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# Speciation

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Introduction to Evolution and Scientific Inquiry  
Dr. Stephanie J. Spielman; [spielman@rowan.edu](mailto:spielman@rowan.edu)

# To study speciation, we must define "species"

- **Speciation** is the process by which new species form, from an *ancestral species*
  - There are *many* definitions ("concepts") that have been proposed for species
- 
1. Morphological Species Concept
  2. Phylogenetic Species Concept
  3. Ecological Species Concept
  4. **Biological Species Concept (the main one we use)**

# Morphological Species Concept

- Defines species based on different morphologies (appearance)
- Commonly used in museum collections which have a single species specimen, and similarly fossil data
- But it has **major problems**:
  - Sexual dimorphism misleads
  - Sometimes there are geographic variants
  - Morphologically different life stages



# MSC tends to oversplit or undersplit species



"Cryptic Species"

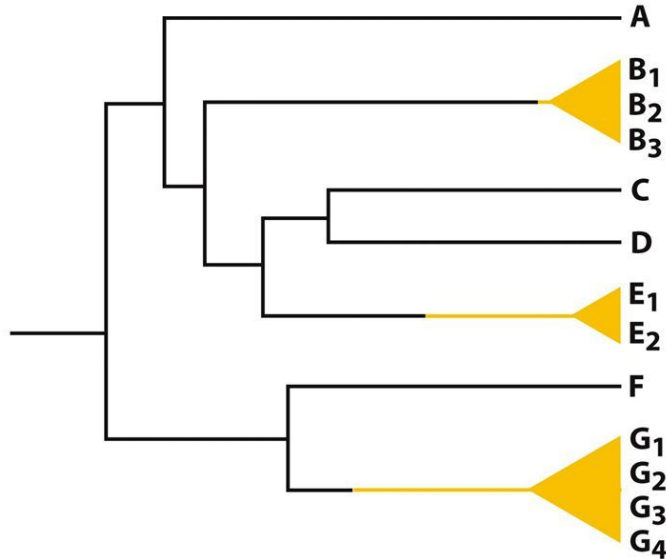


Oak Titmouse  
*Baeolophus inornatus*

Juniper Titmouse  
*Baeolophus ridgwayi*

# Phylogenetic Species Concept

- Defines species as "tips" on evolutionary trees (phylogenies)
  - Stay tuned 1-2 weeks for phylogenies!



# Ecological Species Concept

- Defines species based occupying the same niche (adapted to same ecological resources)

Hawaiian Honeycreepers



# Biological Species Concept (BSC) (this one!!!!)

Most commonly, researchers use this species concept to delimit species

"Species are groups of actually or potentially interbreeding populations which are reproductively isolated from other such groups." - Ernst Mayr (1942)

**Formal definition: Two organisms are the same species if they successfully mate AND produce fertile offspring**

# One species becomes two when....

- A barrier to mating forms
  - Leads to **reproductive isolation**
- Populations start to evolve separately as independent **lineages**
  - Gain separate mutations
  - Experience different selection pressures, differences in strength of genetic drift → different alleles go to fixation
- Over enough time, genetic differences accumulate and species are unable to mate entirely



# Isolation mechanisms (barriers) prevent gene exchange

Over time, populations that stop exchanging genes will **diverge** and accumulate **differences**. If these differences **prevent successful mating**, speciation has occurred.

Pop quiz!! Is speciation the goal of successful evolution?

