Speciation

How are species defined?

Species divergence in allopatry

Species divergence in sympatry

Reuniting

Outline

How are species defined?

- Conceptually, we define species as "evolutionary units":
  - Individuals within a species are evolving together
  - Individuals of different species evolve independently
- It is difficult to make this conceptual definition into a practical definition
  - * i.e., one that we can apply to decide how to group organisms into species
  - Life is complex

An ancestral population

Population splits onto different islands and characteristics diverge

Large ground finch

Medium ground finch

Outline

Biological species concept

- Biological species are defined by reproductive isolation
- Different biological species either:
  - Don't breed in nature
  - Breed but fail to produce offspring
  - Produce **inviable** offspring – offspring do not develop to adulthood
  - Produce **sterile** offspring – offspring that cannot themselves reproduce

Mechanisms of isolation

- Mechanisms of isolation are often divided into two classes:
  - **Prezygotic** isolation refers to any mechanism that prevents successful mating
  - **Postzygotic** isolation refers to any mechanism that prevents offspring from producing offspring of their own
  - "Zygote" means a cell formed by the fusion of a sperm and an egg

Mechanism examples

- Pre- or post-?
  - Different malaria parasites breed inside different hosts
  - Different species of doves can nest together, but eggs fail to hatch or chicks fail to grow
  - The offspring of horses and donkeys grow up to be healthy, infertile adults
  - Sea urchin eggs cannot be penetrated by sperm from other species
  - Species of pine trees release and receive pollen and different times of year

Pre- vs. post-zygotic mechanisms

- Which should be adaptively favored?
  - * Pre-zygotic mechanisms mean less wasted effort
  - * When post-zygotic isolation is happening, there will be natural selection for pre-zygotic isolation
  - * Example: it takes a lot of resources for a horse to birth and raise a mule, but there is no long-term fitness benefit
    - * This is presumably why horses rarely mate with donkeys

Disadvantages of the biological species concept

- * Doesn't apply to asexual species
- * Not practical for extinct species
- * May be hard to evaluate
  - * What if two populations rarely come into contact because of geographic distance?
- *Rings of populations*

Outline

Morphological species concept

- Morphological species are defined to be different if they **look** different
  - Useful for working with fossils, or very diverse groups (e.g., insects)
  - A lot of expertise and experience guides morphospecies decisions
- Disadvantages?
  - * Subjective, prone to disagreements
  - * There are groups that look very similar but can't produce viable offspring
  - * Not clear how definition relates to our conceptual definition of evolutionary units

Meadowlarks (present)

