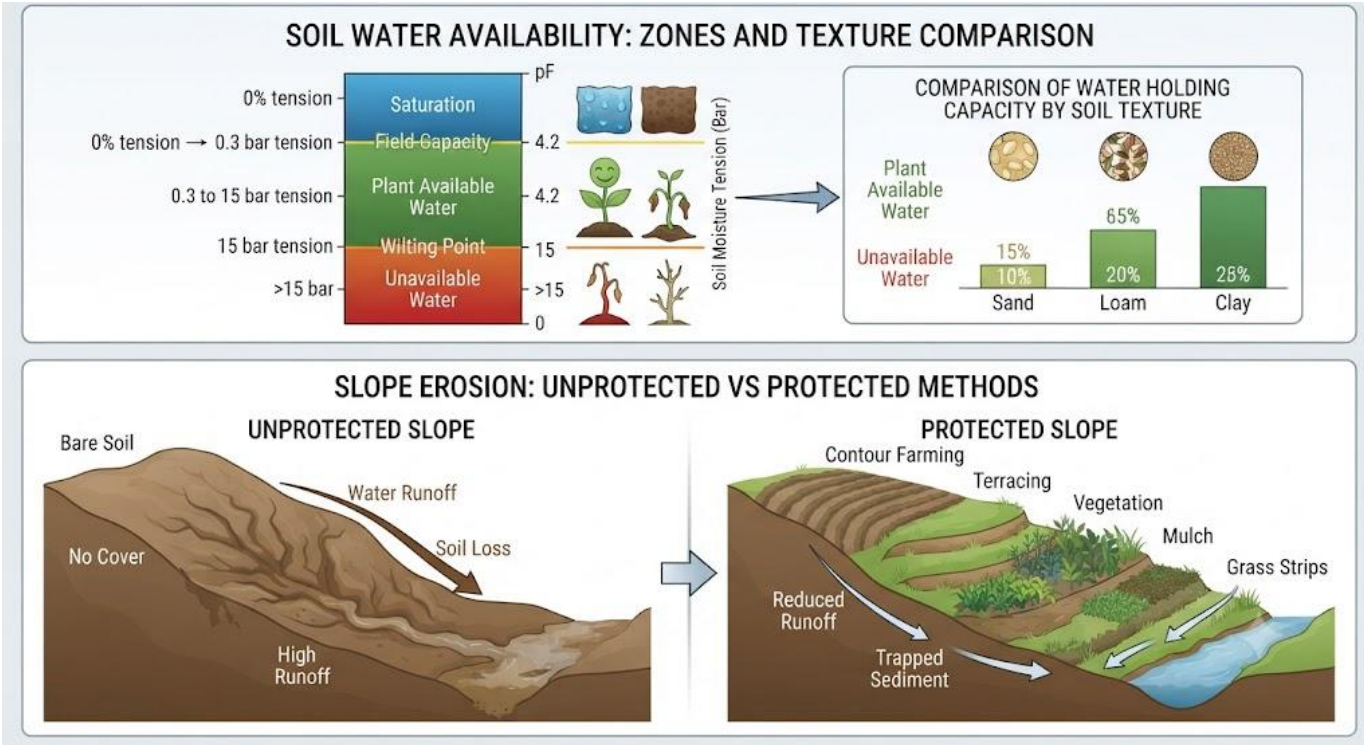

Figure 5.4: Soil-water-plant relationships and soil erosion

Pilot questions 5.4

1. Define plant available water and state the soil water potentials that define its boundaries.
2. Explain why earthworm distribution is strongly correlated with soil moisture.
3. Describe how soil samples are collected for chemical analysis.
4. Explain what a Berlese-Tullgren funnel is used for.
5. Name four methods for alleviating soil erosion.

Series Summary

This Series brought together the physical, chemical, and biological dimensions of soil. Soil is a four-component system of minerals, organic matter, water, and air, whose fertility is determined by texture, structure, pH, and cation exchange capacity. Beneath the surface, a rich community of organisms from bacteria and fungi to earthworms, nematodes, and termites forms the soil food web, driving the decomposition of organic matter and the cycling of nutrients through the bacterial and fungal energy channels. Carbon and nitrogen cycling in particular are central to soil fertility, with multiple microbial transformations converting organic compounds to forms usable by plants and returning gases to the atmosphere.

The relationship between soil, water, and living organisms is intimate: plant available water is determined by soil texture and organic matter, while soil fauna depend on moisture for survival and activity. Soil sampling techniques allow the physical, chemical, and biological condition of soil to be measured and monitored. Finally, soil erosion by water and wind represents a critical environmental threat to agricultural productivity, particularly in Nigeria, and its alleviation through vegetation cover, contour farming, terracing, mulching, and agroforestry is among the most important practical applications of soil science and biogeography together.

