

# Speciation

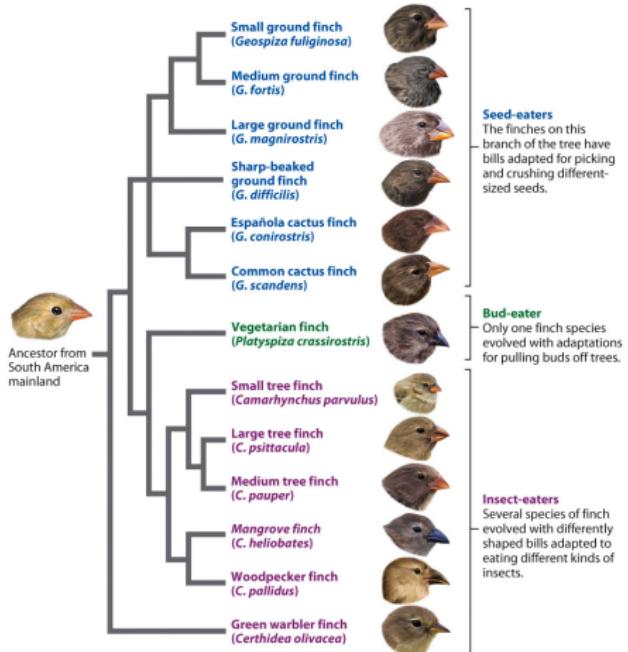
How are species defined?

Species divergence in allopatry

Species divergence in sympatry

Reuniting

# Speciation



► What patterns and processes allowed a single ancestor to diversify into >10 million species?

Figure 21.9 (Part 1)  
Biology: How Life Works  
© Macmillan Learning

# Speciation

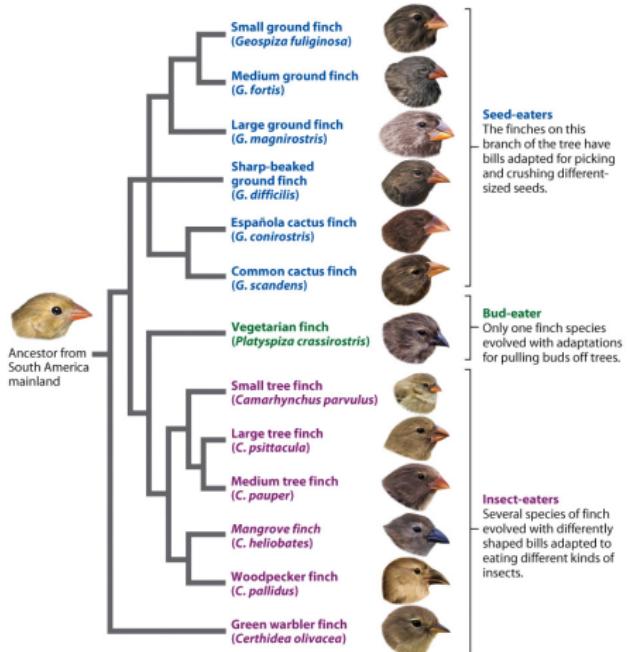


Figure 21.9 (Part 1)  
Biology: How Life Works  
© Macmillan Learning

- ▶ What patterns and processes allowed a single ancestor to diversify into >10 million species?

# Outline

## How are species defined?

Biological species concept

Morphological species concept

Ecological species concept

Phylogenetic species concept

## Species divergence in allopatry

Dispersal

Vicariance

## Species divergence in sympatry

Disruptive selection

Genetic incompatibility

## Reuniting

# How are species defined?

- ▶ Conceptually, we define species as “evolutionary units”:

# How are species defined?

- ▶ Conceptually, we define species as “evolutionary units”:
  - ▶ Individuals within a species are evolving together

# How are species defined?

- ▶ Conceptually, we define species as “evolutionary units”:
  - ▶ Individuals within a species are evolving together
  - ▶ Individuals of different species evolve independently

# 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

# 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
  - ▶ \*

# 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

# 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

# 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

# Outline

How are species defined?

Biological species concept

Morphological species concept

Ecological species concept

Phylogenetic species concept

Species divergence in allopatry

Dispersal

Vicariance

Species divergence in sympatry

Disruptive selection

Genetic incompatibility

Reuniting

# Biological species concept

- Biological species are defined by reproductive isolation

## Biological species concept

- ▶ Biological species are defined by reproductive isolation
- ▶ Different biological species either:

## Biological species concept

- ▶ Biological species are defined by reproductive isolation
- ▶ Different biological species either:
  - ▶ **Don't breed in nature**

## 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

## 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

## 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

# 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:

# Mechanisms of isolation

- ▶ Mechanisms of isolation are often divided into two classes:
  - ▶ **Prezygotic** isolation refers to any mechanism that prevents successful mating

# 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

# 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

# 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-?

## Mechanism examples

- ▶ Pre- or post-?
  - ▶ Different malaria parasites breed inside different hosts

## 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

# 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

# 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

## 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

## 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- vs. post-zygotic mechanisms

- ▶ Which should be adaptively favored?
  - ▶ \*

## Pre- vs. post-zygotic mechanisms

- ▶ Which should be adaptively favored?
  - ▶ \* Pre-zygotic mechanisms mean less wasted effort

## Pre- vs. post-zygotic mechanisms

- ▶ Which should be adaptively favored?
  - ▶ \* Pre-zygotic mechanisms mean less wasted effort
  - ▶ \*

# 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

# 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
  - ▶ \*

## 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

## 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
    - ▶ \*

# 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

# 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



## Disadvantages of the biological species concept

- ▶ \* Doesn't apply to asexual species

## Disadvantages of the biological species concept

- ▶ \* Doesn't apply to asexual species
- ▶ \*

## Disadvantages of the biological species concept

- ▶ \* Doesn't apply to asexual species
- ▶ \* Not practical for extinct species

# Disadvantages of the biological species concept

- ▶ \* Doesn't apply to asexual species
- ▶ \* Not practical for extinct species
- ▶ \*

## Disadvantages of the biological species concept

- ▶ \* Doesn't apply to asexual species
- ▶ \* Not practical for extinct species
- ▶ \* May be hard to evaluate

## Disadvantages of the biological species concept

- ▶ \* Doesn't apply to asexual species
- ▶ \* Not practical for extinct species
- ▶ \* May be hard to evaluate
  - ▶ \*

## 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?

## 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*

## 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

## How are species defined?

Biological species concept

**Morphological species concept**

Ecological species concept

Phylogenetic species concept

## Species divergence in allopatry

Dispersal

Vicariance

## Species divergence in sympatry

Disruptive selection

Genetic incompatibility

## Reuniting

## Morphological species concept

- Morphological species are defined to be different if they **look** different

## 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)

## 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

# 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?

## 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?
  - ▶ \*

## 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

# 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
  - ▶ \*

# 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

# 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
  - ▶ \*

# 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
  - ▶ \* Males and females, different life stages, or specific phenotypes might look very different, but be part of the same population (ADDED)

# 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
  - ▶ \* Males and females, different life stages, or specific phenotypes might look very different, but be part of the same population (ADDED)
  - ▶ \*