Outline

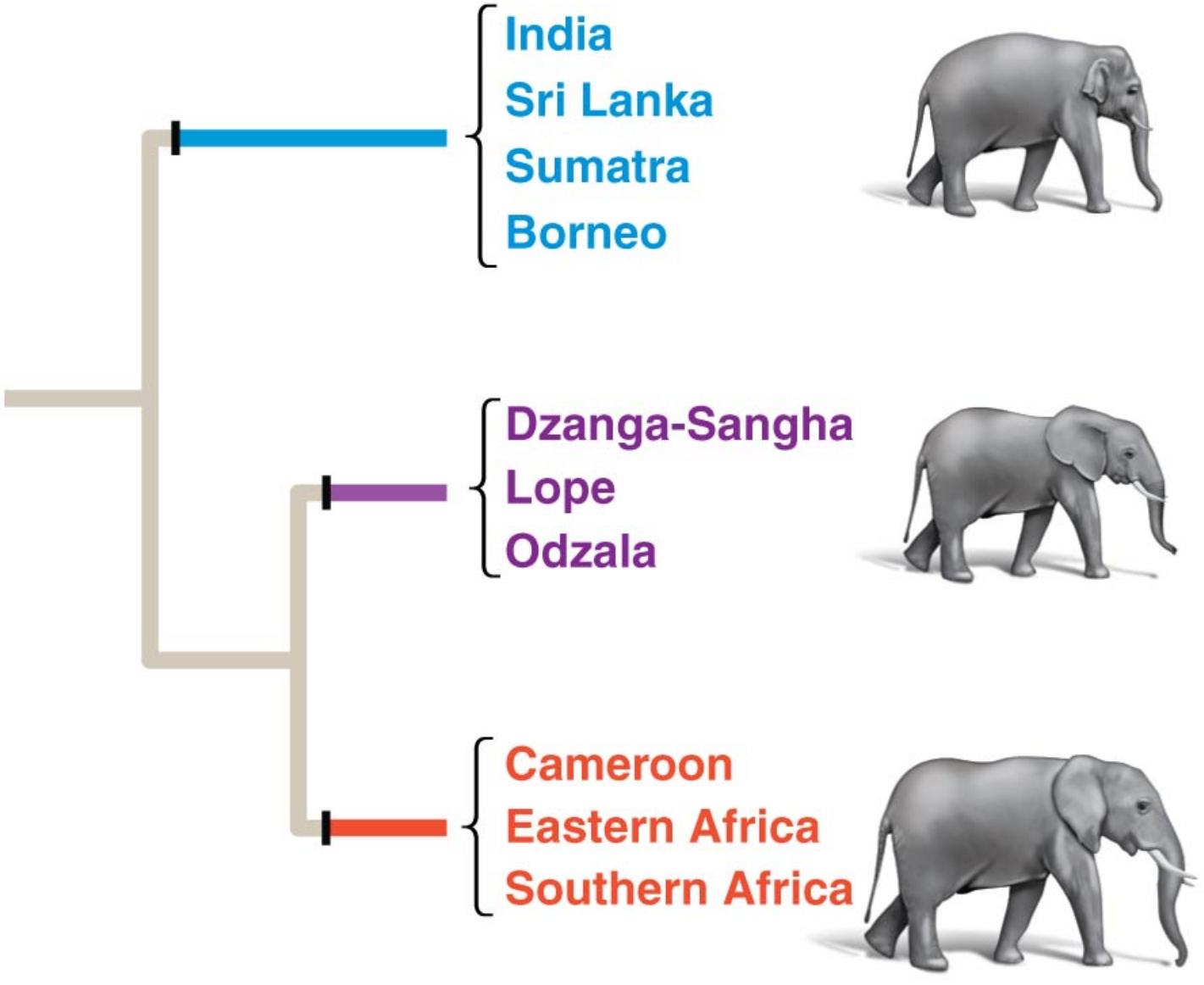
Ecological species concept

- An ecological species is a set of related organisms occupying the same ecological **niche**
  - Exploit similar resources
  - Tolerate similar environments
  - Face similar natural enemies
- Commonly used for small things, particularly small asexual things

Outline

Phylogenetic species concept

- A phylogenetic species is a monophyletic group of *populations*
  - Must not be divisible into smaller species
- A **monophyletic group** is a group *defined by* a single common ancestor
  - All descendants of the ancestor must be in the group


India
Sri Lanka
Sumatra
Borneo
Dzanga-Sangha
Lope
Odzala
Cameroon
Eastern Africa
Southern Africa

Phylogenetic species concept

- Advantages
  - Well defined (as long as you know what a population is)
  - Broadly applicable
- Disadvantages
  - Hard to estimate phylogenies
  - Requires a lot of information about populations
- Believers in the phylogenetic species concept recognize a *lot* of species

Defining species

- Defining species formally can be very tricky
  - No one way is agreed to be the best
- Usually we know more or less what we mean by a species, though

Generating species

- We believe new species are generated from old species
- One species can gradually evolve into another
  - We can't say exactly when the switch occurs
- Species can also **diverge**: one species splits into two species
  - Divergence is the origin of **diversity**

How do species split?

- Genetic isolation
- Genetic divergence
- Which comes first?
  - * Usually isolation: with too much gene flow populations can't diverge
  - * There is often a loop: isolation allows divergence, which causes natural selection for more isolation

Outline

Species divergence in allopatry

- **Allopatry** refers to organisms living apart from each other
- If two populations are isolated from each other, we would expect that they might diverge. Why?
  - * Genetic drift
  - * Natural selection
    - * Different environments, or different adaptive mutations
- How can two populations of the same species be isolated from each other?

Outline

Dispersal

- Isolated populations of the same species can develop if some individuals **disperse** (move) to a new area and **colonize** it (establish a new population).
- Since colonizing populations are usually small, we expect founder effects and drift to be particularly important

