The Origin of Species

Chapter 22

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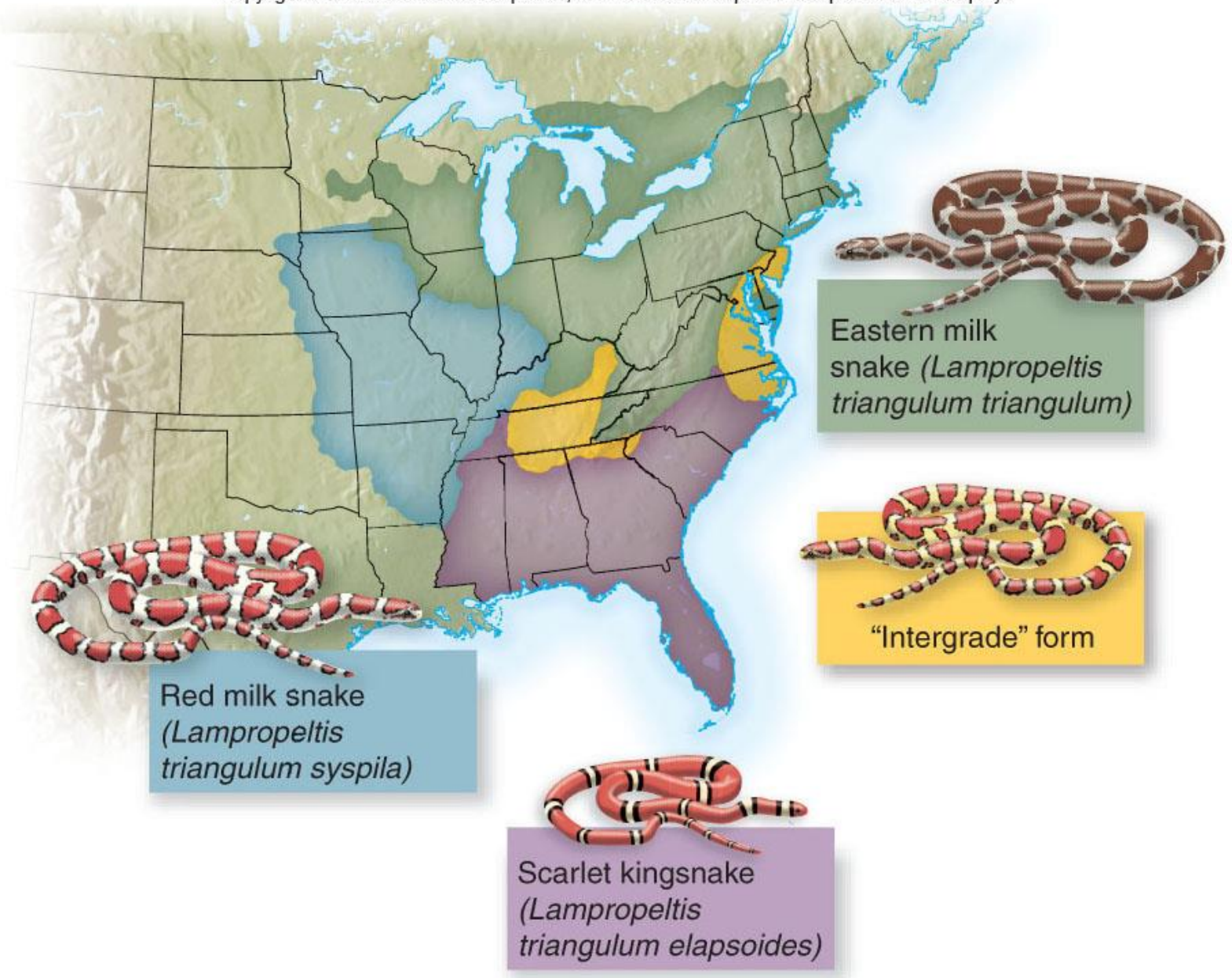
The Nature of Species

- The concept of species must account for two phenomena:
  - The distinctiveness of species that occur together at a single locality
  - The connection that exists among different populations belonging to the same species

- Sympatric species occur together in an area
  - Are distinctive entities
  - Are phenotypically different
  - Utilize different parts of the habitat
  - Behave separately
- Even if they look alike to us, the organisms themselves have no such difficulties

- Subspecies
  - Within a single species, individuals in populations that occur in different areas may be distinct from one another
- Even though geographically distant populations may appear distinct, they are usually connected by intervening populations that are intermediate in their characteristics



Data from R. Conant & J.T. Collins, Reptiles & Amphibians of Eastern/Central North America, 3rd edition, 1991. Houghton Miffl in Company.

The Biological Species Concept

- Species composed of populations whose members mate with each other and produce fertile offspring
- Reproductive isolation – do not mate with each other or do not produce fertile offspring

Gene exhange

- The biological species concept focuses on the ability to exchange genes
  - Prezygotic isolating mechanisms
    - Mechanisms that prevent formation of a zygote
  - Postzygotic isolating mechanisms
    - Mechanisms that prevent development into an adult

- Reproductive isolating mechanisms
  - Prezygotic isolating mechanisms
    - Ecological isolation
    - Behavioral isolation
    - Temporal isolation
    - Mechanical isolation
    - Prevention of gamete fusion
  - Postzygotic isolating mechanisms
    - Hybrid inviability or infertility

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- Ecological isolation
  - Tiglons do not occur in the wild
  - Lions and tiger ranges overlap in India but they use different habitats