## 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
  - ▶ \* Males and females, different life stages, or specific phenotypes might look very different, but be part of the same population (ADDED)
  - ▶ \* Not clear how definition relates to our conceptual definition of evolutionary units

## 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
  - ▶ \* Males and females, different life stages, or specific phenotypes might look very different, but be part of the same population (ADDED)
  - ▶ \* Not clear how definition relates to our conceptual definition of evolutionary units

## Meadowlarks (preview)



# Outline

## How are species defined?

Biological species concept

Morphological species concept

**Ecological species concept**

Phylogenetic species concept

## Species divergence in allopatry

Dispersal

Vicariance

## Species divergence in sympatry

Disruptive selection

Genetic incompatibility

## Reuniting

# Ecological species concept

- ▶ An ecological species is a set of related organisms occupying the same ecological **niche**

# Ecological species concept

- ▶ An ecological species is a set of related organisms occupying the same ecological **niche**
  - ▶ Exploit similar resources

# Ecological species concept

- ▶ An ecological species is a set of related organisms occupying the same ecological **niche**
  - ▶ Exploit similar resources
  - ▶ Tolerate similar environments

# 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

# 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

## 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
  - ▶ \*

# 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
  - ▶ \* **Bacteria, archaea**

# 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
  - ▶ \* **Bacteria, archaea**

# Outline

## How are species defined?

Biological species concept

Morphological species concept

Ecological species concept

**Phylogenetic species concept**

## Species divergence in allopatry

Dispersal

Vicariance

## Species divergence in sympatry

Disruptive selection

Genetic incompatibility

## Reuniting

# Phylogenetic species concept

- A phylogenetic species is a monophyletic group of *populations*

# Phylogenetic species concept

- ▶ A phylogenetic species is a monophyletic group of *populations*
  - ▶ Must not be divisible into smaller groups

# Phylogenetic species concept

- ▶ A phylogenetic species is a monophyletic group of *populations*
  - ▶ Must not be divisible into smaller groups
- ▶ A **monophyletic group** is a group *defined by* a single common ancestor

# Phylogenetic species concept

- ▶ A phylogenetic species is a monophyletic group of *populations*
  - ▶ Must not be divisible into smaller groups
- ▶ A **monophyletic group** is a group *defined by* a single common ancestor
  - ▶ And consisting of all descendants of the ancestor

# Phylogenetic species concept

- ▶ A phylogenetic species is a monophyletic group of *populations*
  - ▶ Must not be divisible into smaller groups
- ▶ A **monophyletic group** is a group *defined by* a single common ancestor
  - ▶ And consisting of all descendants of the ancestor

## Book's version of Phylogenetic species concept

- Mammals could all be one species?

## Book's version of Phylogenetic species concept

- ▶ Mammals could all be one species?
  - ▶ \*

## Book's version of Phylogenetic species concept

- ▶ Mammals could all be one species?
  - ▶ \* Not if we start from populations and take the smallest group

## Book's version of Phylogenetic species concept

- ▶ Mammals could all be one species?
  - ▶ \* Not if we start from populations and take the smallest group
- ▶ A group of *siblings* and *cousins* could make a species?

## Book's version of Phylogenetic species concept

- ▶ Mammals could all be one species?
  - ▶ \* Not if we start from populations and take the smallest group
- ▶ A group of siblings and cousins could make a species?
  - ▶ \*

## Book's version of Phylogenetic species concept

- ▶ Mammals could all be one species?
  - ▶ \* Not if we start from populations and take the smallest group
- ▶ A group of siblings and cousins could make a species?
  - ▶ \*

## Book's version of Phylogenetic species concept

- ▶ Mammals could all be one species?
  - ▶ \* Not if we start from populations and take the smallest group
- ▶ A group of siblings and cousins could make a species?
  - ▶ \*
- ▶ Exercise: what does your family tree look like?

## Book's version of Phylogenetic species concept

- ▶ Mammals could all be one species?
  - ▶ \* Not if we start from populations and take the smallest group
- ▶ A group of siblings and cousins could make a species?
  - ▶ \*
- ▶ Exercise: what does your family tree look like?
  - ▶ \*

## Book's version of Phylogenetic species concept

- ▶ Mammals could all be one species?
  - ▶ \* Not if we start from populations and take the smallest group
- ▶ A group of siblings and cousins could make a species?
  - ▶ \*
- ▶ Exercise: what does your family tree look like?
  - ▶ \* Small groups do *not* make distinct groups in sexual species

## Book's version of Phylogenetic species concept

- ▶ Mammals could all be one species?
  - ▶ \* Not if we start from populations and take the smallest group
- ▶ A group of siblings and cousins could make a species?
  - ▶ \*
- ▶ Exercise: what does your family tree look like?
  - ▶ \* Small groups do *not* make distinct groups in sexual species
  - ▶ \*

## Book's version of Phylogenetic species concept

- ▶ Mammals could all be one species?
  - ▶ \* Not if we start from populations and take the smallest group
- ▶ A group of siblings and cousins could make a species?
  - ▶ \*
- ▶ Exercise: what does your family tree look like?
  - ▶ \* Small groups do *not* make distinct groups in sexual species
  - ▶ \* Plus, we can start by defining populations

## Book's version of Phylogenetic species concept

- ▶ Mammals could all be one species?
  - ▶ \* Not if we start from populations and take the smallest group
- ▶ A group of siblings and cousins could make a species?
  - ▶ \*
- ▶ Exercise: what does your family tree look like?
  - ▶ \* Small groups do *not* make distinct groups in sexual species
  - ▶ \* Plus, we can start by defining populations
- ▶ *Science is not really about trust*

## Book's version of Phylogenetic species concept

- ▶ Mammals could all be one species?
  - ▶ \* Not if we start from populations and take the smallest group
- ▶ A group of siblings and cousins could make a species?
  - ▶ \*
- ▶ Exercise: what does your family tree look like?
  - ▶ \* Small groups do *not* make distinct groups in sexual species
  - ▶ \* Plus, we can start by defining populations
- ▶ *Science is not really about trust*

## Phylogenetic species concept

## ► Advantages

# Phylogenetic species concept

- ▶ Advantages
  - ▶ Well defined (as long as you know what a population is)

# Phylogenetic species concept

- ▶ Advantages
  - ▶ Well defined (as long as you know what a population is)
  - ▶ Broadly applicable

# Phylogenetic species concept

- ▶ Advantages
  - ▶ Well defined (as long as you know what a population is)
  - ▶ Broadly applicable
- ▶ Disadvantages

# Phylogenetic species concept

- ▶ Advantages
  - ▶ Well defined (as long as you know what a population is)
  - ▶ Broadly applicable
- ▶ Disadvantages
  - ▶ Need to estimate phylogenies; can be hard

# Phylogenetic species concept

- ▶ Advantages
  - ▶ Well defined (as long as you know what a population is)
  - ▶ Broadly applicable
- ▶ Disadvantages
  - ▶ Need to estimate phylogenies; can be hard
  - ▶ Requires a lot of information about populations

# Phylogenetic species concept

- ▶ Advantages
  - ▶ Well defined (as long as you know what a population is)
  - ▶ Broadly applicable
- ▶ Disadvantages
  - ▶ Need to estimate phylogenies; can be hard
  - ▶ Requires a lot of information about populations

# Applications

- Believers in the phylogenetic species concept recognize a lot of species

# Applications

- ▶ Believers in the phylogenetic species concept recognize a lot of species
  - ▶ e.g., two species of African elephant

# Applications

- ▶ Believers in the phylogenetic species concept recognize a lot of species
  - ▶ e.g., two species of African elephant
- ▶ ... and can answer practical questions:

# Applications

- ▶ Believers in the phylogenetic species concept recognize a lot of species
  - ▶ e.g., two species of African elephant
- ▶ ... and can answer practical questions:
  - ▶ Should we consider Sri Lankan and Indian elephants as separate species?