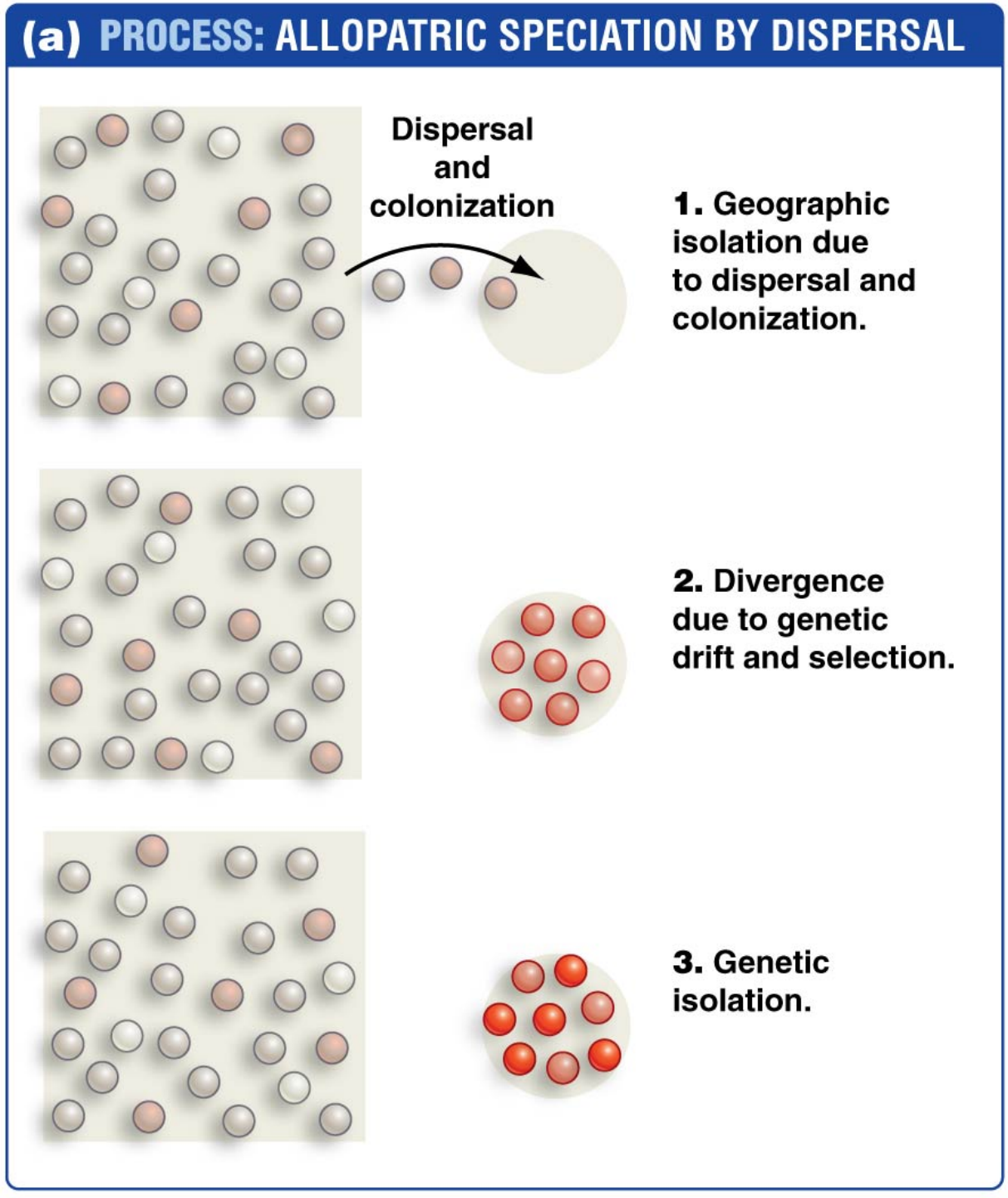
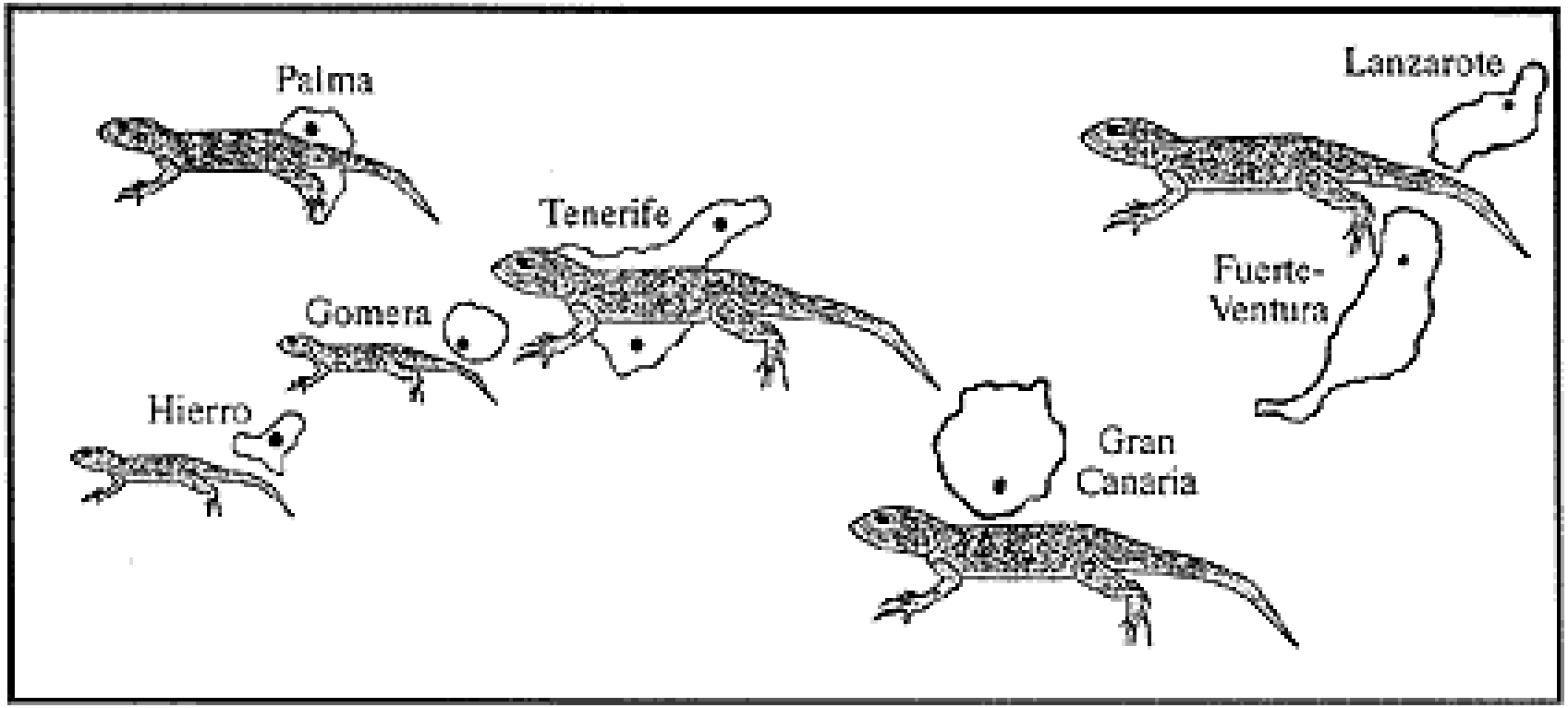