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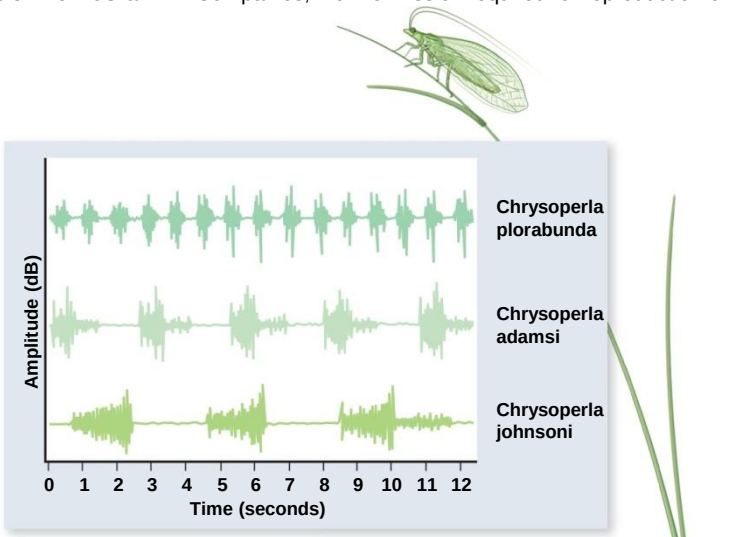
- Behavioral isolation
  - Blue-fotted boobies select mates after an elaborate courtship display
  - Will not mate with other boobies

- Sympatric species avoid mating with members of the wrong species in a variety of ways, including differences in:
  - Visual signals
  - Sound production
  - Chemical signals: pheromones
  - Electrical signals: electroreception



- Lacewings rely on auditory signals to attract mates
- Females are able to distinguish calls of different species

- Temporal isolation
  - 2 species of wild lettuce grow along roadsides in the SE U.S.
  - Hybrids can be made experimentally and are fertile
  - Rare in nature because one flowers in early spring and the other in summer

- Mechanical isolation
  - Structure of the male and female copulatory organs may be incompatible
  - Bees may carry the pollen of one species on a certain place on their bodies; if this area does not come into contact with the receptive structures of the flowers of another plant species, the pollen is not transferred

- Prevention of gamete fusion
  - In animals that shed gametes directly into water, the eggs and sperm derived from different species may not attract or fuse with one another
  - In plants, the growth of pollen tubes may be impeded in hybrids between different species

- Postzygotic isolating mechanisms
  - Leopard frogs form a group of related species
    - Many hybrids cannot be produced even in the laboratory
  - Hybrids that do survive may be weaker
  - Hybrids may be sterile – mules
    - Abnormal sex organs
    - Failure to form gametes

- Criticisms of biological species concept:
  - Reproductive isolation may not be the only force maintaining species integrity
  - Interspecific hybridization
    - 50% of California plant species, in one study, not well defined by genetic isolation
    - 10% of world′s 9500 bird species known to hybridize in nature

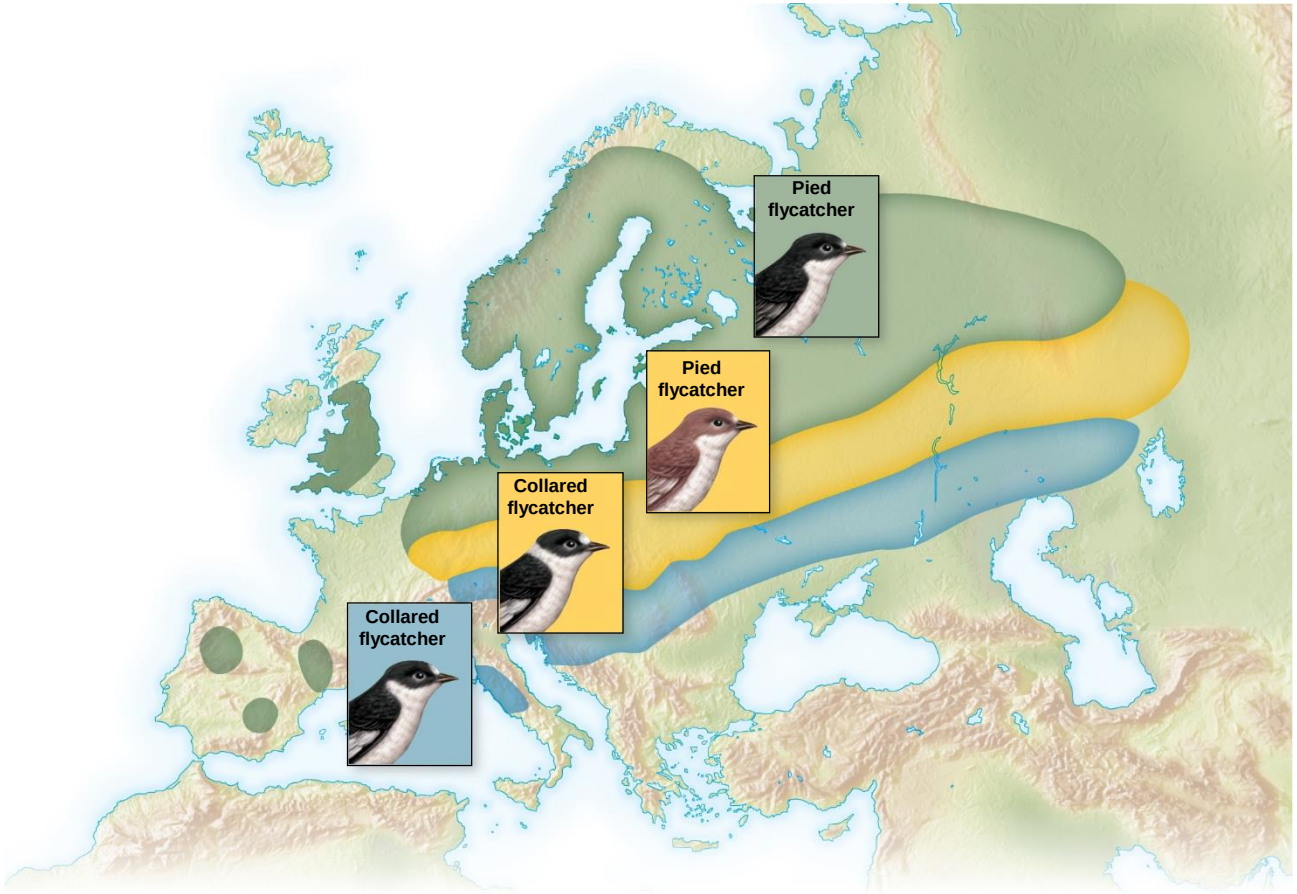
- Ecological species concept
  - Distinctions among species are maintained by natural selection
  - Stabilizing selection maintains the species′ adaptations
  - Hybrids are quickly eliminated from gene pool