# Applications

- ▶ Believers in the phylogenetic species concept recognize a lot of species
  - ▶ e.g., two species of African elephant
- ▶ ... and can answer practical questions:
  - ▶ Should we consider Sri Lankan and Indian elephants as separate species?

# African Bush Elephant



# African Forest Elephant



# Sri Lankan Elephant



# Indian Elephant



## Limitations

- The answer might be different for different sets of genes

# Limitations

- ▶ The answer might be different for different sets of genes
  - ▶ immune genes might group species that we don't want to group

# Limitations

- ▶ The answer might be different for different sets of genes
  - ▶ immune genes might group species that we don't want to group
  - ▶ male- or female-linked genes might give different answers than other genes

# Limitations

- ▶ The answer might be different for different sets of genes
  - ▶ immune genes might group species that we don't want to group
  - ▶ male- or female-linked genes might give different answers than other genes
    - ▶ *If we focus on mitochondria, then maybe you and your cousins are a species*

# Limitations

- ▶ The answer might be different for different sets of genes
  - ▶ immune genes might group species that we don't want to group
  - ▶ male- or female-linked genes might give different answers than other genes
    - ▶ *If we focus on mitochondria, then maybe you and your cousins are a species*
- ▶ Answer might also differ depending on how you define populations

# Limitations

- ▶ The answer might be different for different sets of genes
  - ▶ immune genes might group species that we don't want to group
  - ▶ male- or female-linked genes might give different answers than other genes
    - ▶ *If we focus on mitochondria, then maybe you and your cousins are a species*
- ▶ Answer might also differ depending on how you define populations
  - ▶ \*

# Limitations

- ▶ The answer might be different for different sets of genes
  - ▶ immune genes might group species that we don't want to group
  - ▶ male- or female-linked genes might give different answers than other genes
    - ▶ *If we focus on mitochondria, then maybe you and your cousins are a species*
- ▶ Answer might also differ depending on how you define populations
  - ▶ \* Especially for asexual species

# Limitations

- ▶ The answer might be different for different sets of genes
  - ▶ immune genes might group species that we don't want to group
  - ▶ male- or female-linked genes might give different answers than other genes
    - ▶ *If we focus on mitochondria, then maybe you and your cousins are a species*
- ▶ Answer might also differ depending on how you define populations
  - ▶ \* Especially for asexual species

# Defining species

- Defining species formally can be very tricky

# Defining species

- ▶ Defining species formally can be very tricky
  - ▶ No one way is agreed to be the best

## 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

## 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

# Generating species

- ▶ We believe new species are generated from old species
- ▶ One species can gradually evolve into another

## 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

# 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

# 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**

# 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

# How do species split?

- ▶ Genetic isolation
- ▶ Genetic divergence

# How do species split?

- ▶ Genetic isolation
- ▶ Genetic divergence
- ▶ Which comes first?

# How do species split?

- ▶ Genetic isolation
- ▶ Genetic divergence
- ▶ Which comes first?
  - ▶ \*

# How do species split?

- ▶ Genetic isolation
- ▶ Genetic divergence
- ▶ Which comes first?
  - ▶ \* Usually isolation: with too much gene flow populations can't diverge

# How do species split?

- ▶ Genetic isolation
- ▶ Genetic divergence
- ▶ Which comes first?
  - ▶ \* Usually isolation: with too much gene flow populations can't diverge
  - ▶ \*

# 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 can cause natural selection for more isolation

# 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 can cause natural selection for more isolation

# Outline

How are species defined?

- Biological species concept

- Morphological species concept

- Ecological species concept

- Phylogenetic species concept

Species divergence in allopatry

- Dispersal

- Vicariance

Species divergence in sympatry

- Disruptive selection

- Genetic incompatibility

Reuniting

# Species divergence in allopatry

- **Allopatry** refers to organisms living apart from each other

## 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?

# 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?
  - ▶ \*

## 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

# 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
  - ▶ \*

# 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

# 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
  - ▶ \*

# 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 responses to similar situations

# 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 responses to similar situations
- ▶ How can two populations of the same species be isolated from each other?

# 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 responses to similar situations
- ▶ How can two populations of the same species be isolated from each other?

# Outline

How are species defined?

- Biological species concept

- Morphological species concept

- Ecological species concept

- Phylogenetic species concept

Species divergence in allopatry

- Dispersal

- Vicariance

Species divergence in sympatry

- Disruptive selection

- Genetic incompatibility

Reuniting

# 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).

# 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

# 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

## Peripatric speciation

- ▶ Populations on small islands are likely to be founded later, by small groups, and to have smaller populations

## Peripatric speciation

- ▶ Populations on small islands are likely to be founded later, by small groups, and to have smaller populations
  - ▶ \*

## Peripatric speciation

- ▶ Populations on small islands are likely to be founded later, by small groups, and to have smaller populations
  - ▶ \* more opportunity for genetic drift

## Peripatric speciation

- ▶ Populations on small islands are likely to be founded later, by small groups, and to have smaller populations
  - ▶ \* more opportunity for genetic drift
- ▶ Islands may also have different biological or physical environments

# Peripatric speciation

- ▶ Populations on small islands are likely to be founded later, by small groups, and to have smaller populations
  - ▶ \* more opportunity for genetic drift
- ▶ Islands may also have different biological or physical environments
  - ▶ Uniform weather, fewer food species, fewer competitors

# Peripatric speciation

- ▶ Populations on small islands are likely to be founded later, by small groups, and to have smaller populations
  - ▶ \* more opportunity for genetic drift
- ▶ Islands may also have different biological or physical environments
  - ▶ Uniform weather, fewer food species, fewer competitors
  - ▶ \*

## Peripatric speciation

- ▶ Populations on small islands are likely to be founded later, by small groups, and to have smaller populations
  - ▶ \* more opportunity for genetic drift
- ▶ Islands may also have different biological or physical environments
  - ▶ Uniform weather, fewer food species, fewer competitors
  - ▶ \* more opportunity for natural selection

## Peripatric speciation

- ▶ Populations on small islands are likely to be founded later, by small groups, and to have smaller populations
  - ▶ \* more opportunity for genetic drift
- ▶ Islands may also have different biological or physical environments
  - ▶ Uniform weather, fewer food species, fewer competitors
  - ▶ \* more opportunity for natural selection



The three mainland subspecies of *Tanysiptera* are similar to one another (and colored similarly on the map), but island subspecies are more distinct (and colored differently), suggesting faster genetic divergence on island populations.