**NO. Evolution does not have any goals at all.**

# Types of isolation mechanisms/barriers to mating

- **Prezygotic barriers**

- Prevent zygote from being formed in the first place

- **Postzygotic barriers**

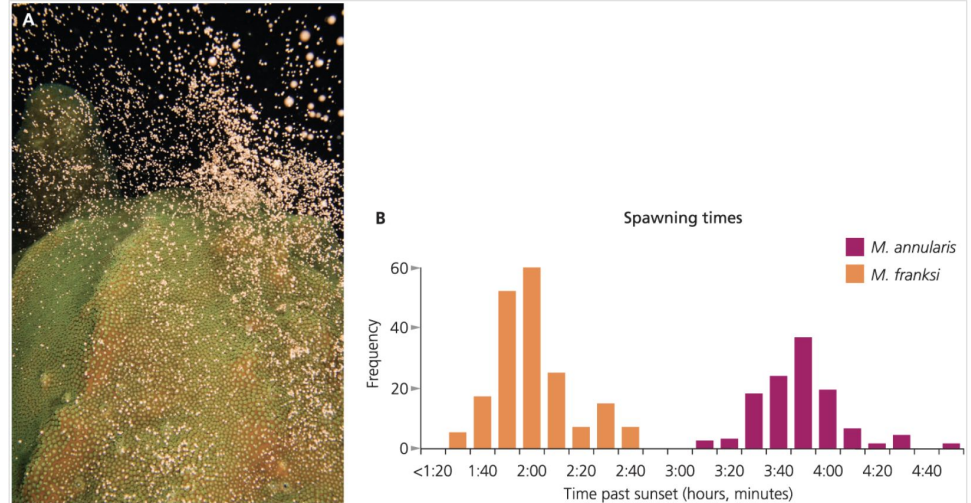
- Prevent a formed zygote from being viable

- Reminder: zygote = sperm + egg fused into a single cell

# Types of prezygotic barriers

- Barriers which prevent mating in the first place
  - Temporal isolation: different times of emergence
  - Ecological isolation: live in different habitats
  - Behavioral isolation: Divergence of mating behaviors (bird songs, frog chirps)
- Barriers which prevent a successful mating (even if attempted)
  - Mechanical isolation: morphological incompatibility ("parts don't fit")

# Example of temporal reproductive isolation

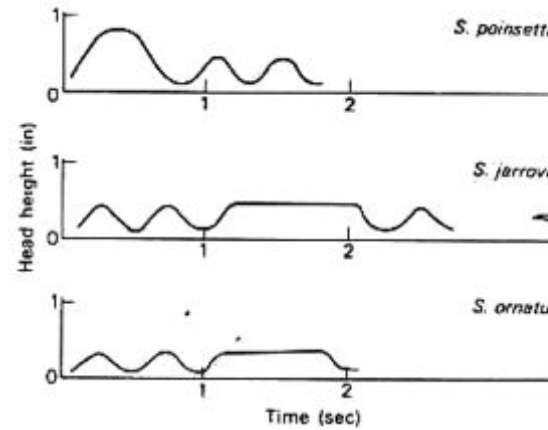
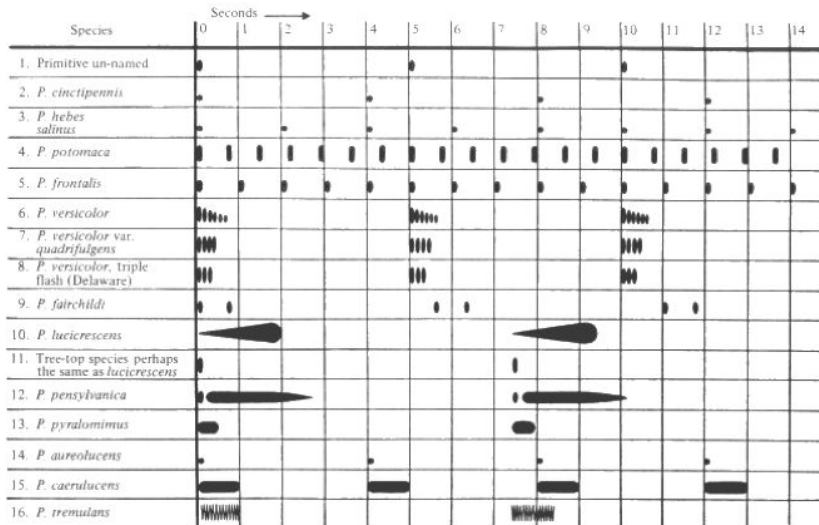


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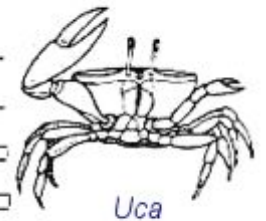
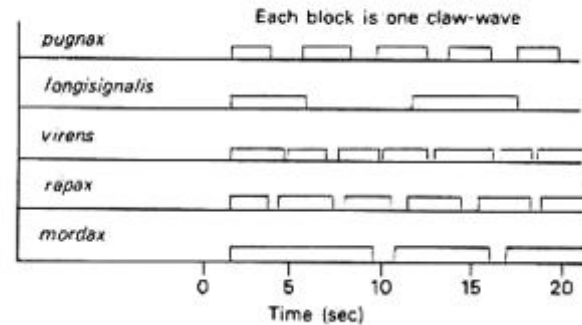
A: Universal Images Group / Superstock, Inc.