- Other weaknesses of biological species concept
  - Difficult to apply the concept to populations that are geographically separated in nature
  - Many species that do not hybridize in the wild will do so in captivity
  - Many organisms are asexual

Reproductive Isolation

- Cladogenesis
  - One ancestral species becomes divided into two descendant species
- If species are defined by the existence of reproductive isolation,
  - Then the process of speciation is identical to the evolution of reproductive isolating mechanisms

- Selection may reinforce isolating mechanisms
  - Formation of species a continuous process
  - 2 populations may be only partially reproductively isolated
  - Reinforcement – initially incomplete isolating mechanisms are reinforced by natural selection until they are completely effective
  - Reinforcement is not inevitable – hybrids may be inferior but may still be fertile – serve as conduit of genetic exchange

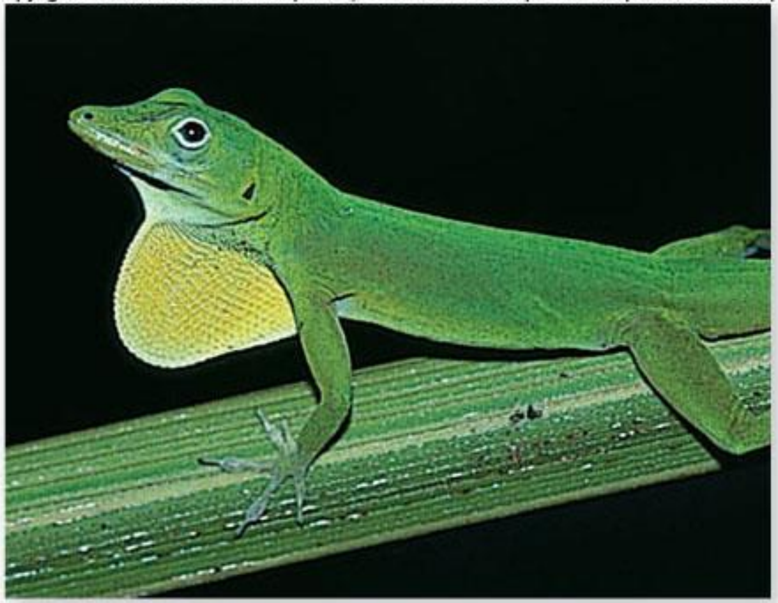


- Pied flycatcher and collared flycatcher appear very similar where they occur alone
- In areas where they are sympatric, differences in color and pattern allow individuals to avoid hybridizing

Genetic Drift

- Random changes may cause reproductive isolation
  - Genetic drift in small populations
  - Founder effects
  - Population bottlenecks
- Hawaiian Islands: *Drosophila* differ in courtship behavior
  - Changes in courtship behavior between ancestor and descendant population may be the result of founder events

- Adaptation can lead to speciation
  - As populations of a species adapt to different circumstances, they likely accumulate many differences that may lead to reproductive isolation
  - Changes in dewlap color related to environment
    - If you can't be seen, you don't mate
    - Could lead to reproductive isolation from ancestral population



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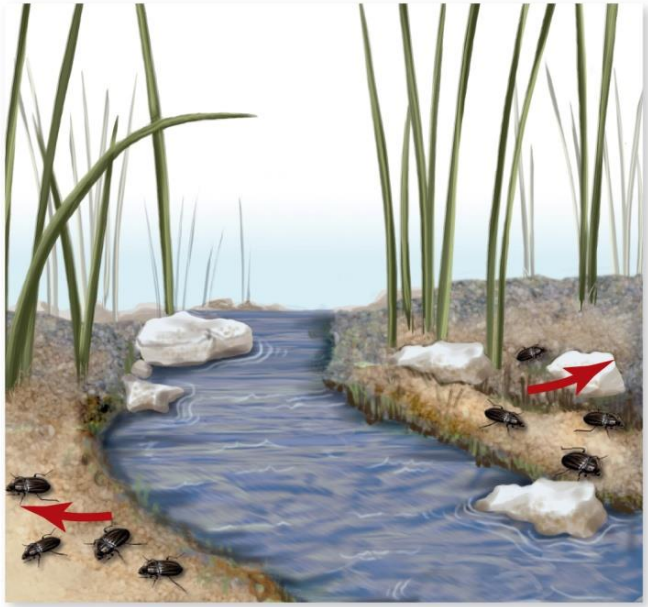
Geography of Speciation

- Speciation is a 2-part process
  - Initially identical populations must diverge
  - Reproductive isolation must evolve to maintain these differences
- Homogenizing effect of gene flow erases differences
- Speciation more likely in geographically isolated populations

a.