The eight subspecies on New Guinea and nearby islands are marked in different colors.



C.H. Greenewalt/VIREO

**Figure 21.8**  
*Biology: How Life Works*  
© Macmillan Learning

# Outline

How are species defined?

- Biological species concept

- Morphological species concept

- Ecological species concept

- Phylogenetic species concept

Species divergence in allopatry

- Dispersal

- Vicariance

Species divergence in sympatry

- Disruptive selection

- Genetic incompatibility

Reuniting

# Vicariance

- ▶ Isolated populations of the same species can develop when a population is split by a geographical or ecological barrier

# 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.

# 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

# 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

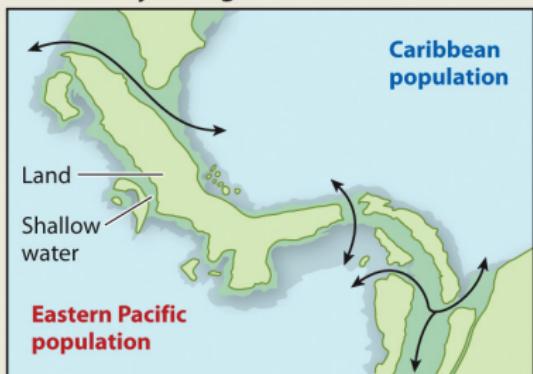
# Vicariance

- ▶ 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

# Example: Shrimp

Interbreeding between eastern Pacific and Caribbean populations of *Alpheus* was possible through the corridors that existed before the final formation of the Isthmus of Panama.

3.5 million years ago



Interbreeding between eastern Pacific and Caribbean populations is no longer possible because of the geographic barrier.

Today



Figure 21.7 (Part 1)  
Biology: How Life Works  
© Macmillan Learning

# Shrimp

The closing of marine corridors resulted over time in the speciation of *Alpheus* into eastern Pacific and Caribbean species.

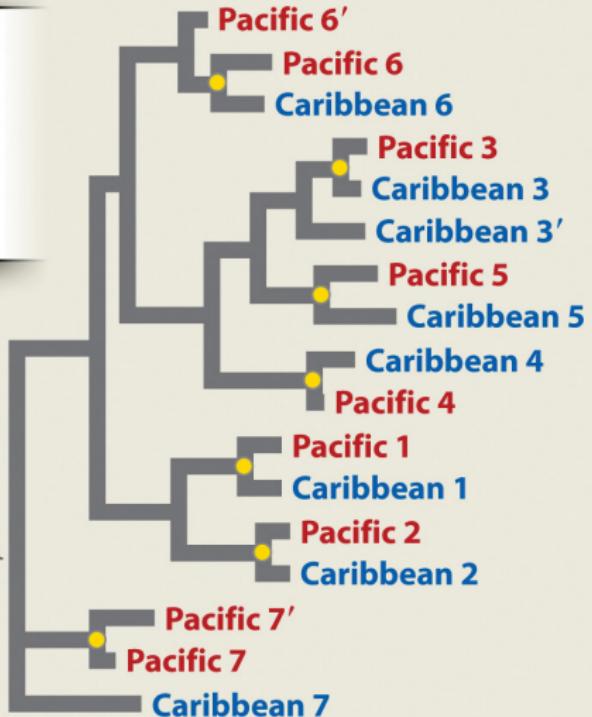
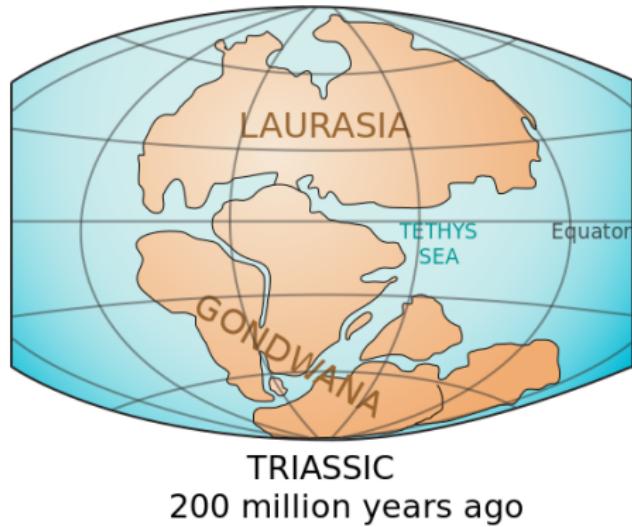


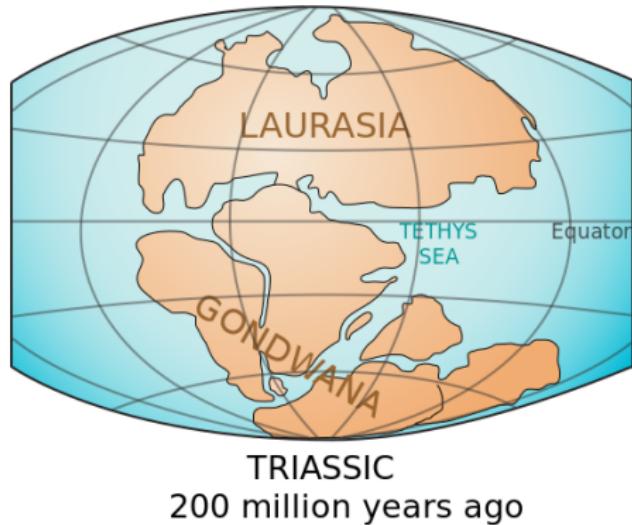
Figure 21.7 (Part 2)  
Biology: How Life Works  
© Macmillan Learning

