## Speciation

How are species defined?

Species divergence in allopatry

Species divergence in sympatry

Reuniting

#### 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

#### Reuniting

Fusion

Reinforcement

Hybrid zones

Exclusion

New species

► Conceptually, we define species as "evolutionary units":

- ► Conceptually, we define species as "evolutionary units":
  - ► Individuals within a species are evolving together

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

- ► 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

- 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
  - \*

- ► 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

- ► 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

- ► 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** 

@ 2014 Pearson Education, Inc.

#### 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

#### Reuniting

Fusion

Reinforcemen<sup>-</sup>

Hybrid zones

Exclusion

New species

► Biological species are defined by reproductive isolation

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

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

- ▶ Biological species are defined by reproductive isolation
- Different biological species either:
  - Don't breed in nature
  - ► Breed but fail to produce offspring

- ▶ 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 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 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 are often divided into two classes:

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

- 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 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 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

► Pre- or post-?

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

- 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

- 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

- 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

- 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- 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

► Which should be adaptively favored?

Which should be adaptively favored?

**▶** <sup>3</sup>

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

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

- Which should be adaptively favored?
  - \* Pre-zygotic mechanisms mean less wasted effort
  - ► \* 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
  - ► \* Example: it takes a lot of resources for a horse to birth and raise a mule, but there is no long-term fitness benefit



▶ \* Doesn't apply to asexual species

▶ \* Doesn't apply to asexual species

**▶** \*

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

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

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

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

- \* 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?

- \* 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?

#### 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

#### Reuniting

Fusior

Reinforcemen<sup>-</sup>

Hybrid zones

Exclusion

New species

 Morphological species are defined to be different if they look different

- 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 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 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 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 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 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
  - , a

- 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 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 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

- 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





#### 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

#### Reuniting

Fusion

Reinforcement

Hybrid zones

Exclusion

New species

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

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

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

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

- ► 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

- ► 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

#### 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

#### Reuniting

Fusion

Reinforcement

Hybrid zones

Exclusion

New species

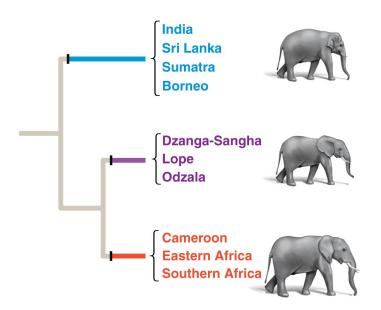
► A phylogenetic species is a monophyletic group of populations

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

- ▶ 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

- ▶ 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

- ► 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



Advantages

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

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

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

- Advantages
  - Well defined (as long as you know what a population is)
  - ▶ Broadly applicable
- Disadvantages
  - ► Hard to estimate phylogenies

- 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

- 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

- 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 formally can be very tricky

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

- 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 be a species, though

- 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 be a species, though

► We believe new species are generated from old species

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

- ▶ 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

- ▶ 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

- 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

► Genetic isolation

- Genetic isolation
- ► Genetic divergence

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

- Genetic isolation
- ► Genetic divergence
- Which comes first?
  - **,**

- Genetic isolation
- Genetic divergence
- Which comes first?
  - ► \* Isolation is necessary: with too much gene flow populations can't diverge

- Genetic isolation
- Genetic divergence
- Which comes first?
  - ► \* Isolation is necessary: with too much gene flow populations can't diverge
    - \*

- Genetic isolation
- Genetic divergence
- Which comes first?
  - \* Isolation is necessary: with too much gene flow populations can't diverge
  - \* There can also be a loop: if species diverge, there can be natural selection for increased isolation

- Genetic isolation
- Genetic divergence
- Which comes first?
  - \* Isolation is necessary: with too much gene flow populations can't diverge
  - \* There can also be a loop: if species diverge, there can be natural selection for increased isolation
    - **\***

- Genetic isolation
- Genetic divergence
- Which comes first?
  - \* Isolation is necessary: with too much gene flow populations can't diverge
  - \* There can also be a loop: if species diverge, there can be natural selection for increased isolation
    - \* Don't want to waste resources on less-fit hybrid offspring

- Genetic isolation
- Genetic divergence
- Which comes first?
  - \* Isolation is necessary: with too much gene flow populations can't diverge
  - \* There can also be a loop: if species diverge, there can be natural selection for increased isolation
    - \* Don't want to waste resources on less-fit hybrid offspring

#### 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

#### Reuniting

Fusion

Reinforcement

Hybrid zones

Exclusion

New species

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

- 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?