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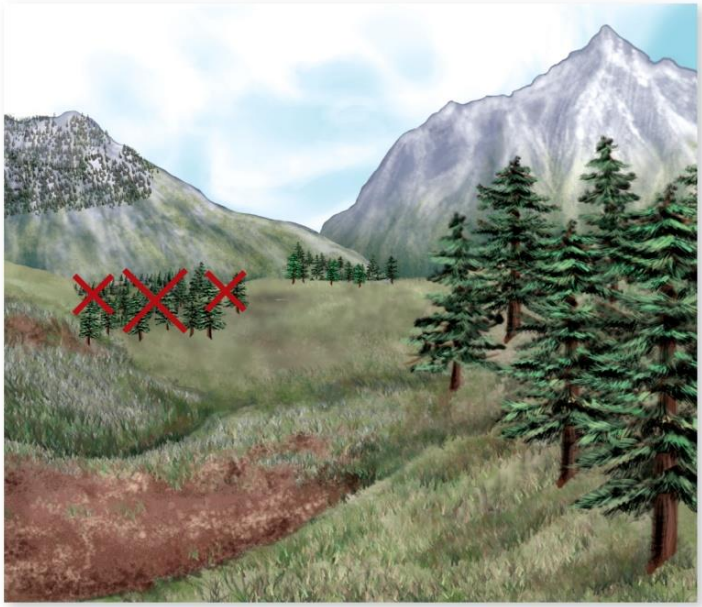
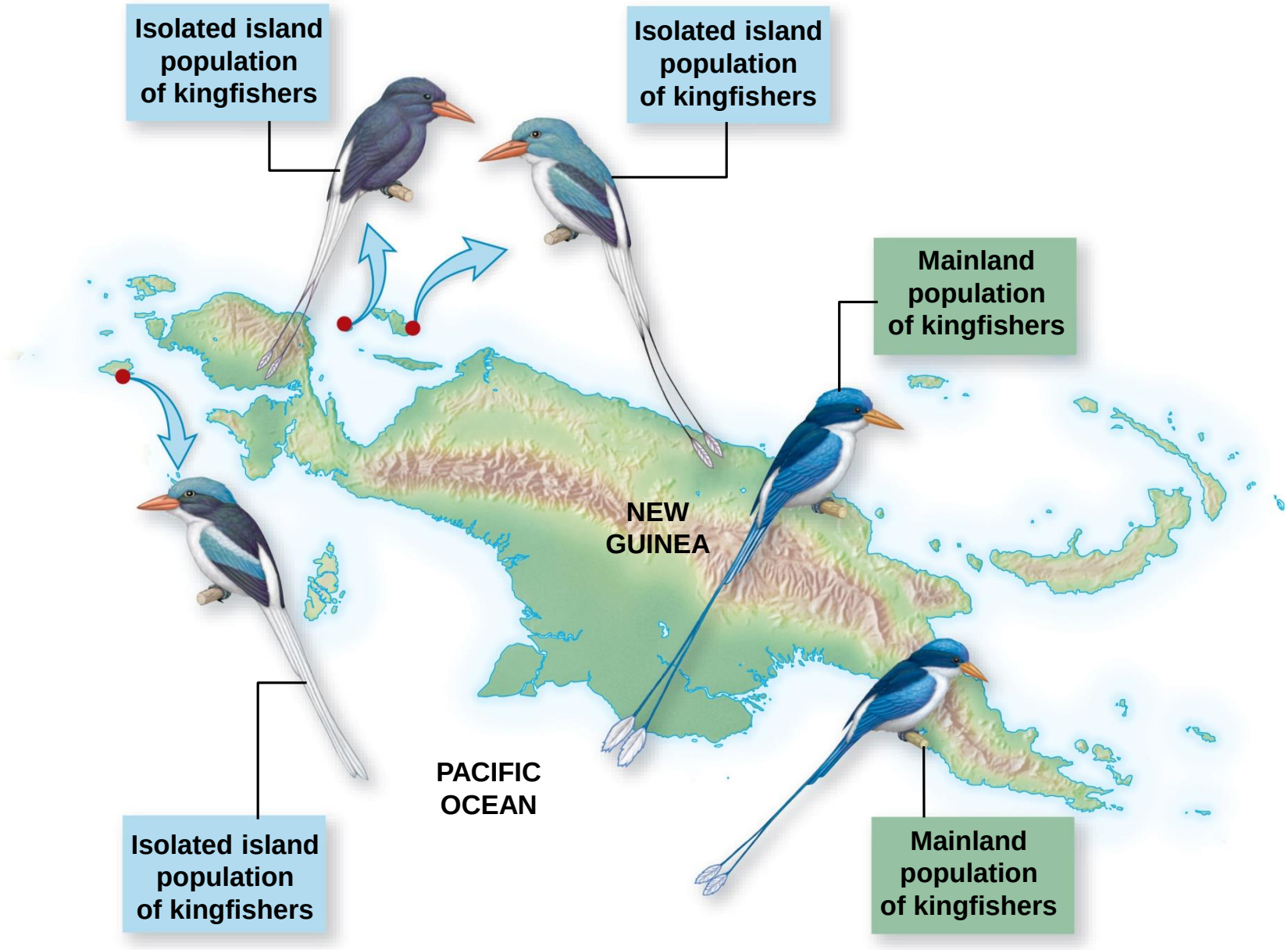


c.

Allopatric speciation

- Geographically separated, or allopatric, populations appear much more likely to have evolved substantial differences leading to speciation
- Little paradise kingfisher varies little throughout range
  - Isolated populations are strikingly different from each other and mainland population