## Example: ratites

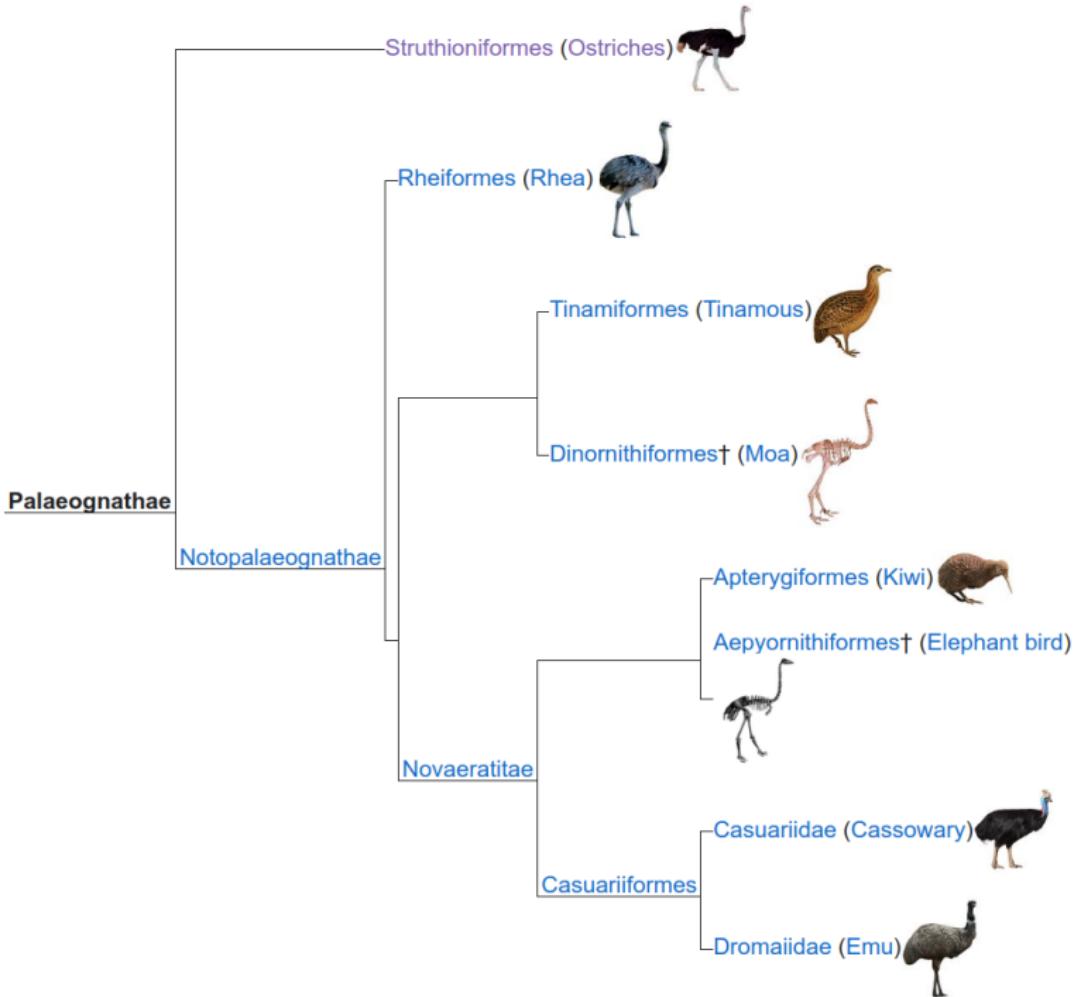


- ▶ The ancestors of today's ostriches, emus, etc. were isolated when the super-continent of Gondwanaland drifted apart starting about 140 million years ago

## Example: ratites



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



## Exercise: What is a biological “island”?

► \*

## Exercise: What is a biological “island”?

► \*

## Exercise: What is a biological “island”?

- ▶ \*
- ▶ Examples:

# Exercise: What is a biological “island”?

- ▶ \*
- ▶ Examples:
  - ▶ \*

## Exercise: What is a biological “island”?

- ▶ \*
- ▶ Examples:
  - ▶ \* An island can be an island

# Exercise: What is a biological “island”?

- ▶ \*
- ▶ Examples:
  - ▶ \* An island can be an island
  - ▶ \*

## Exercise: What is a biological “island”?

- ▶ \*
- ▶ Examples:
  - ▶ \* An island can be an island
  - ▶ \*

## Exercise: What is a biological “island”?

- ▶ \*
- ▶ Examples:
  - ▶ \* An island can be an island
  - ▶ \*
  - ▶ \*

## Exercise: What is a biological “island”?

- ▶ \*
- ▶ Examples:
  - ▶ \* An island can be an island
  - ▶ \*
  - ▶ \*

# Exercise: What is a biological “island”?

- ▶ \*
- ▶ Examples:
  - ▶ \* An island can be an island
  - ▶ \*
  - ▶ \*
  - ▶ \*

## Exercise: What is a biological “island”?

- ▶ \*
- ▶ Examples:
  - ▶ \* An island can be an island
  - ▶ \*
  - ▶ \*
  - ▶ \*

## Exercise: What is a biological “island”?

- ▶ \*
- ▶ Examples:
  - ▶ \* An island can be an island
  - ▶ \*
  - ▶ \*
  - ▶ \*

# Outline

How are species defined?

- Biological species concept

- Morphological species concept

- Ecological species concept

- Phylogenetic species concept

Species divergence in allopatry

- Dispersal

- Vicariance

Species divergence in sympatry

- Disruptive selection

- Genetic incompatibility

Reuniting

## Species divergence in sympatry

- **Sympatry** refers to organisms living in the same geographic area

# 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.

## 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.
  - ▶ \*

## 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

## 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
  - ▶ \*

# 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

# 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
- ▶ What are some ways it can happen

# 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
- ▶ What are some ways it can happen
  - ▶ \*

# 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
- ▶ What are some ways it can happen
  - ▶ \* Disruptive selection

# 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
- ▶ What are some ways it can happen
  - ▶ \* Disruptive selection
  - ▶ \*

# 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
- ▶ What are some ways it can happen
  - ▶ \* Disruptive selection
  - ▶ \* Genetic incompatibility

# 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
- ▶ What are some ways it can happen
  - ▶ \* Disruptive selection
  - ▶ \* Genetic incompatibility

# Outline

How are species defined?

- Biological species concept

- Morphological species concept

- Ecological species concept

- Phylogenetic species concept

Species divergence in allopatry

- Dispersal

- Vicariance

Species divergence in sympatry

- Disruptive selection**

- Genetic incompatibility

Reuniting

## Divergence by partitioning habitats

- Insects that feed on many different plants may be subject to disruptive selection

## Divergence by partitioning habitats

- ▶ Insects that feed on many different plants may be subject to disruptive selection
  - ▶ An individual may do most of its feeding on one particular plant

## Divergence by partitioning habitats

- ▶ Insects that feed on many different plants may be subject to disruptive selection
  - ▶ An individual may do most of its feeding on one particular plant
- ▶ In some cases, gene flow will prevent divergence

## Divergence by partitioning habitats

- ▶ Insects that feed on many different plants may be subject to disruptive selection
  - ▶ An individual may do most of its feeding on one particular plant
- ▶ In some cases, gene flow will prevent divergence
  - ▶ \*

## Divergence by partitioning habitats

- ▶ Insects that feed on many different plants may be subject to disruptive selection
  - ▶ An individual may do most of its feeding on one particular plant
- ▶ In some cases, gene flow will prevent divergence
  - ▶ \* When genes from two populations mix, the populations become more similar (NEW)

## Divergence by partitioning habitats

- ▶ Insects that feed on many different plants may be subject to disruptive selection
  - ▶ An individual may do most of its feeding on one particular plant
- ▶ In some cases, gene flow will prevent divergence
  - ▶ \* When genes from two populations mix, the populations become more similar (NEW)
- ▶ In other cases, individuals may mate preferentially with individuals with the same host plant, and divergence may occur

## Divergence by partitioning habitats

- ▶ Insects that feed on many different plants may be subject to disruptive selection
  - ▶ An individual may do most of its feeding on one particular plant
- ▶ In some cases, gene flow will prevent divergence
  - ▶ \* When genes from two populations mix, the populations become more similar (NEW)
- ▶ In other cases, individuals may mate preferentially with individuals with the same host plant, and divergence may occur
  - ▶ \*