- ▶ 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?
  - \*

- 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

- 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
  - \*

- 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

- 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 mutations

## 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?

## 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

### 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

### Reuniting

Fusion

Reinforcement

Hybrid zones

Exclusion

New species

# Dispersal

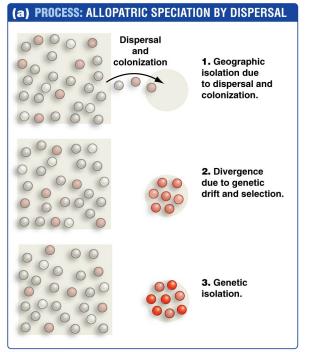
Isolated populations of the same species can develop if some individuals disperse (move) to a new area and colonize it (establish a new population).

## Dispersal

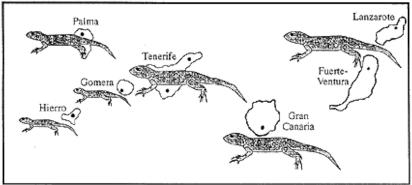
- Isolated populations of the same species can develop if some individuals disperse (move) to a new area and colonize it (establish a new population).
- ► Since colonizing populations are usually small, we expect founder effects and drift to be particularly important

## 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



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



### 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

### Reuniting

Fusion

Reinforcemen<sup>-</sup>

Hybrid zones

Exclusion

New species

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

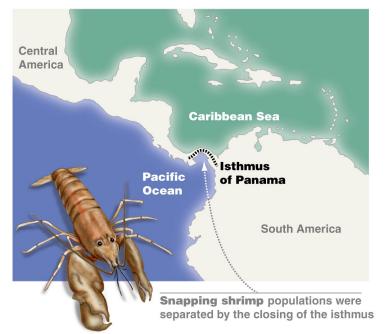
- ▶ Isolated populations of the same species can develop when a population is split by a geographical or ecological barrier
- ► Such splits are called **vicariance** events.

- ▶ 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

- 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

- 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

#### (a) Vicariance event: The closing of the Isthmus of Panama



### 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

# 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

### 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

### Reuniting

Fusion

Reinforcemen

Hybrid zones

Exclusion

New species

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

- 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.

- 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.
  - **▶** <sup>≯</sup>

- 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

- 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
- Are there exceptions to this expectation?

- 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
- Are there exceptions to this expectation?
  - **▶** ≯

- 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
- Are there exceptions to this expectation?
  - ▶ \* Seed crackers?

- 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
- Are there exceptions to this expectation?
  - ► \* Seed crackers?

- 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
- Are there exceptions to this expectation?
  - ▶ \* Seed crackers?
    - ▶ \* We don't really know yet

- 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
- Are there exceptions to this expectation?
  - ▶ \* Seed crackers?
    - ▶ \* We don't really know yet
  - \*

- 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
- Are there exceptions to this expectation?
  - ▶ \* Seed crackers?
    - ▶ \* We don't really know yet
  - \* Hawthorn flies

- 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
- Are there exceptions to this expectation?
  - ▶ \* Seed crackers?
    - ▶ \* We don't really know yet
  - ▶ \* Hawthorn flies
  - \*

- 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
- Are there exceptions to this expectation?
  - ▶ \* Seed crackers?
    - ▶ \* We don't really know yet
  - \* Hawthorn flies
  - ▶ \* Soapberry bugs

- 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
- Are there exceptions to this expectation?
  - ▶ \* Seed crackers?
    - ▶ \* We don't really know yet
  - \* Hawthorn flies
  - ▶ \* Soapberry bugs

# Divergence by partitioning habitats

► Insects that feed on many different plants may be subject to divergent selection

## 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

## 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

## 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

## 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



► Divergence in sympatry is an exciting field

- Divergence in sympatry is an exciting field
  - ► When can disruptive selection overcome gene flow?

- Divergence in sympatry is an exciting field
  - ▶ When can disruptive selection overcome gene flow?
  - ▶ Is this an important component of how diversity evolves?

- Divergence in sympatry is an exciting field
  - ▶ When can disruptive selection overcome gene flow?
  - Is this an important component of how diversity evolves?
- Divergence can also occur when mutation causes genetic incompatibility (see book if you are curious about mechanisms)

- Divergence in sympatry is an exciting field
  - ▶ When can disruptive selection overcome gene flow?
  - Is this an important component of how diversity evolves?
- Divergence can also occur when mutation causes genetic incompatibility (see book if you are curious about mechanisms)
  - ► If two populations are in the same place, but can't produce fertile offspring, they are reproductively isolated

- Divergence in sympatry is an exciting field
  - ▶ When can disruptive selection overcome gene flow?
  - Is this an important component of how diversity evolves?
- Divergence can also occur when mutation causes genetic incompatibility (see book if you are curious about mechanisms)
  - ▶ If two populations are in the same place, but can't produce fertile offspring, they are reproductively isolated
  - ▶ In what way are they not isolated?