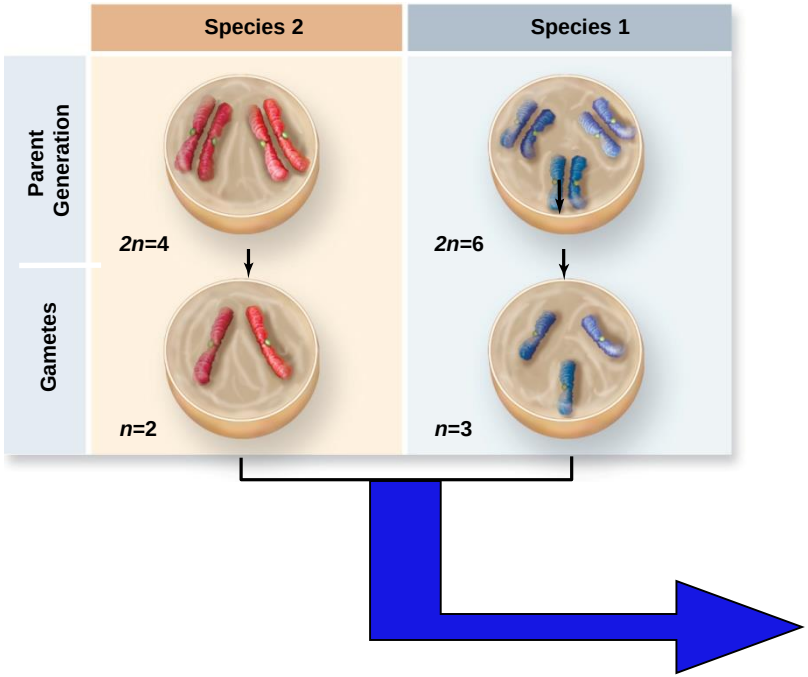


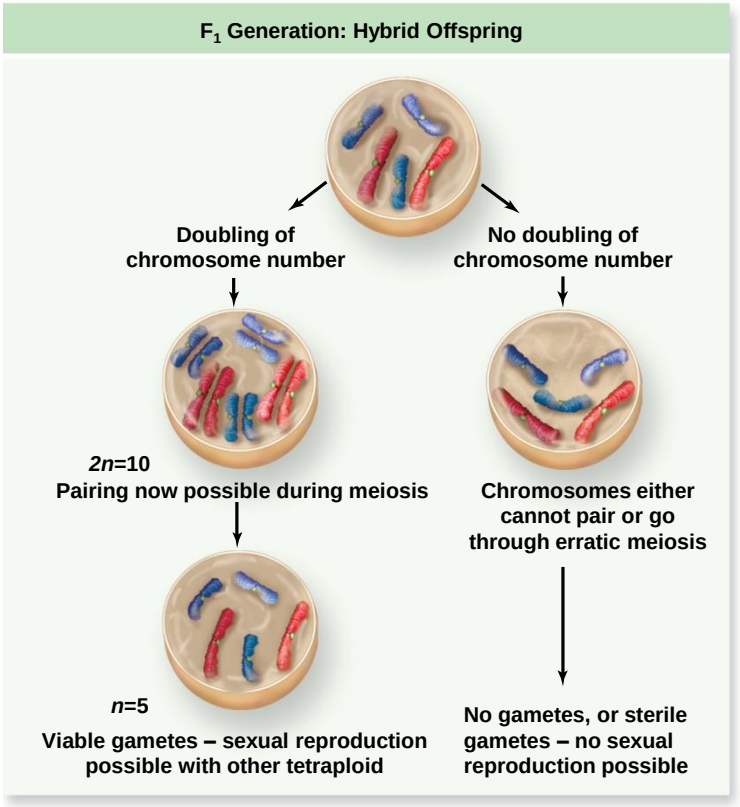
Sympatric speciation

- One species splits into two at a single locality, without the two new species ever having been geographically separated
- One type occurs commonly as the result of polyploidy
  - Individuals that have more than two sets of chromosomes

- 2 ways polyploidy occurs
  - Autoploidy
    - All the chromosomes arise from a single species
    - Error in cell division produces tetraploids
    - Cannot produce fertile offspring with normal diploids

- Allopolyploidy
  - Two species hybridize
  - Resulting offspring have one copy of the chromosomes of each species
  - Infertile: cannot reproduce with either species – can’t produce gametes
  - Can reproduce asexually
  - Can become fertile if chromosomes spontaneously doubled (polyploidy)



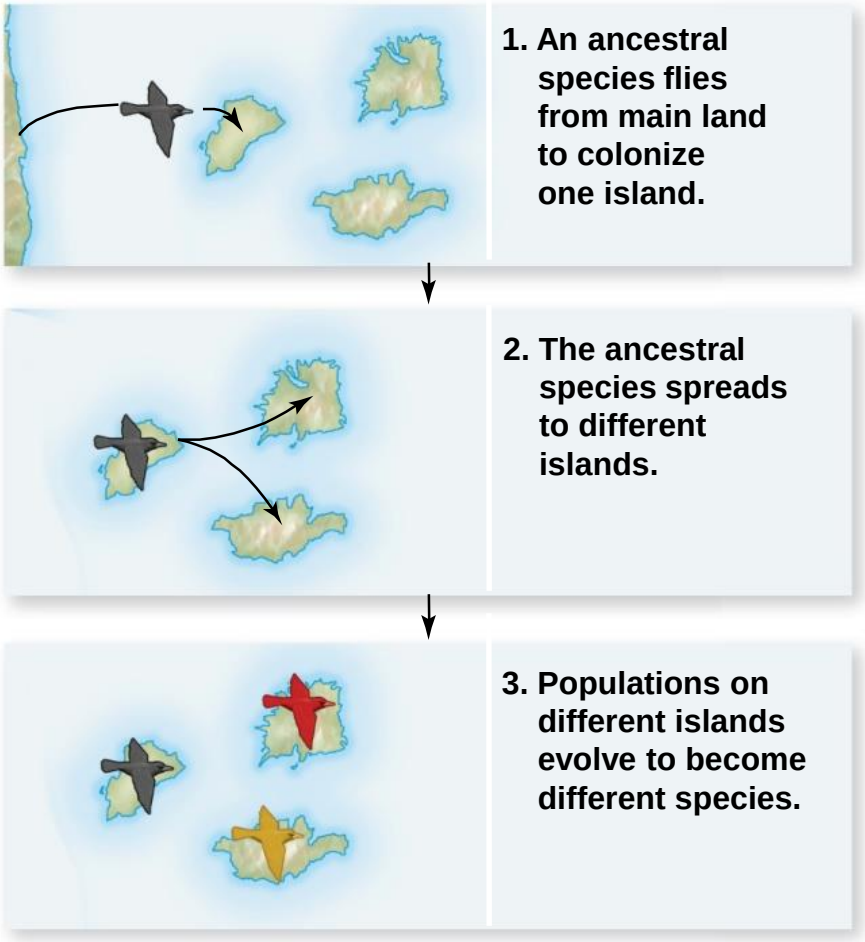


- Sympatric speciation may occur over the course of multiple generations through disruptive selection
  - Cause a population to contain individuals exhibiting two different phenotypes
- Two phenotypes would have to evolve reproductive isolating mechanisms
- Two phenotypes could be retained as polymorphism within a single population

Adaptive radiations

- Closely related species that have recently evolved from a common ancestor by adapting to different parts of the environment
- Occurs
  - In an environment with few other species and many resources
    - Hawaiian and Galápagos Islands
  - Catastrophic event leading to extinction of other species

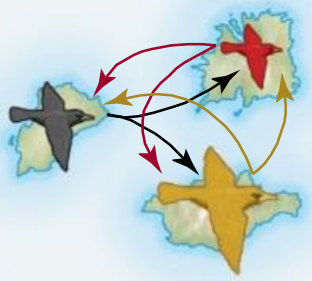
- Key innovation
  - New trait evolves within a species allowing it to use resources that were previously inaccessible
    - Lungs in fish
    - Wings in birds
  - Requires both speciation and adaptation to different habitats
    - Island archipelago example



or

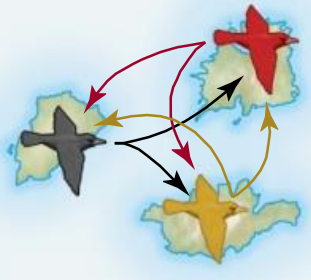
a.