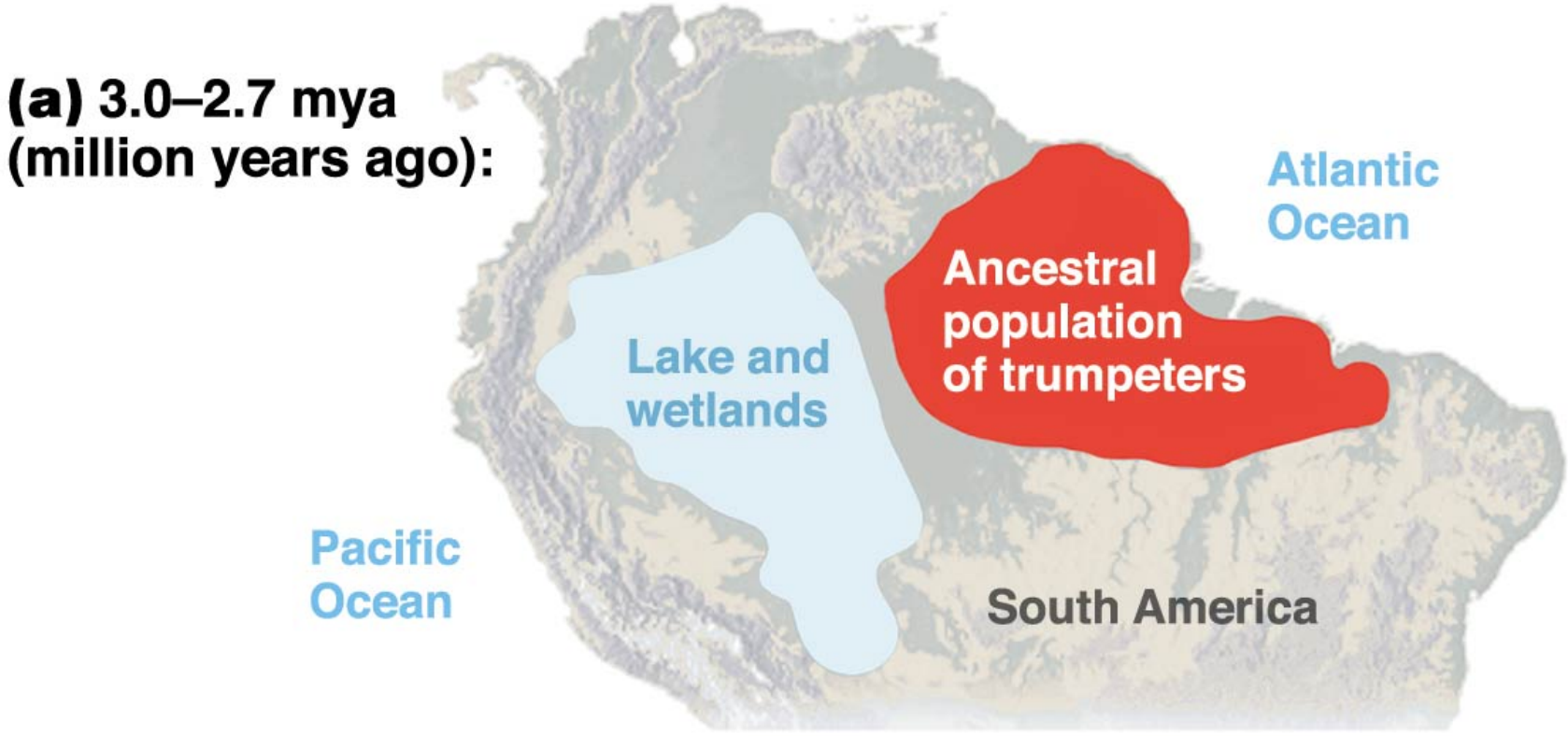
Figure 2. The relative sizes of typical lizards from each population are shown. (Redrawn from Thorpe et al., 1994.)