**Figure 13.4** A: Corals reproduce by releasing gametes into the water. B: This graph shows how two species of *Montastraea* corals remain reproductively isolated: by spawning at different times after sunset. (Data from [Leviton et al. 2004](#))

# Examples of behavioral isolation (strongly related to female preference!!)



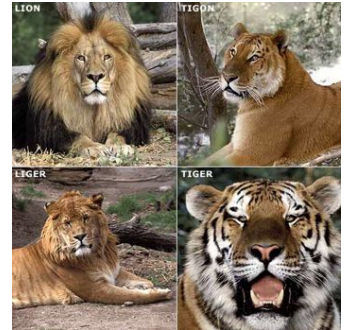
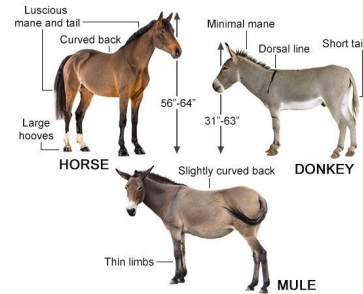
*Scleropor* lizards



*Uca*

# Types of postzygotic barriers

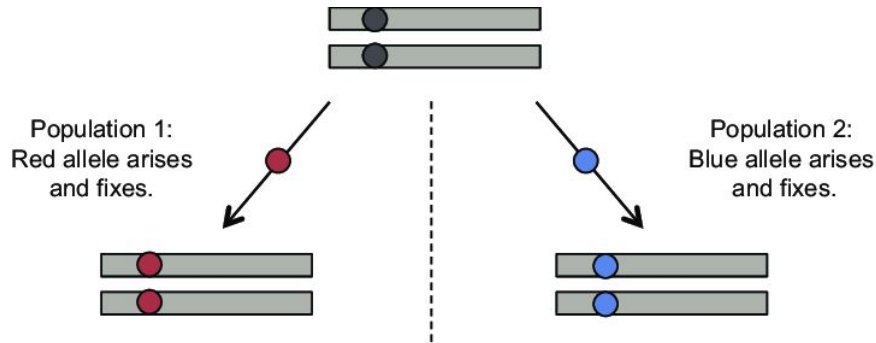
- Gametic mortality
  - sperm transferred but does not fertilize eggs
- Zygotic mortality
  - egg is fertilized but zygote dies
- Hybrid inviability or sterility
  - Hybrid offspring is either inviable (incomplete development) or sterile (looks fine but can't reproduce)



# The genetic basis of postzygotic barriers: Hybrid inviability

## Example: Single gene locus

New population alleles produce LOW FITNESS hybrids

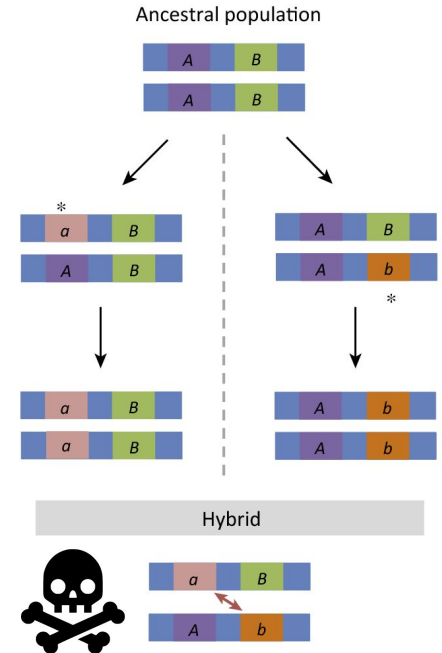


Red and blue alleles are incompatible in  $F_1$  hybrids.