4. Species evolve different adaptations in allopatry.

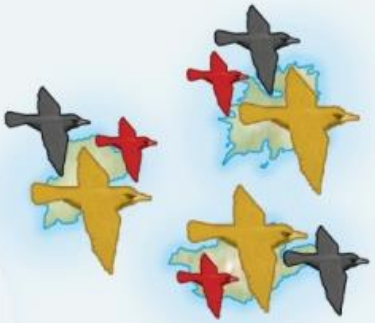


5. Colonization of islands.

b.

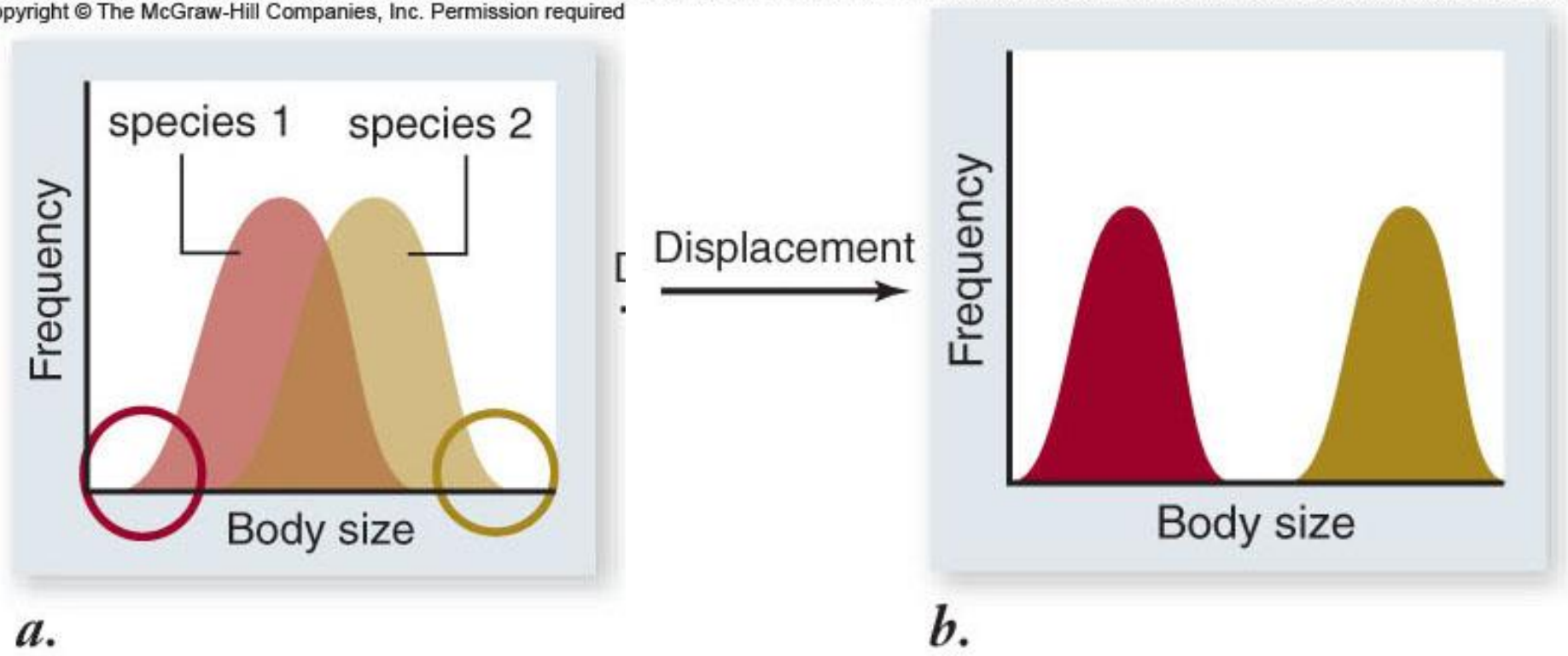


4. Colonization of islands.



5. Species evolve different adaptations to minimize competition with other species (character displacement).

- Character displacement
  - Natural selection in each species favors those individuals that use resources not used by the other species
    - Greater fitness
    - Trait differences in resource use will increase in frequency over time
    - Species will diverge



Individuals in each species that are most different from the other species (circled) will be favored by natural selection, because they will not have to compete with the other species

Hawaiian *Drosophila*

- > 1,000 species of *Drosophila* on Hawaiian Islands
- Diversity of morphological and behavioral traits
- Empty habitats resulted in fruit flies that are:
  - Predators
  - Herbivores
  - Nectar eaters
  - Parasites
  - Detritivores