Outline

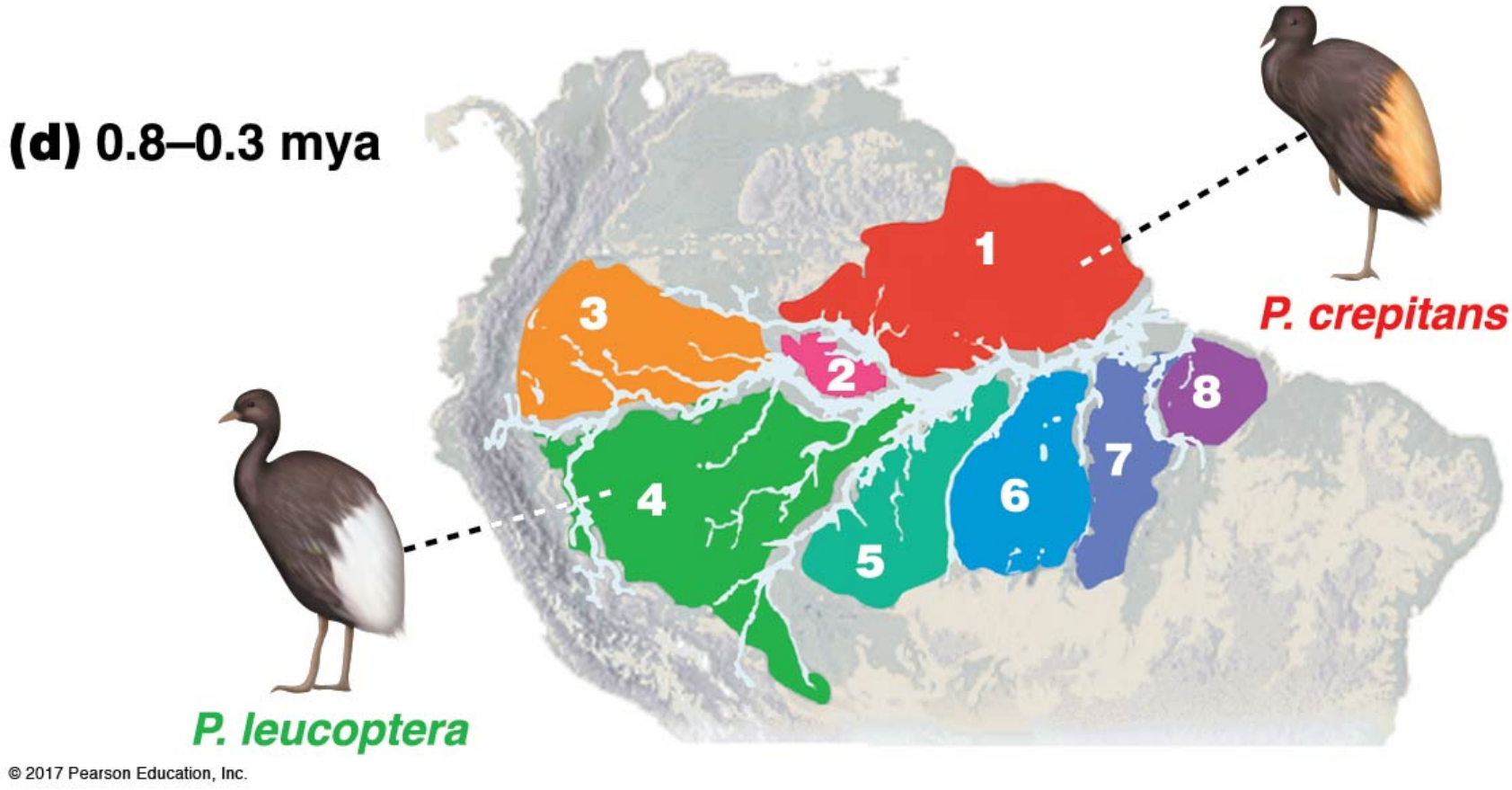
Vicariance

- Isolated populations of the same species can develop when a population is split by a geographical or ecological barrier
- Such splits are called **vicariance** events.
  - Rivers change course, mountains appear or disappear, continents split and join
  - When temperature changes, some species may only be able to survive in "refuges", small, protected parts of their original range

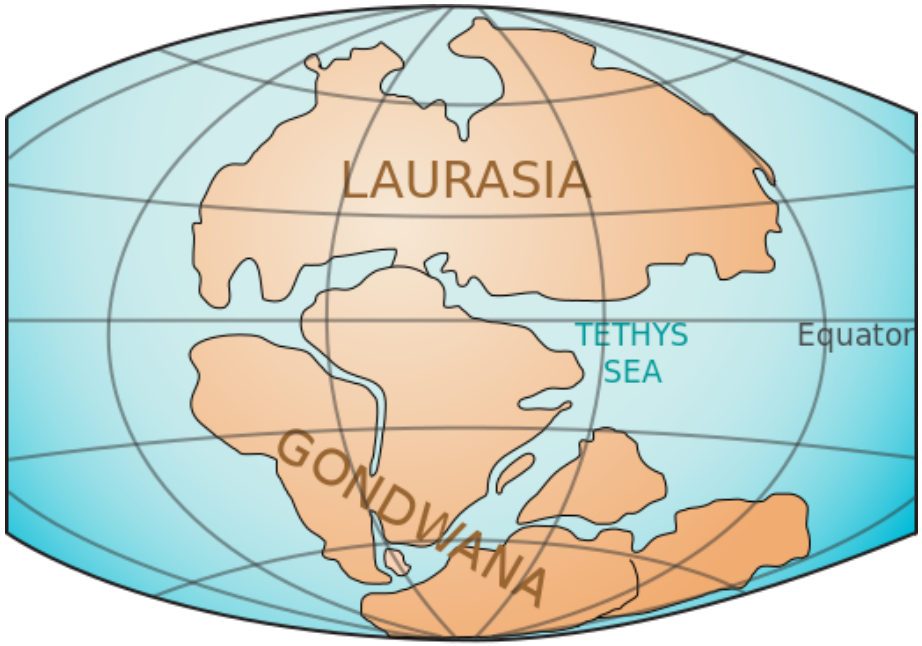


(b) 2.7–2.0 mya

(c) 2.0–1.0 mya



Example: ratites



TRIASSIC
200 million years ago

- The ancestors of today's ostriches, emus, etc. were isolated when the super-continent of Gondwanaland drifted apart starting about 140 million years ago

Outline

Species divergence in sympatry

- **Sympatry** refers to organisms living in the same geographic area
- In general, it should be hard for populations of the same species living in sympatry to diverge.
  - * Gene flow
  - * Competition
- Are there exceptions to this expectation?
  - * Seed crackers?
  - * Hawthorn flies
  - * Soapberry bugs

Outline

Divergence by partitioning habitats

- Insects that feed on many different plants may be subject to divergent selection
  - An individual may do most of its feeding on one particular plant
- In some cases, gene flow will prevent divergence
- In other cases, individuals may mate preferentially with individuals with the same host plant, and divergence may occur