### Example: Two gene loci interact (epistasis!)

New population alleles when combined produce LOW FITNESS hybrids



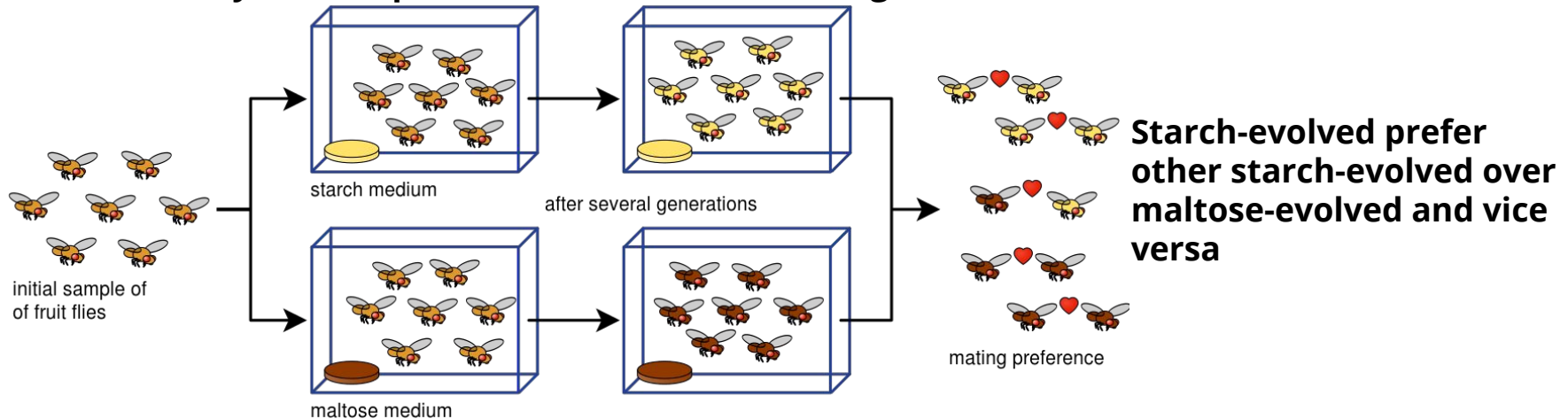
# Testing the evolution of isolation mechanisms

"Reproductive isolation as a consequence of **adaptive divergence**..."

REPRODUCTIVE ISOLATION AS A CONSEQUENCE OF ADAPTIVE DIVERGENCE IN  
*DROSOPHILA PSEUDOOBSCURA*

DIANE M. B. DODD<sup>1</sup>  
<sup>1</sup>Department of Biology, Yale University, New Haven, CT

One year of separation aka isolation (30-40 generations)



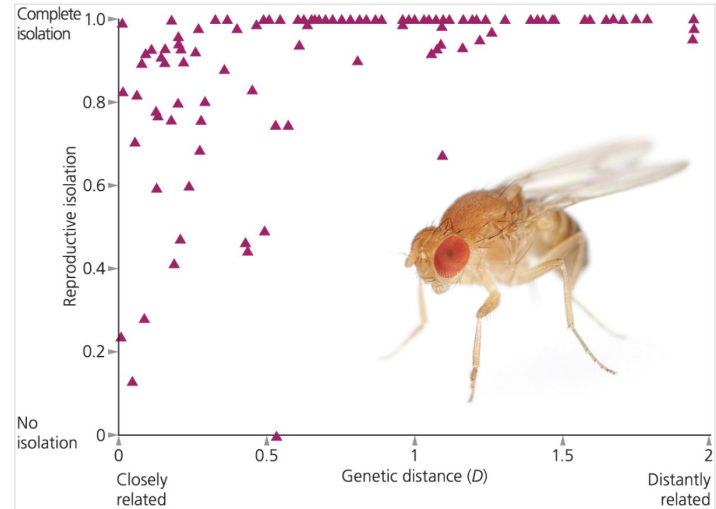


# Pleiotropy: another fancy vocabulary word

- Pleiotropy: when a gene affects more than one phenotype.
  - Phenotype 1: Food metabolism
  - Phenotype 2: Mating preference
- Genes involved with *Drosophila* **adapting to** different food sources **also affected mating preferences**
- A prezygotic barrier to mating formed because of genes related to **food metabolism**