Hawaiian *Drosophila*

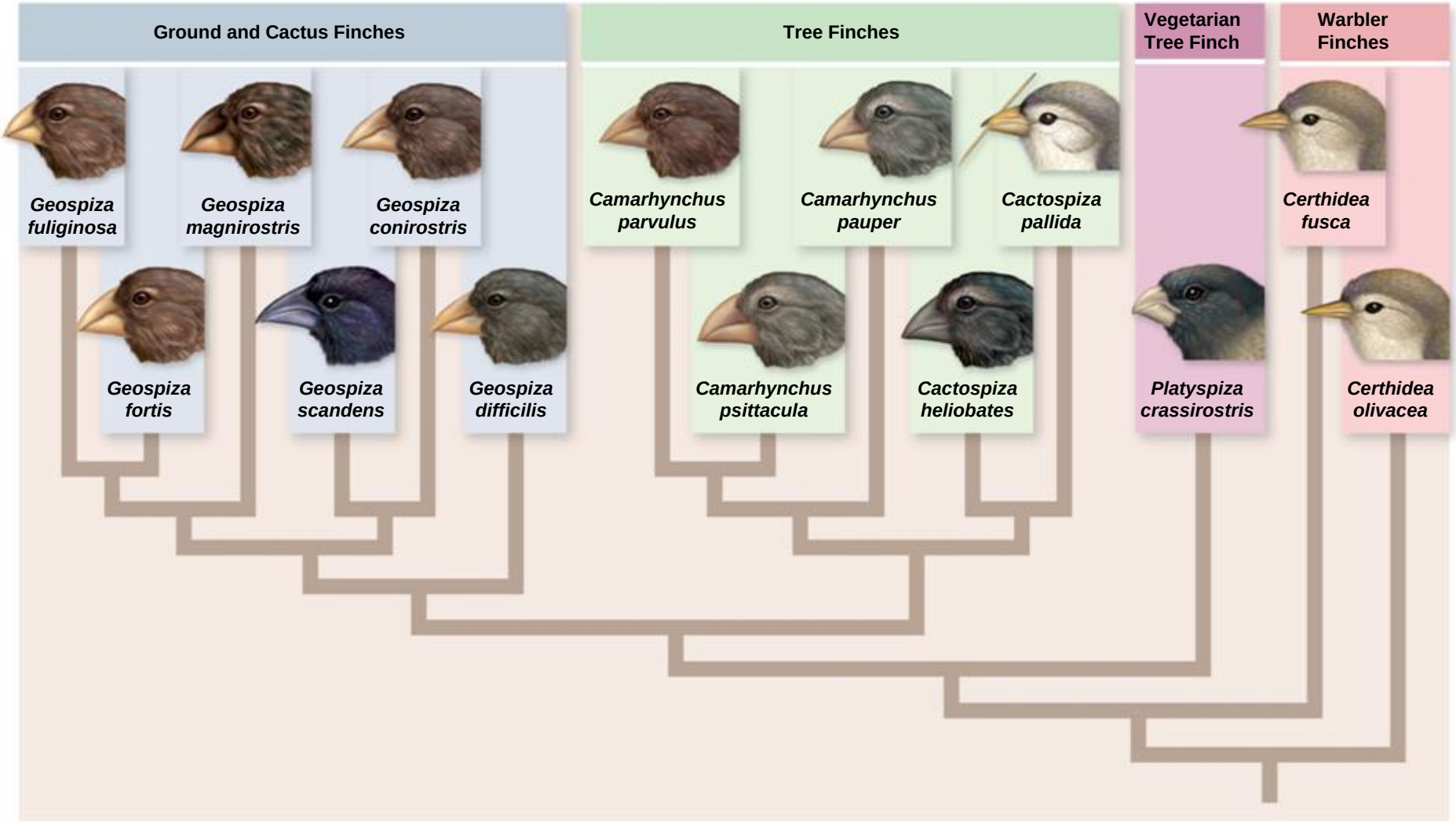
Drosophila heteroneura

Drosophila digressa

Darwin’s finches

- Ancestors reached these islands before other land birds
- Subjected to different selective pressures as they adopted new lifestyles
- Geographic isolation on many islands
- Diverse population, some evolved into separate species
- Occupy many different habitats

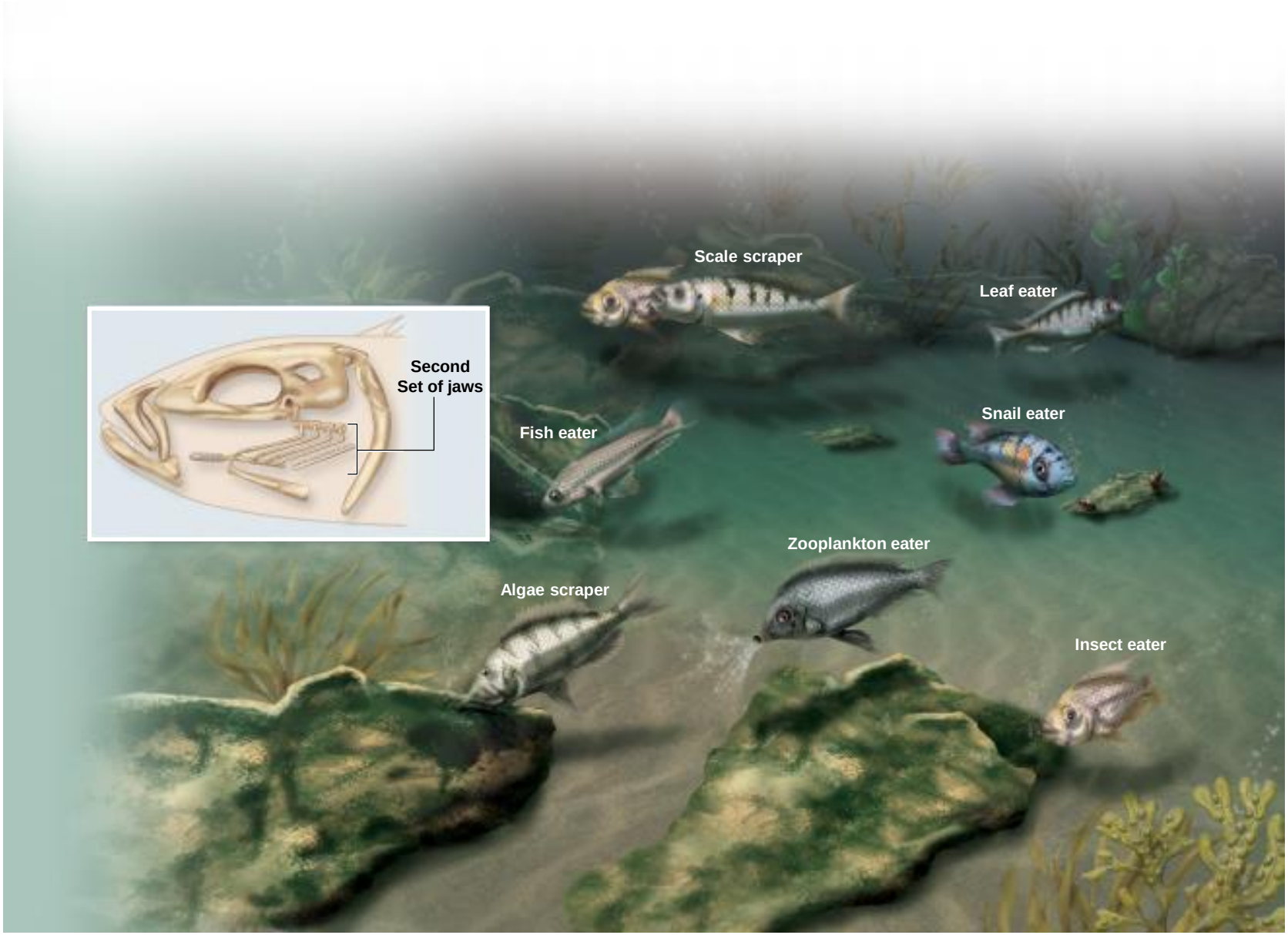
- Differences between species likely resulted from character displacement as initially similar species diverged to minimize competitive pressures
- Ground finches
  - Feed on seeds: size of bill relates to size of seed they eat
- Tree finches
  - All eat insects: one species uses a tool to get insects
- Vegetarian finch
  - Eats buds from branches
- Warbler finches
  - Eat insects from leaves and branches