Glossary of Terms

- **Ammonification:** the microbial decomposition of organic nitrogen compounds in dead organic matter to release ammonium ions into the soil.
- **Cation exchange capacity (CEC):** a measure of the soil ability to hold positively charged nutrient ions on clay and humus surfaces, preventing their loss by leaching.
- **Detritivore:** an organism that obtains energy by feeding on dead organic matter (detritus), including earthworms, millipedes, and many fungi and bacteria.
- **Denitrification:** the microbial conversion of nitrate to gaseous nitrogen (N2 or N2O) under anaerobic conditions, causing nitrogen loss from soil.

- **Field capacity:** the soil water content remaining after free drainage has ceased, representing the upper boundary of plant available water.
- **Humus:** the stable, dark fraction of soil organic matter formed by the advanced decomposition and transformation of plant and animal residues, contributing to soil structure and fertility.
- **Nitrification:** the microbial oxidation of ammonium to nitrite and then to nitrate, carried out by Nitrosomonas and Nitrobacter bacteria.
- **Permanent wilting point:** the soil water content at which plants can no longer extract water from the soil, representing the lower boundary of plant available water.
- **Soil horizon:** a layer in the soil profile with distinct characteristics (colour, texture, organic matter content) that differ from adjacent layers above and below.
- **Soil texture:** the relative proportions of sand, silt, and clay particle size classes in a soil, determining drainage, aeration, and nutrient retention properties.

Concept Check Questions [Series 5]

Objective Questions

1. Soil texture is defined by the relative proportions of sand, ________ , and clay. (Linked to SLO 5.1)
2. The ________ horizon is the topsoil layer rich in organic matter and biological activity. (Linked to SLO 5.1)
3. ________ are the most numerically abundant soil organisms, carrying out decomposition and nitrification. (Linked to SLO 5.2)
4. ________ is the conversion of nitrate to gaseous N2 under anaerobic conditions, causing nitrogen loss from soil. (Linked to SLO 5.3)
5. ________ farming reduces soil erosion by ploughing along contour lines rather than up and down slopes. (Linked to SLO 5.4)

Short-Answer Questions

1. Define cation exchange capacity and explain why it matters for soil fertility. (Linked to SLO 5.1)
2. Name four groups of soil fauna and state the role of each. (Linked to SLO 5.2)
3. Name the four major transformations in the soil nitrogen cycle. (Linked to SLO 5.3)
4. Define plant available water and state what determines it. (Linked to SLO 5.4)
5. Name four methods for alleviating soil erosion. (Linked to SLO 5.4)

Long-Answer Questions

1. Describe the physical and chemical properties of soil that determine its fertility. (Linked to SLO 5.1)
2. Describe soil organisms and the soil food web, and explain nutrient cycling in soil. (Linked to SLOs 5.2, 5.3)
3. Explain plant and animal soil-water relationships and the causes and alleviation of soil erosion. (Linked to SLO 5.4)

Answers to Concept Check Questions [Series 5]

Objective Questions

1. Silt.
2. A.
3. Bacteria.
4. Denitrification.
5. Contour.

Short-Answer Questions

1. CEC is the ability of soil to hold positively charged nutrient cations on clay and humus surfaces; high CEC soils retain more nutrients and are more fertile.
2. Earthworms (mix and aerate soil, nutrient-rich casts), millipedes (fragment litter), nematodes (feed on bacteria, fungi, roots), termites (decompose wood, modify soil structure).
3. Nitrogen fixation, ammonification, nitrification, and denitrification.
4. Plant available water is the fraction of soil water between field capacity and permanent wilting point from which roots can extract water; it is determined by soil texture and organic matter content.
5. Vegetation cover, contour farming, terracing, and mulching (or grass strips, windbreaks, agroforestry).

Long-Answer Questions

1. Soil consists of mineral particles, organic matter, water, and air. Texture (sand, silt, clay proportions) determines drainage and nutrient retention. Structure (aggregate formation) determines porosity and root penetration. Soil profile (O, A, B, C, R horizons) shows the vertical organisation. pH affects nutrient availability (optimum 6-7 for most crops). CEC (clay and humus surfaces holding cations) determines fertilty; liming improves CEC in acid soils.
2. Soil fauna (earthworms, nematodes, millipedes, termites, collembolans, mites) form the detrital community. Bacteria and fungi are the primary decomposers, with bacteria more abundant and fungi important for lignin decomposition. The soil food web has bacterial and fungal channels rising through protozoa and nematodes to predatory arthropods. Carbon

cycling converts plant litter through humus to CO_2. Nitrogen cycling involves fixation, ammonification, nitrification, and denitrification; phosphorus cycling lacks an atmospheric phase and is constrained by soil pH.