# The relationship between reproductive isolation and genetic distance

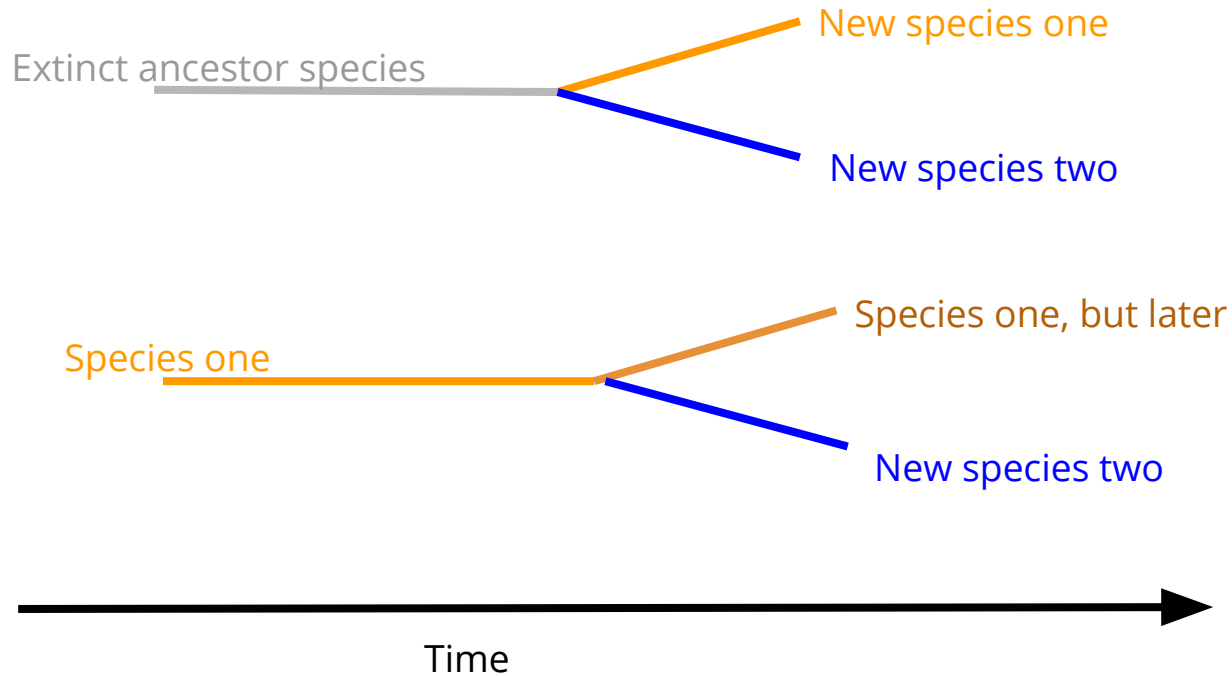
- Genetic distance example:
  - Species 1: ACCTAAGGCC
  - Species 2: ACCTACGGCA
  - 3/10 differ = **0.3 genetic distance**
- Also called **P-distance**
  - Proportion of differences
- Genetic distance can be  $> 1$  when **more than 1 mutation** occurs at each DNA position