Lake Victoria cichlid fishes

- Immense, shallow, freshwater sea in equatorial East Africa
- Was home to over 300 species of cichlid until recently
- Sequencing of cytochrome *b* gene reveals first cichlids arrived 200,000 years ago
- Changes in water level encouraged species formation
- Lake dry down 14,000 years ago may have stimulated speciation by isolating populations

- Cichlids are small, perchlike fishes
- Males very colorful
- Sense of diversity in how they eat
  - Mud biters, algae scrapers, leaf chewers, snail crushers, zooplankton eaters, insect eaters, prawn eaters, fish eaters
- Abrupt extinction in the last several decades
  - 1950s: Nile perch introduced into lake
  - 1990s: 70% of cichlids extinct



New Zealand alpine buttercups

- Speciation and diversification have been promoted by repeated cycles of glacial advance and retreat
- 14 species occupy 5 distinct habitats
  - Snowfields: 2130–2740 m elevation
  - Snowline fringe: 1220–2130 m elevation
  - Stony debris: slopes at 610 to 1830 m
  - Sheltered: 305–1830 m
  - Boggy habitats: 760–1525 m elevation

a.

Glaciers link alpine zones into one continuous range.

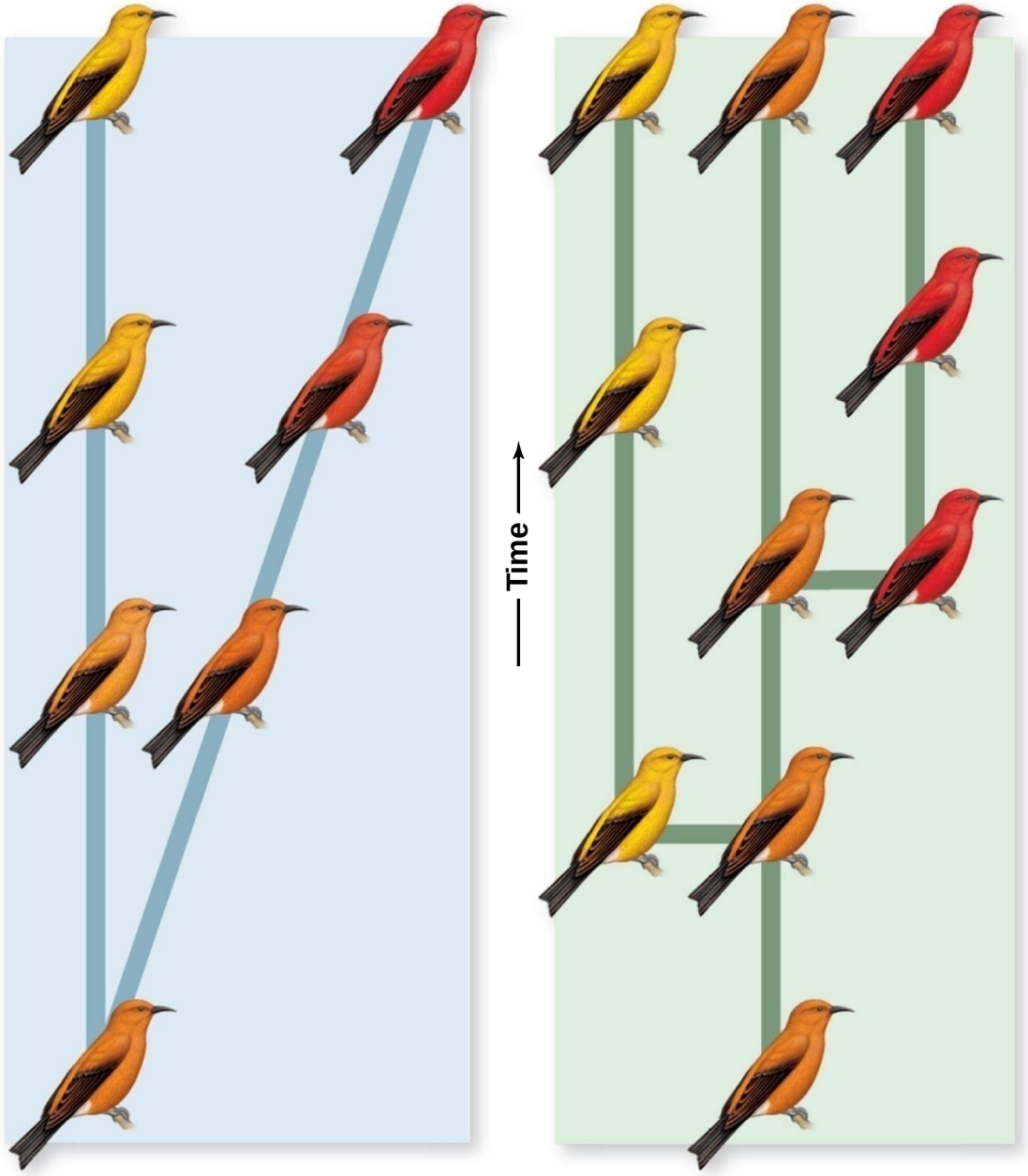
Mountain populations become isolated, permitting divergence and speciation.

Alpine zones are reconnected. Separately evolved species come back into contact.

b.

The Pace of Evolution

- Gradualism
  - Accumulation of small changes
  - Standard view for a long time
- Punctuated equilibrium
  - Long periods of stasis followed by rapid change
  - Stabilizing and oscillating selection is responsible for stasis
- Gradualism and punctuated equilibrium are two ends of a continuum



a. **Gradualism** ***b.*** **Punctuated equilibrium**