Whitney Cranshaw, Colorado State University, Bugwood.org

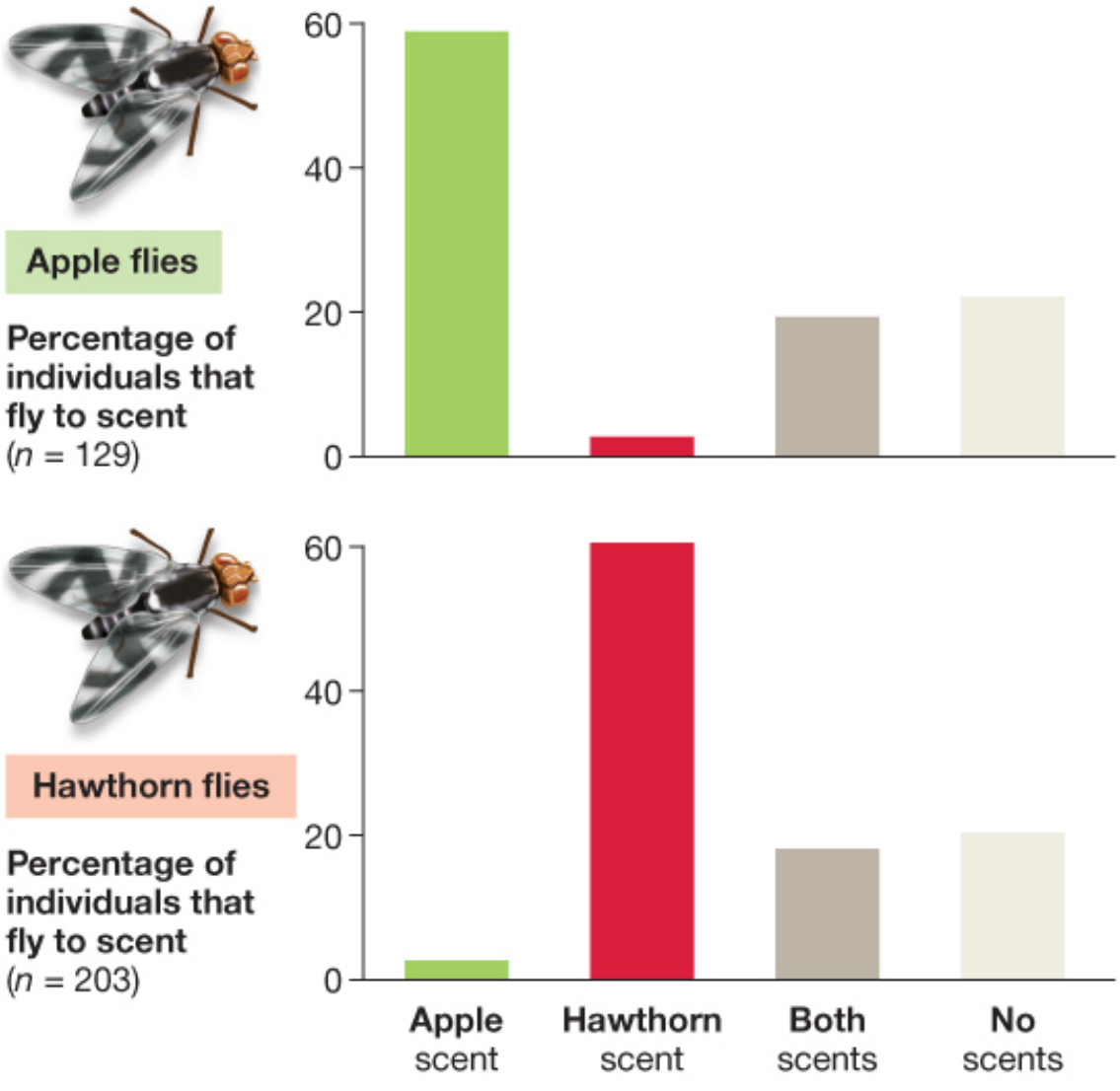


Figure 24.8 Disruptive Selection on Fruit Preference in Flies. Each fly was tested with four types of scent, one at a time, in a laboratory setting.

SOURCE: Based on data from Dambroski, H. R., C. Linn Jr., S. H. Berlocher, et al. 2005. *Evolution* 59: 1953–1964.

Outline

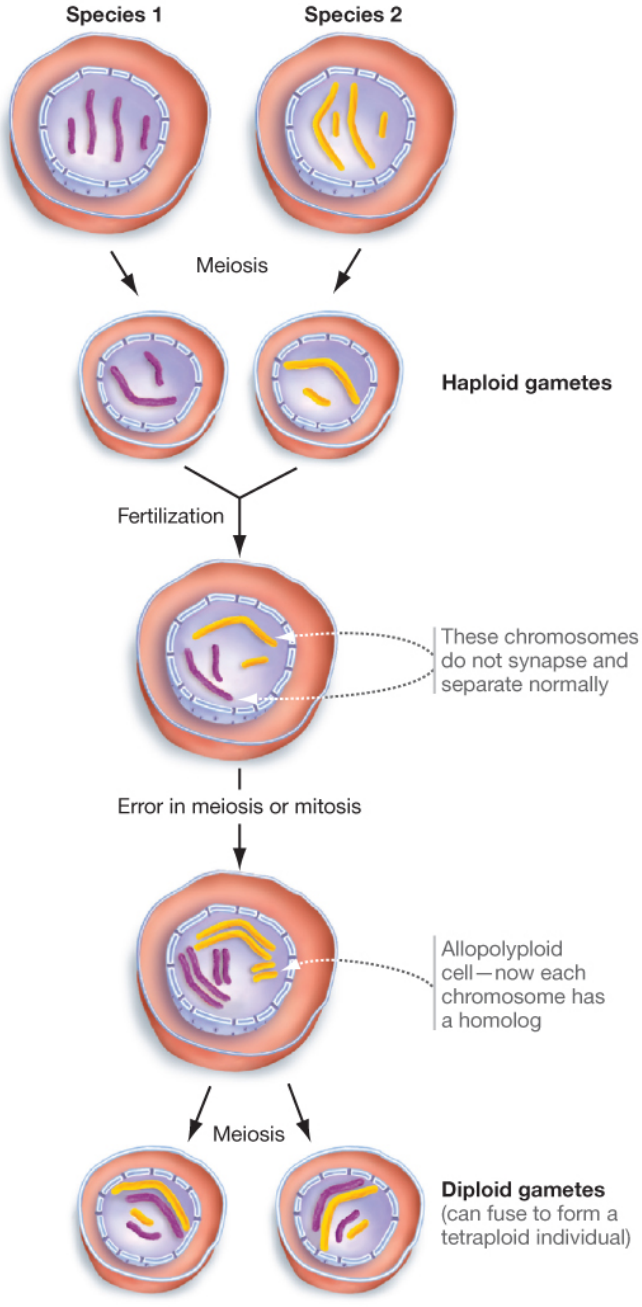
Genetic incompatibility

- Divergence can also occur when mutation causes genetic incompatibility
  - If two populations are in the same place, but can't produce fertile offspring, they are reproductively isolated
- Genetic incompatibility is less likely to produce divergence than physical separation
  - * The populations will still compete, and one may drive the other extinct
  - * Or, reproductive isolation and disruptive selection may work together to make divergence more likely
    - * or less unlikely

Polyploidy

- Reproductive mistakes can occur that produce individuals with extra copies of each chromosome
- Sometimes these **polyploid** individuals survive, and can even mate
- This produces instant reproductive isolation
- It can also provide material for new genetic innovation
  - * Two copies of each gene, so it may be possible to keep one and mutate one

(a) If chromosome doubling occurs, allopolyploid offspring can be fertile and form new species.