## Divergence by partitioning habitats

- ▶ Insects that feed on many different plants may be subject to disruptive selection
  - ▶ An individual may do most of its feeding on one particular plant
- ▶ In some cases, gene flow will prevent divergence
  - ▶ \* When genes from two populations mix, the populations become more similar (NEW)
- ▶ In other cases, individuals may mate preferentially with individuals with the same host plant, and divergence may occur
  - ▶ \* More opportunity to meet individuals in the same place or same timing

## Divergence by partitioning habitats

- ▶ Insects that feed on many different plants may be subject to disruptive selection
  - ▶ An individual may do most of its feeding on one particular plant
- ▶ In some cases, gene flow will prevent divergence
  - ▶ \* When genes from two populations mix, the populations become more similar (NEW)
- ▶ In other cases, individuals may mate preferentially with individuals with the same host plant, and divergence may occur
  - ▶ \* More opportunity to meet individuals in the same place or same timing
  - ▶ \*

## Divergence by partitioning habitats

- ▶ Insects that feed on many different plants may be subject to disruptive selection
  - ▶ An individual may do most of its feeding on one particular plant
- ▶ In some cases, gene flow will prevent divergence
  - ▶ \* When genes from two populations mix, the populations become more similar (NEW)
- ▶ In other cases, individuals may mate preferentially with individuals with the same host plant, and divergence may occur
  - ▶ \* More opportunity to meet individuals in the same place or same timing
  - ▶ \* Natural selection to mate with similar individuals to increase fitness

## Divergence by partitioning habitats

- ▶ Insects that feed on many different plants may be subject to disruptive selection
  - ▶ An individual may do most of its feeding on one particular plant
- ▶ In some cases, gene flow will prevent divergence
  - ▶ \* When genes from two populations mix, the populations become more similar (NEW)
- ▶ In other cases, individuals may mate preferentially with individuals with the same host plant, and divergence may occur
  - ▶ \* More opportunity to meet individuals in the same place or same timing
  - ▶ \* Natural selection to mate with similar individuals to increase fitness

# Hawthorn flies

- ▶ Apples are ready before hawthorns, so there should be disruptive selection



wikipedia/Apple\_maggot

# Hawthorn flies

- ▶ Apples are ready before hawthorns, so there should be disruptive selection
- ▶ There is already evidence that reproductive isolation is evolving:



wikipedia/Apple\_maggot

# Hawthorn flies

- ▶ Apples are ready before hawthorns, so there should be disruptive selection
- ▶ There is already evidence that reproductive isolation is evolving:
  - ▶ Flies raised on each type of fruit prefer to seek mates on the same type of fruit



wikipedia/Apple\_maggot

# Hawthorn flies

- ▶ Apples are ready before hawthorns, so there should be disruptive selection
- ▶ There is already evidence that reproductive isolation is evolving:
  - ▶ Flies raised on each type of fruit prefer to seek mates on the same type of fruit
- ▶ What might happen next?



wikipedia/Apple\_maggot

# Hawthorn flies

- ▶ Apples are ready before hawthorns, so there should be disruptive selection
- ▶ There is already evidence that reproductive isolation is evolving:
  - ▶ Flies raised on each type of fruit prefer to seek mates on the same type of fruit
- ▶ What might happen next?

▶ \*



wikipedia/Apple\_maggot

# Hawthorn flies

- ▶ Apples are ready before hawthorns, so there should be disruptive selection
- ▶ There is already evidence that reproductive isolation is evolving:
  - ▶ Flies raised on each type of fruit prefer to seek mates on the same type of fruit
- ▶ What might happen next?
  - ▶ \* Less gene flow; more fruit-specific adaptation; more divergence



wikipedia/Apple\_maggot

# Hawthorn flies

- ▶ Apples are ready before hawthorns, so there should be disruptive selection
- ▶ There is already evidence that reproductive isolation is evolving:
  - ▶ Flies raised on each type of fruit prefer to seek mates on the same type of fruit
- ▶ What might happen next?
  - ▶ \* Less gene flow; more fruit-specific adaptation; more divergence



wikipedia/Apple\_maggot

# Outline

How are species defined?

- Biological species concept

- Morphological species concept

- Ecological species concept

- Phylogenetic species concept

Species divergence in allopatry

- Dispersal

- Vicariance

Species divergence in sympatry

- Disruptive selection

- Genetic incompatibility

Reuniting

# Genetic incompatibility

- Divergence can also occur when mutation causes genetic incompatibility

## 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

- ▶ 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

## 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
  - ▶ \*

# 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

# 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
  - ▶ \*

# 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
  - ▶ \* But reproductive isolation can sometimes work together with natural selection to make divergence possible

# 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
  - ▶ \* But reproductive isolation can sometimes work together with natural selection to make divergence possible

# Hybridization

- Some species seem to have arisen as hybrids between two other species

# Hybridization

- ▶ Some species seem to have arisen as hybrids between two other species
- ▶ Why is this surprising?

# Hybridization

- ▶ Some species seem to have arisen as hybrids between two other species
- ▶ Why is this surprising?
  - ▶ \*

# Hybridization

- ▶ Some species seem to have arisen as hybrids between two other species
- ▶ Why is this surprising?
  - ▶ \* If they can breed successfully, how are they separate species?

# Hybridization

- ▶ Some species seem to have arisen as hybrids between two other species
- ▶ Why is this surprising?
  - ▶ \* If they can breed successfully, how are they separate species?
  - ▶ \*

# Hybridization

- ▶ Some species seem to have arisen as hybrids between two other species
- ▶ Why is this surprising?
  - ▶ \* If they can breed successfully, how are they separate species?
  - ▶ \* And how did the hybrids stay separate?

# Hybridization

- ▶ Some species seem to have arisen as hybrids between two other species
- ▶ Why is this surprising?
  - ▶ \* If they can breed successfully, how are they separate species?
  - ▶ \* And how did the hybrids stay separate?
- ▶ What do we conclude?

# Hybridization

- ▶ Some species seem to have arisen as hybrids between two other species
- ▶ Why is this surprising?
  - ▶ \* If they can breed successfully, how are they separate species?
  - ▶ \* And how did the hybrids stay separate?
- ▶ What do we conclude?
  - ▶ \*

# Hybridization

- ▶ Some species seem to have arisen as hybrids between two other species
- ▶ Why is this surprising?
  - ▶ \* If they can breed successfully, how are they separate species?
  - ▶ \* And how did the hybrids stay separate?
- ▶ What do we conclude?
  - ▶ \* The successful hybrid is probably a rare event that can't easily happen often

# Hybridization

- ▶ Some species seem to have arisen as hybrids between two other species
- ▶ Why is this surprising?
  - ▶ \* If they can breed successfully, how are they separate species?
  - ▶ \* And how did the hybrids stay separate?
- ▶ What do we conclude?
  - ▶ \* The successful hybrid is probably a rare event that can't easily happen often

## Example: sunflowers

- ▶ For example, sunflowers were found that resembled observed, not-very-successful natural hybrids of two other species

## Example: sunflowers

- ▶ For example, sunflowers were found that resembled observed, not-very-successful natural hybrids of two other species
- ▶ Scientists hypothesized the third species was a hybrid