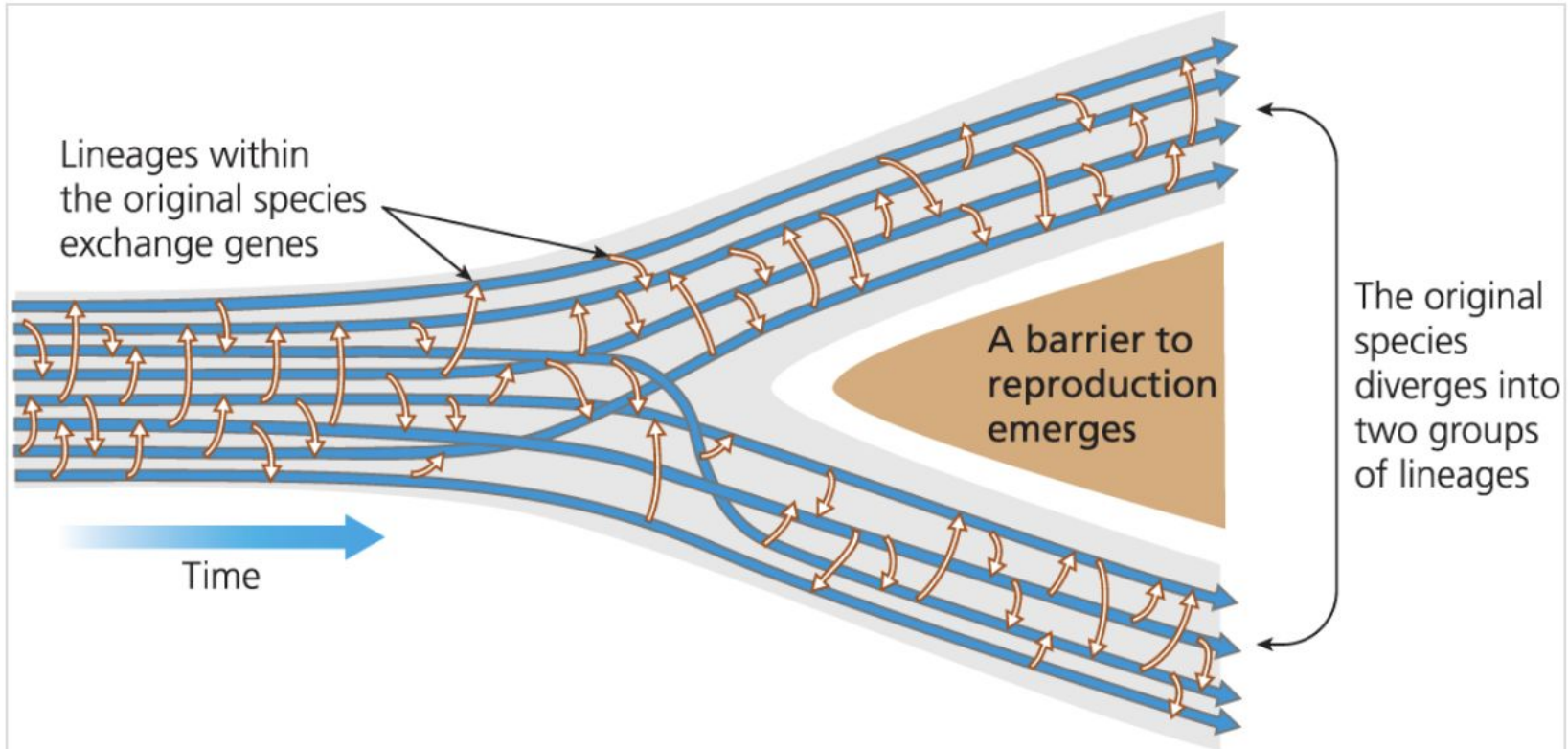
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photo by Antagain / E+ / Getty Images

**Figure 13.14** This graph shows how reproductive isolation evolved among species of *Drosophila*. The genetic distance ( $D$ ) between two species increases with time. It takes roughly a million years for  $D$  to reach a value of 1. By then, a typical pair of *Drosophila* species no longer interbreeds. (Data from [Coyne and Orr 2004](#))

# We call this process cladogenesis



**Lineage ~ population (interbreeding group of organisms of the same species)**



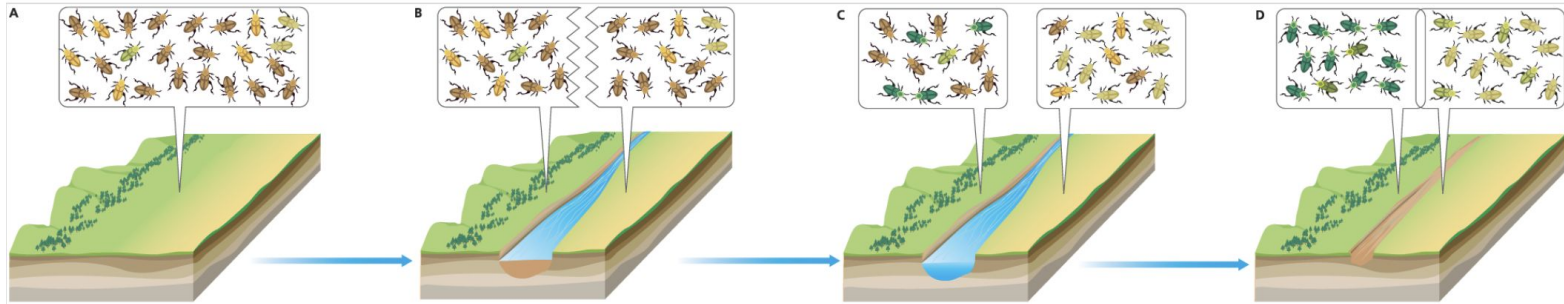
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# Two main models of speciation (there are others)

- **Allopatric speciation:** Species form in **different** environments
  - allopatric = live in non-overlapping geographic areas
- **Sympatric speciation:** Species form in the **same** environment
  - sympatric = live in the same geographic area
- Which do you think is more common? Why?