(b) An allopolyploid species that formed recently.

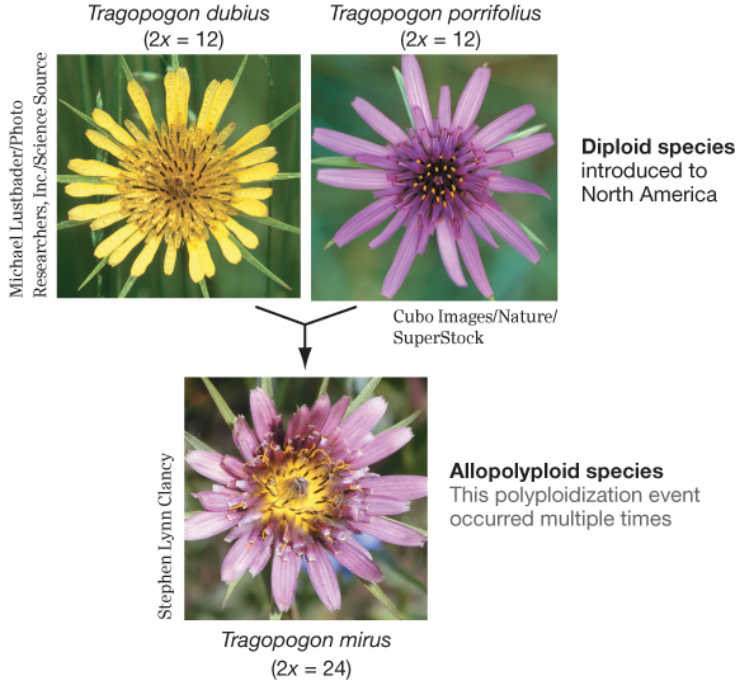


Figure 24.10 Allopolyploids Can Form New Species.

Outline

Reuniting

- What happens when isolated populations come back into contact?
- Usually this happens when a geographic barrier disappears
  - a land bridge forms between an island and the continent
  - a river changes course

Outline

Fusion

- When two isolated populations come into contact, they may **fuse** – go back together
  - Adaptive differences may be small
  - Adaptive differences may be overwhelmed by gene flow

Outline

Reinforcement

- In some cases, hybrid offspring may have low fitness
  - * Incompatible alleles
  - * Disruptive selection
- In these cases we expect natural selection for traits that **reinforce** the distinction between the two species
  - They avoid mating, using coloration, timing, courtship rituals

Meadowlarks (present)

Meadowlarks

- Eastern and Western meadowlarks have hybrid zones in the Great Plains
- Hybrids don't reproduce well
  - Probably due to incompatible alleles after evolving separately
- They have evolved to avoid inter-breeding:
  - * They have different songs

Sticklebacks

- Closely related freshwater sticklebacks live on the bottom (benthic) or in the water column (limnetic)
- Benthic sticklebacks arrived first (from the ocean), and are highly adapted to live on the bottom
- Limnetic sticklebacks arrived later
  - * Adapted to live in the water column
- The two groups evolved to avoiding breeding with each other
  - * Courtship rituals