- Divergence in sympatry is an exciting field
  - ▶ When can disruptive selection overcome gene flow?
  - Is this an important component of how diversity evolves?
- Divergence can also occur when mutation causes genetic incompatibility (see book if you are curious about mechanisms)
  - ▶ If two populations are in the same place, but can't produce fertile offspring, they are reproductively isolated
  - ▶ In what way are they not isolated?

**>** 3

- Divergence in sympatry is an exciting field
  - When can disruptive selection overcome gene flow?
  - Is this an important component of how diversity evolves?
- Divergence can also occur when mutation causes genetic incompatibility (see book if you are curious about mechanisms)
  - ▶ If two populations are in the same place, but can't produce fertile offspring, they are reproductively isolated
  - In what way are they not isolated?
    - ▶ \* They can still compete, and one may drive the other extinct

- Divergence in sympatry is an exciting field
  - ▶ When can disruptive selection overcome gene flow?
  - Is this an important component of how diversity evolves?
- Divergence can also occur when mutation causes genetic incompatibility (see book if you are curious about mechanisms)
  - ▶ If two populations are in the same place, but can't produce fertile offspring, they are reproductively isolated
  - In what way are they not isolated?
    - ▶ \* They can still compete, and one may drive the other extinct
    - \*

- Divergence in sympatry is an exciting field
  - ▶ When can disruptive selection overcome gene flow?
  - Is this an important component of how diversity evolves?
- Divergence can also occur when mutation causes genetic incompatibility (see book if you are curious about mechanisms)
  - ▶ If two populations are in the same place, but can't produce fertile offspring, they are reproductively isolated
  - In what way are they not isolated?
    - ▶ \* They can still compete, and one may drive the other extinct
    - ▶ \* Reproductive isolation can *combine with* disruptive selection

- Divergence in sympatry is an exciting field
  - ▶ When can disruptive selection overcome gene flow?
  - Is this an important component of how diversity evolves?
- Divergence can also occur when mutation causes genetic incompatibility (see book if you are curious about mechanisms)
  - ▶ If two populations are in the same place, but can't produce fertile offspring, they are reproductively isolated
  - In what way are they not isolated?
    - ▶ \* They can still compete, and one may drive the other extinct
    - ▶ \* Reproductive isolation can *combine with* disruptive selection

## Outline

### How are species defined?

Biological species concept

Morphological species concept

Esplanical species concept

Phylogenetic species concept

## Species divergence in allopatry

Dispersal

Vicariance

## Species divergence in sympatry

### Reuniting

**Fusion** 

Reinforcement

Hybrid zones

Exclusion

New species

► What happens when isolated populations come back into contact?

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

- 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

- 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

- 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

### 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

### Reuniting

#### **Fusion**

Reinforcement

Hybrid zones

Exclusion

New species

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

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

- 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

- 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

#### 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

### Reuniting

Fusion

#### Reinforcement

Hybrid zones

Exclusion

New species

► In some cases, hybrid offspring may have low fitness

▶ In some cases, hybrid offspring may have low fitness

**▶** \*

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

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

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

- ▶ 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

- ▶ 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

- ▶ 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





## 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

### Reuniting

Fusior

Reinforcemen<sup>-</sup>

Hybrid zones

Exclusion

New species

# 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
- ▶ In this case, should we 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
- ▶ In this case, should we consider the species to be different?

# 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

## Reuniting

Fusion

Reinforcement

Hybrid zones

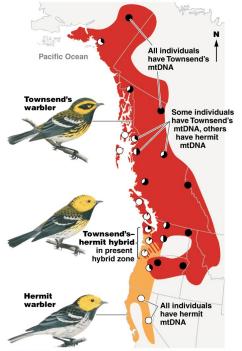
Exclusion

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

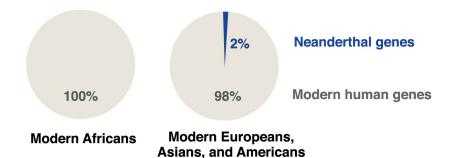
- ► One species might eliminate the other species, either by competition, or by better success in mating
  - Warblers competing for mates

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

- ► 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

### 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

## Reuniting

Fusion

Reinforcement

Hybrid zones

Exclusion

► There is evidence that in some cases hybridization between related species may lead to creation of new species

- ► There is evidence that in some cases hybridization between related species may lead to creation of new species
  - Some combination of genes from the two species may lead to a new adaptation

- ► There is evidence that in some cases hybridization between related species may lead to creation of new species
  - Some combination of genes from the two species may lead to a new adaptation
  - ► Sunflower example, p. 516–518

- ► There is evidence that in some cases hybridization between related species may lead to creation of new species
  - Some combination of genes from the two species may lead to a new adaptation
  - ▶ Sunflower example, p. 516–518



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

- ► 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

- ► 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

- ► 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

- ► 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

- ► 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

- ► 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