# Allopatric speciation

A single species **diverges** over time due to geographic barriers.

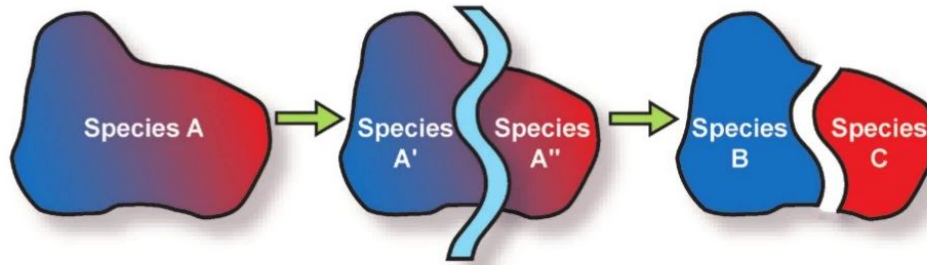


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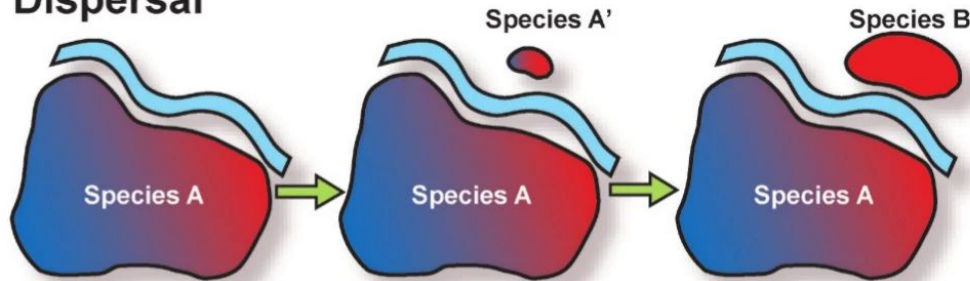
**Figure 13.8** Allopatric speciation is the result of geographic isolation. A: Here, a population begins with a continuous geographic range. It contains genetic variation, but gene flow ensures that new mutations can spread across the range once they arise. B: A river divides the population into two subpopulations. C: The change of allele frequencies in the two subpopulations is no longer linked. They become increasingly divergent. D: The river later dries up, allowing the two subpopulations to make contact. During their separation, reproductive barriers may evolve, reducing the gene flow between the two subpopulations.