## Example: sunflowers

- ▶ For example, sunflowers were found that resembled observed, not-very-successful natural hybrids of two other species
- ▶ Scientists hypothesized the third species was a hybrid
- ▶ Breeding experiments and genetic observations supported this hypothesis

## Example: sunflowers

- ▶ For example, sunflowers were found that resembled observed, not-very-successful natural hybrids of two other species
- ▶ Scientists hypothesized the third species was a hybrid
- ▶ Breeding experiments and genetic observations supported this hypothesis
- ▶ Part of the reason for survival is probably that the new species has a surprising adaptation

## Example: sunflowers

- ▶ For example, sunflowers were found that resembled observed, not-very-successful natural hybrids of two other species
- ▶ Scientists hypothesized the third species was a hybrid
- ▶ Breeding experiments and genetic observations supported this hypothesis
- ▶ Part of the reason for survival is probably that the new species has a surprising adaptation
  - ▶ They do best in drier patches than either of the parents

## Example: sunflowers

- ▶ For example, sunflowers were found that resembled observed, not-very-successful natural hybrids of two other species
- ▶ Scientists hypothesized the third species was a hybrid
- ▶ Breeding experiments and genetic observations supported this hypothesis
- ▶ Part of the reason for survival is probably that the new species has a surprising adaptation
  - ▶ They do best in drier patches than either of the parents
  - ▶ \*

## Example: sunflowers

- ▶ For example, sunflowers were found that resembled observed, not-very-successful natural hybrids of two other species
- ▶ Scientists hypothesized the third species was a hybrid
- ▶ Breeding experiments and genetic observations supported this hypothesis
- ▶ Part of the reason for survival is probably that the new species has a surprising adaptation
  - ▶ They do best in drier patches than either of the parents
  - ▶ \* Less likely to be driven extinct by competition

## Example: sunflowers

- ▶ For example, sunflowers were found that resembled observed, not-very-successful natural hybrids of two other species
- ▶ Scientists hypothesized the third species was a hybrid
- ▶ Breeding experiments and genetic observations supported this hypothesis
- ▶ Part of the reason for survival is probably that the new species has a surprising adaptation
  - ▶ They do best in drier patches than either of the parents
  - ▶ \* Less likely to be driven extinct by competition

# Hybrid sunflowers

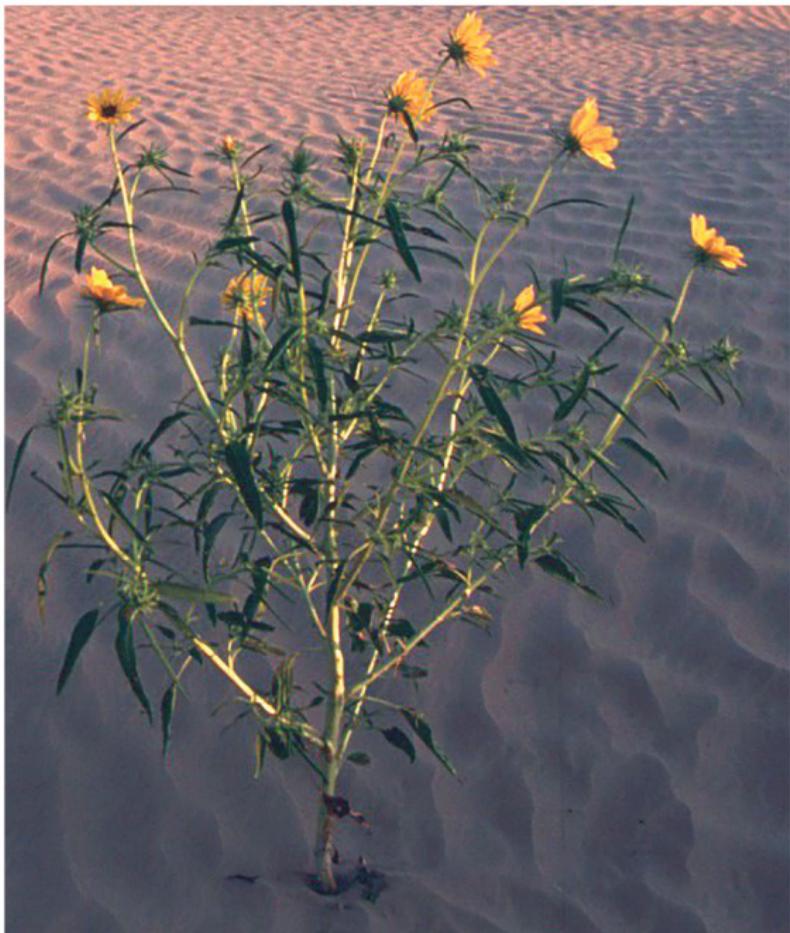


photo by Jason Rick, courtesy of Loren Rieseberg

# Polyplody

- Reproductive mistakes can occur that produce individuals with extra copies of each chromosome

# Polyplody

- ▶ Reproductive mistakes can occur that produce individuals with extra copies of each chromosome
- ▶ Usually, these **polyploid** individuals don't survive, or can't mate

# Polyplody

- ▶ Reproductive mistakes can occur that produce individuals with extra copies of each chromosome
- ▶ Usually, these **polyploid** individuals don't survive, or can't mate
  - ▶ \*

# Polyplody

- ▶ Reproductive mistakes can occur that produce individuals with extra copies of each chromosome
- ▶ Usually, these **polyploid** individuals don't survive, or can't mate
  - ▶ \* Would need a lot of things to balance perfectly

# Polyplody

- ▶ Reproductive mistakes can occur that produce individuals with extra copies of each chromosome
- ▶ Usually, these **polyploid** individuals don't survive, or can't mate
  - ▶ \* Would need a lot of things to balance perfectly
  - ▶ \*

# Polyplody

- ▶ Reproductive mistakes can occur that produce individuals with extra copies of each chromosome
- ▶ Usually, these **polyploid** individuals don't survive, or can't mate
  - ▶ \* Would need a lot of things to balance perfectly
  - ▶ \* Would probably need to mate with themselves, or other polyploids

# Polyplody

- ▶ Reproductive mistakes can occur that produce individuals with extra copies of each chromosome
- ▶ Usually, these **polyploid** individuals don't survive, or can't mate
  - ▶ \* Would need a lot of things to balance perfectly
  - ▶ \* Would probably need to mate with themselves, or other polyploids
- ▶ Sometimes, however, they do survive and persist!

# Polyplody

- ▶ Reproductive mistakes can occur that produce individuals with extra copies of each chromosome
- ▶ Usually, these **polyploid** individuals don't survive, or can't mate
  - ▶ \* Would need a lot of things to balance perfectly
  - ▶ \* Would probably need to mate with themselves, or other polyploids
- ▶ Sometimes, however, they do survive and persist!