Outline

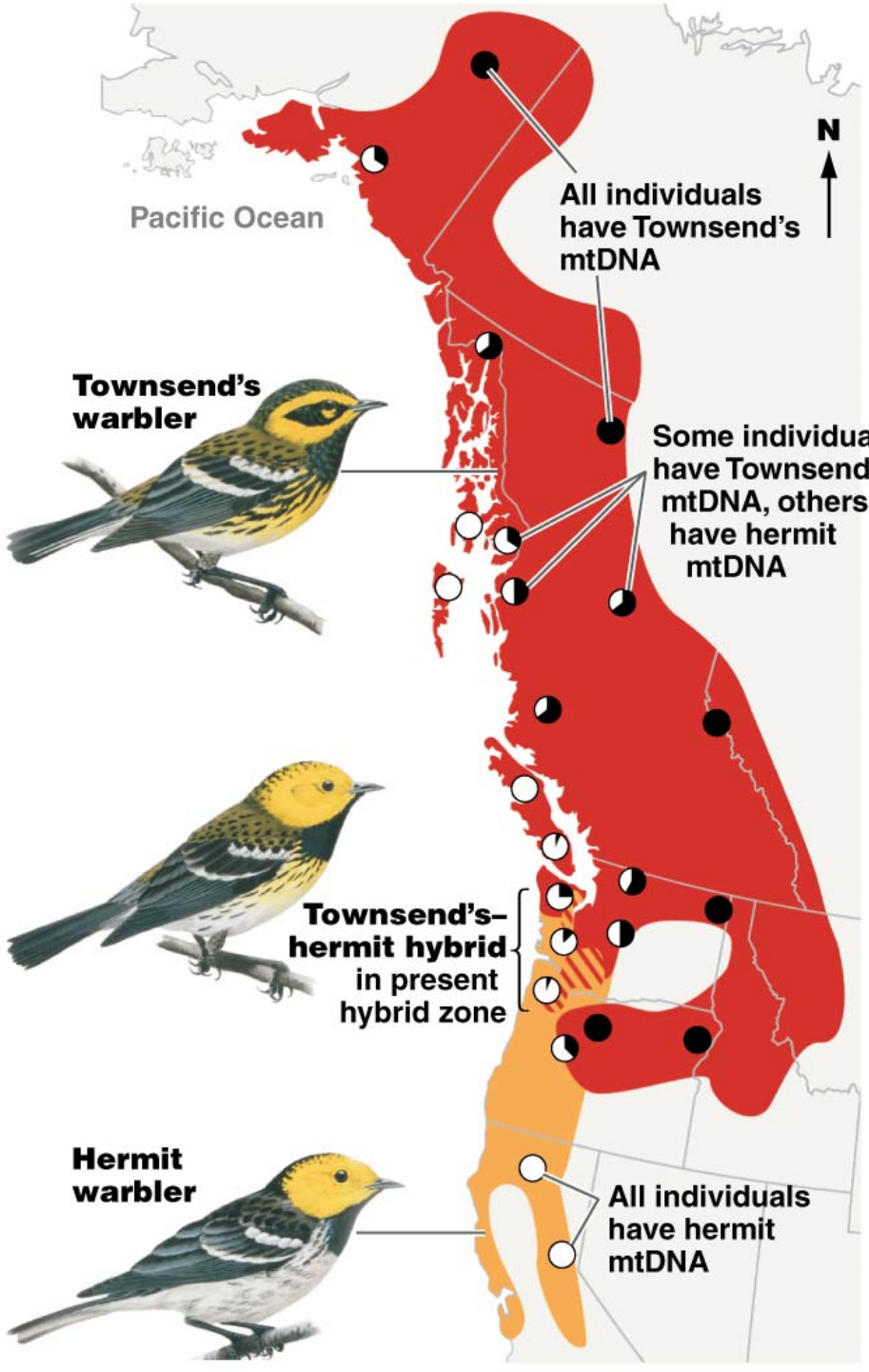
Hybrid zones

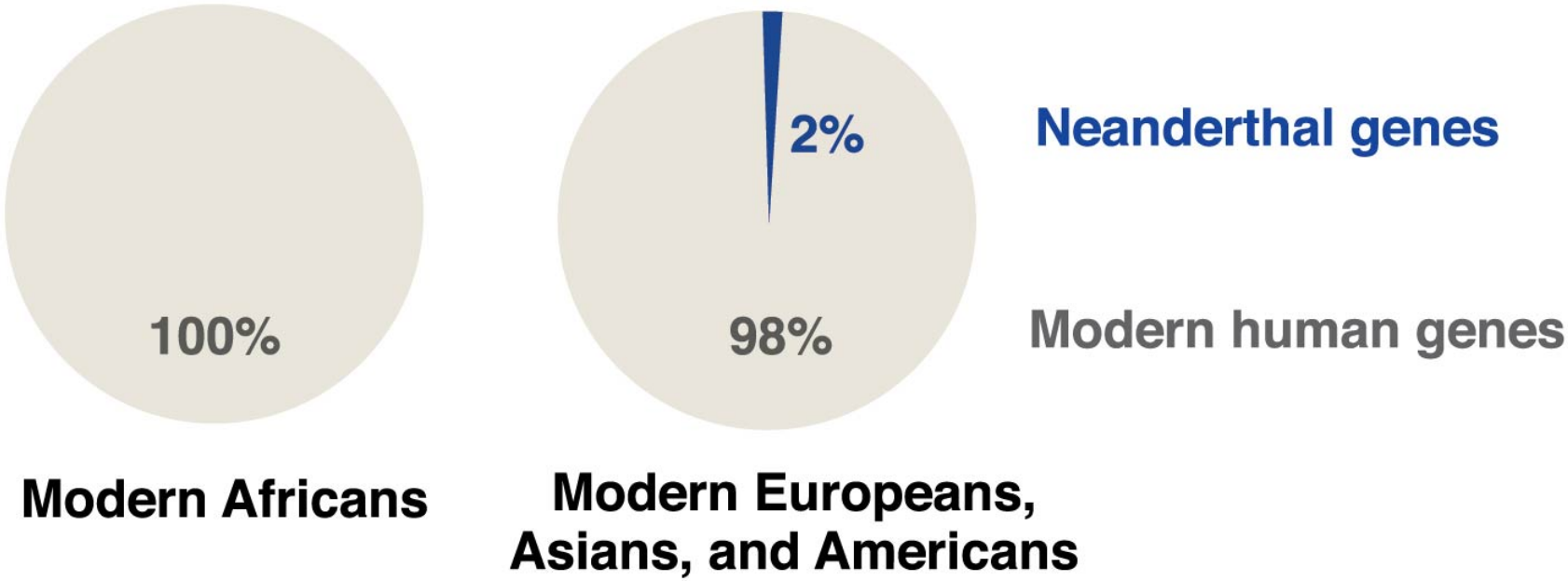
- When hybrid offspring are functional, and well-adapted to the overlap zone, there may be a zone where hybrids occur
- Not always clear when we should consider the species to be different
  - What if species B has hybrid zones with A and C but A and C don't mate in nature?

Outline

Exclusion

- One species might eliminate the other species, either by competition, or by better success in mating
  - Warblers competing for mates
  - Modern humans





***Source*: Prüfer, K., et al. 2014. *Nature* 505: 43–49.**

Outline

Sunflowers

- A cool species of sunflower
  - Resembles natural hybrids from a hybrid zone
  - Is that how it arose?
- Breeding experiments suggest that it's likely
- Why is this surprising?
  - * Rarely seems to happen
  - * If the hybrid has high fitness, why would reproductive isolation evolve?
- How did it happen?
  - * Probably because of an unusual adaptation: the hybrids live in drier climates than either of the "parent" species

Conclusion

- The diversity we see in the world arises from speciation events; mostly by single species splitting into two
- Species splits typically involve isolation and divergence
  - Isolation can happen allopatrically or sympatrically
  - New species can also sometimes arise from hybridization between related species
- Defining species can be complicated
  - Particularly if we want definitions that include both asexual and sexual species