3. Plant available water lies between field capacity and wilting point; clay-rich organic soils hold more available water. Soil fauna (especially earthworms) require moisture for respiration and activity. Soil sampling uses augers for chemical analysis and Berlese-Tullgren funnels for mesofauna. Erosion is caused by raindrop impact, surface runoff, and rill/gully formation; it is alleviated by vegetation cover, contour farming, terracing, mulching, grass strips, and agroforestry.

Answers to Pilot Questions [Series 5]

Part 5.1

1. Mineral particles, organic matter, water, and air.
2. Soil texture is the relative proportions of sand, silt, and clay; sand (0.05-2 mm), silt (0.002-0.05 mm), clay (less than 0.002 mm).
3. horizon: organic layer of litter and humus at the surface. A horizon: topsoil, dark, rich in organic matter and biological activity.
4. Most nutrients are most available at near-neutral pH (6-7); acid soils have toxic aluminium and manganese, while alkaline soils cause micronutrient deficiencies.
5. CEC is the ability of soil to hold positively charged nutrient ions on clay and humus surfaces; high CEC soils retain more nutrients, preventing leaching and maintaining plant availability.

Part 5.2

1. Detritus organisms feed on dead organic matter; four groups: earthworms, millipedes, nematodes, and termites.
2. Earthworms ingest and mix soil, produce nutrient-rich casts, and aerate the soil; their abundance indicates active biological cycling and good soil structure.
3. Nitrogen fixation (by Rhizobium, Azotobacter), nitrification (by Nitrosomonas, Nitrobacter), denitrification (by denitrifying bacteria), and ammonification (by general decomposer bacteria and fungi).

4. Fungi decompose complex organic compounds including lignin that most bacteria cannot efficiently break down, and mycorrhizal fungi transfer nutrients from soil directly to plant roots.
5. The bacterial channel is fast-cycling and associated with wetter, nutrient-rich soils; the fungal channel is slower-cycling and associated with drier, more acidic, organic-rich soils such as forest floors.

Part 5.3

1. Plant litter falls to the soil surface; macrofauna fragment it; bacteria and fungi mineralise organic compounds to CO2, water, and nutrients; a fraction is incorporated into microbial biomass; through successive processing, stable humus compounds form that persist for decades to millennia.
2. Soils contain more carbon than the atmosphere and all living vegetation combined; land use change that converts soils from carbon sinks to sources contributes significantly to climate change.
3. Nitrogen fixation (Rhizobium, Azotobacter), ammonification (decomposer bacteria and fungi), nitrification (Nitrosomonas to nitrite, Nitrobacter to nitrate), denitrification (denitrifying bacteria under anaerobic conditions).
4. Acid tropical soils have high iron and aluminium oxide contents that fix phosphorus in unavailable forms; at low pH, phosphorus precipitates as iron and aluminium phosphates, making it inaccessible to plants.
5. A nutrient pool is the quantity of a nutrient held in a particular form (living organisms, dead organic matter, soil solution, adsorbed, or mineral); a nutrient flux is the rate of transfer of nutrient between pools.

Part 5.4

1. Plant available water is the soil water held between field capacity (approximately -0.03 MPa) and permanent wilting point (approximately -1.5 MPa).
2. Earthworms require moist skin for cutaneous gas exchange (respiration); desiccation rapidly kills them, so their distribution and seasonal activity are strongly linked to soil moisture availability.

3. A soil auger or core sampler is used to collect multiple cores from across the sampling area to a specified depth (0-15 cm topsoil); cores are composited, air-dried, sieved, and sent for laboratory analysis.
4. A Berlese-Tullgren funnel applies heat from above a soil sample; small arthropods (mites, collembolans) move downward away from the heat and fall through the funnel into a collecting vessel for identification and counting.
5. Vegetation cover, contour farming, terracing, and mulching.

References and Attribution

Textual References (Books and External Sources)

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Figures, Plates, Tables, and Boxes

- Figure 5.1: Soil composition, texture, and profile Attribution: AI generated. Suggested OER search string: "soil texture triangle sand silt clay soil profile horizons O A B C R horizon organic matter OER".
- Figure 5.2: Soil organisms and food web Attribution: AI generated. Suggested OER search string: "soil food web detritus organisms earthworm nematode bacteria fungi soil microbiology decomposition trophic levels OER".
- Figure 5.3: Soil nutrient cycling Attribution: AI generated. Suggested OER search string: "soil nitrogen cycle fixation nitrification denitrification nutrient pools carbon cycle phosphorus soil biology OER".
- Figure 5.4: Soil-water-plant relationships and soil erosion Attribution: AI generated. Suggested OER search string: "soil water plant available field capacity wilting point erosion contour farming terracing mulch agroforestry OER".