# Polyplody and speciation

- Polyploidy produces instant reproductive isolation

# Polyplody and speciation

- ▶ Polyploidy produces instant reproductive isolation
- ▶ But new polyploid individuals still face another obstacle

# Polyplody and speciation

- ▶ Polyploidy produces instant reproductive isolation
- ▶ But new polyploid individuals still face another obstacle
  - ▶ \*

# Polyplody and speciation

- ▶ Polyplody produces instant reproductive isolation
- ▶ But new polyploid individuals still face another obstacle
  - ▶ \* Need to compete with the ancestral species

# Polyplody and speciation

- ▶ Polyplody produces instant reproductive isolation
- ▶ But new polyploid individuals still face another obstacle
  - ▶ \* Need to compete with the ancestral species
- ▶ Polyplody can also provide material for new genetic innovation

# Polyplody and speciation

- ▶ Polyplody produces instant reproductive isolation
- ▶ But new polyploid individuals still face another obstacle
  - ▶ \* Need to compete with the ancestral species
- ▶ Polyplody can also provide material for new genetic innovation
  - ▶ \*

# Polyplody and speciation

- ▶ Polyploidy produces instant reproductive isolation
- ▶ But new polyploid individuals still face another obstacle
  - ▶ \* Need to compete with the ancestral species
- ▶ Polyploidy can also provide material for new genetic innovation
  - ▶ \* Two copies of each gene, so it may be possible to keep one and mutate one

# Polyplody and speciation

- ▶ Polyplody produces instant reproductive isolation
- ▶ But new polyploid individuals still face another obstacle
  - ▶ \* Need to compete with the ancestral species
- ▶ Polyplody can also provide material for new genetic innovation
  - ▶ \* Two copies of each gene, so it may be possible to keep one and mutate one
- ▶ Polyplody events can involve individuals of the same, or different, species

# Polyplody and speciation

- ▶ Polyploidy produces instant reproductive isolation
- ▶ But new polyploid individuals still face another obstacle
  - ▶ \* Need to compete with the ancestral species
- ▶ Polyploidy can also provide material for new genetic innovation
  - ▶ \* Two copies of each gene, so it may be possible to keep one and mutate one
- ▶ Polyploidy events can involve individuals of the same, or different, species

## Example: clawed frogs

- The Evans lab here at Mac studies an amazingly polyploid system



## Example: clawed frogs

- ▶ The Evans lab here at Mac studies an amazingly polyploid system
- ▶ Current species have up to six times as many chromosomes as their ancestors after multiple polyploidy event



## Example: clawed frogs

- ▶ The Evans lab here at Mac studies an amazingly polyploid system
- ▶ Current species have up to six times as many chromosomes as their ancestors after multiple polyploidy event



# Outline

How are species defined?

- Biological species concept

- Morphological species concept

- Ecological species concept

- Phylogenetic species concept

Species divergence in allopatry

- Dispersal

- Vicariance

Species divergence in sympatry

- Disruptive selection

- Genetic incompatibility

## Reuniting

# Reuniting

- What happens when isolated populations come back into contact?

# Reuniting

- ▶ What happens when isolated populations come back into contact?
- ▶ Usually this happens when a geographic barrier disappears

# 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

# 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

# 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
- ▶ Observing what happened (or is happening) in this case can give insight into what constitutes speciation

# 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
- ▶ Observing what happened (or is happening) in this case can give insight into what constitutes speciation

# Fusion

- When two isolated populations come into contact, they may **fuse** – go back together

# Fusion

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

# 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

# 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

# Reinforcement

- ▶ In some cases, hybrid offspring may have low fitness

# Reinforcement

- ▶ In some cases, hybrid offspring may have low fitness
  - ▶ \*

# Reinforcement

- ▶ In some cases, hybrid offspring may have low fitness
  - ▶ \* Incompatible alleles

# Reinforcement

- ▶ In some cases, hybrid offspring may have low fitness
  - ▶ \* Incompatible alleles
  - ▶ \*

# Reinforcement

- ▶ In some cases, hybrid offspring may have low fitness
  - ▶ \* Incompatible alleles
  - ▶ \* Disruptive selection

# 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

# 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

# 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 (repeat)



# Meadowlarks

- Eastern and Western meadowlarks have hybrid zones in the Great Plains

# Meadowlarks

- ▶ Eastern and Western meadowlarks have hybrid zones in the Great Plains
- ▶ Hybrids don't reproduce well

# 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

# 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:

# 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:
  - ▶ \*

# 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

# 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

# Hybrid zones

- When hybrid offspring are functional, and well-adapted to the overlap zone, there may be a zone where hybrids occur

## 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

## 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?

## 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?

## Exclusion

- One species might eliminate the other species, either by competition, or by better success in mating

# Exclusion

- ▶ One species might eliminate the other species, either by competition, or by better success in mating
  - ▶ Warblers

# Exclusion

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

# Exclusion

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

# Mating success

- In some reuniting areas, we see zones where there is convincing evidence for better mating success of one species than the other



# Mating success

- ▶ In some reuniting areas, we see zones where there is convincing evidence for better mating success of one species than the other
  - ▶ Most genes are dominated by one species, but mitochondrial genes are mixed between two species



# Mating success

- ▶ In some reuniting areas, we see zones where there is convincing evidence for better mating success of one species than the other
  - ▶ Most genes are dominated by one species, but mitochondrial genes are mixed between two species

▶ \*



# Mating success

- ▶ In some reuniting areas, we see zones where there is convincing evidence for better mating success of one species than the other
  - ▶ Most genes are dominated by one species, but mitochondrial genes are mixed between two species
    - ▶ \* Males, but not females of the dominant species have been doing better



# Mating success

- ▶ In some reuniting areas, we see zones where there is convincing evidence for better mating success of one species than the other
  - ▶ Most genes are dominated by one species, but mitochondrial genes are mixed between two species
    - ▶ \* Males, but not females of the dominant species have been doing better
    - ▶ \*



# Mating success

- ▶ In some reuniting areas, we see zones where there is convincing evidence for better mating success of one species than the other
  - ▶ Most genes are dominated by one species, but mitochondrial genes are mixed between two species
    - ▶ \* Males, but not females of the dominant species have been doing better
    - ▶ \* Mitochondrial genes are inherited only from the mother



# Mating success

- ▶ In some reuniting areas, we see zones where there is convincing evidence for better mating success of one species than the other
  - ▶ Most genes are dominated by one species, but mitochondrial genes are mixed between two species
    - ▶ \* Males, but not females of the dominant species have been doing better
    - ▶ \* Mitochondrial genes are inherited only from the mother



# Modern humans

- Modern humans spread through the world and out-competed earlier human populations

# Modern humans

- ▶ Modern humans spread through the world and out-competed earlier human populations
- ▶ There is evidence that there was some inter-breeding, though

# Modern humans

- ▶ Modern humans spread through the world and out-competed earlier human populations
- ▶ There is evidence that there was some inter-breeding, though
- ▶ Modern *non-African* populations show evidence of pre-modern genes

## Modern humans

- ▶ Modern humans spread through the world and out-competed earlier human populations
- ▶ There is evidence that there was some inter-breeding, though
- ▶ Modern *non-African* populations show evidence of pre-modern genes

# Modern humans



wikipedia/humans

# Conclusion

- The diversity we see in the world arises from speciation events; mostly by single species splitting into two

# 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

# 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

## 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

# 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

# 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

# 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