# Allopatric speciation can occur via dispersal or vicariance

**Vicariance**



**Dispersal**

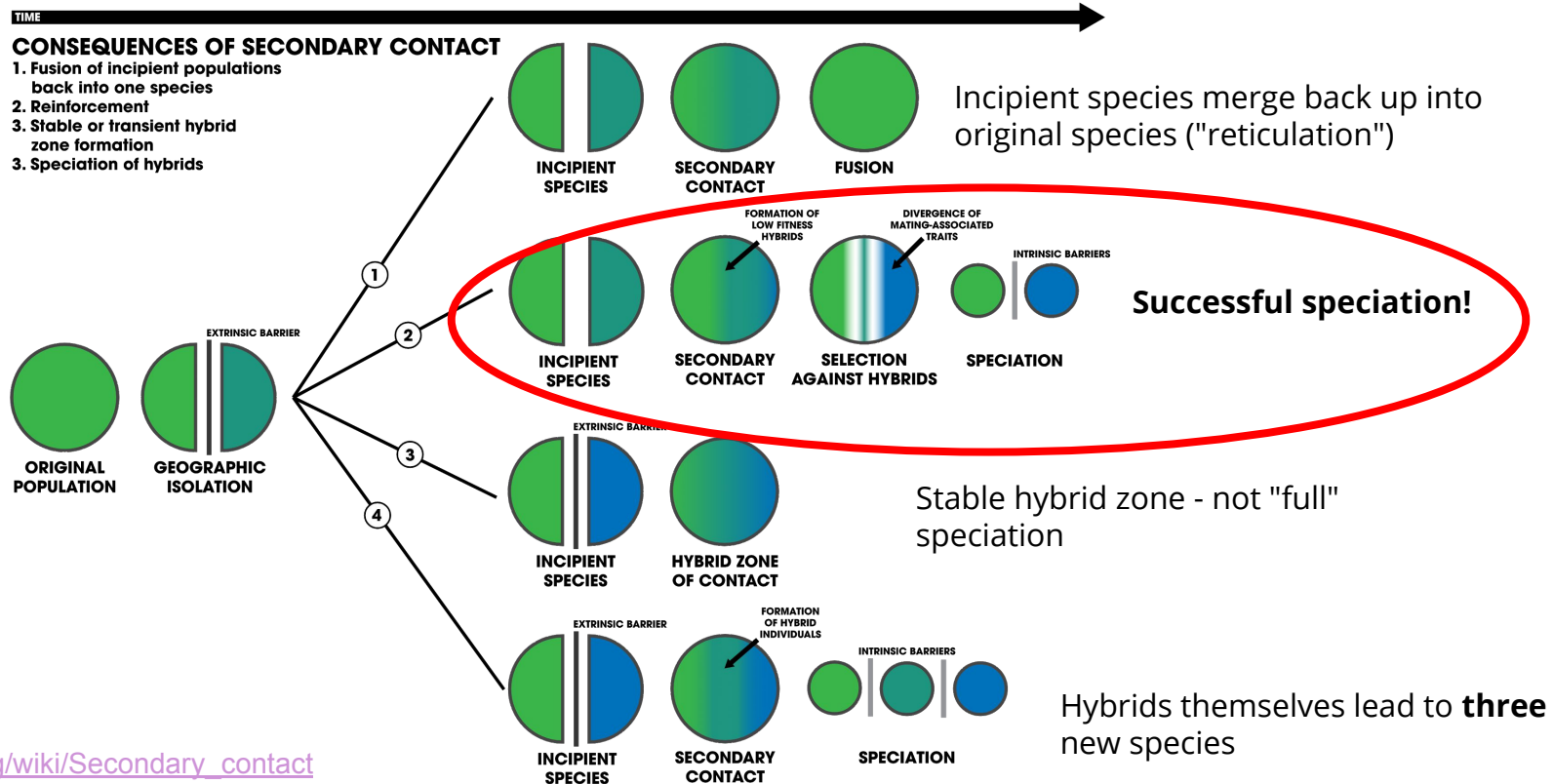


# Geographic separation does not always lead to full speciation

- Successful allopatric speciation relies on incipient species remaining isolated if/when re-introduced
  - Incipient species = two populations in the process of diverging into two species
- Re-introduction is called **secondary contact**

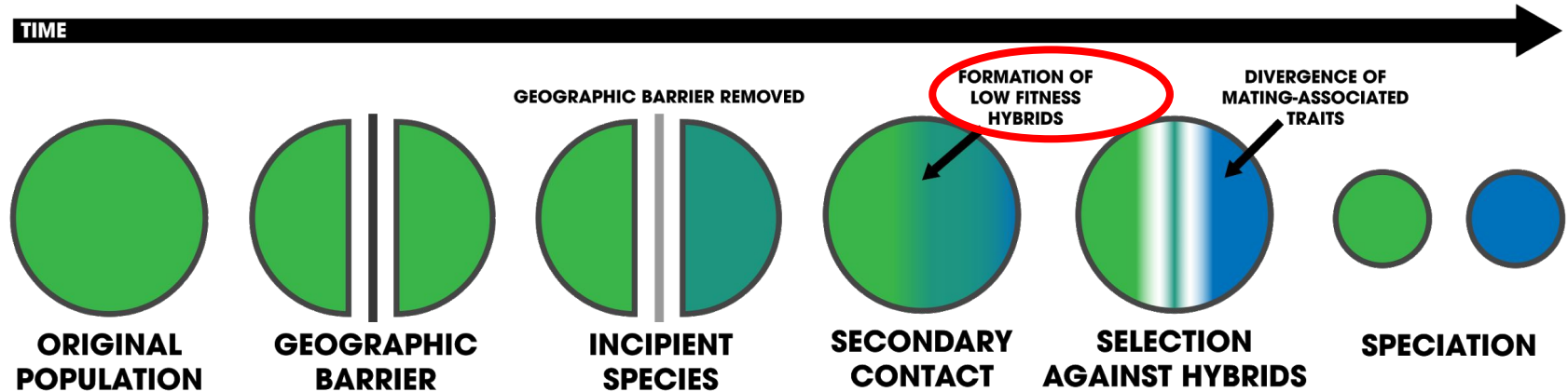


# Upon secondary contact, incipient species could...

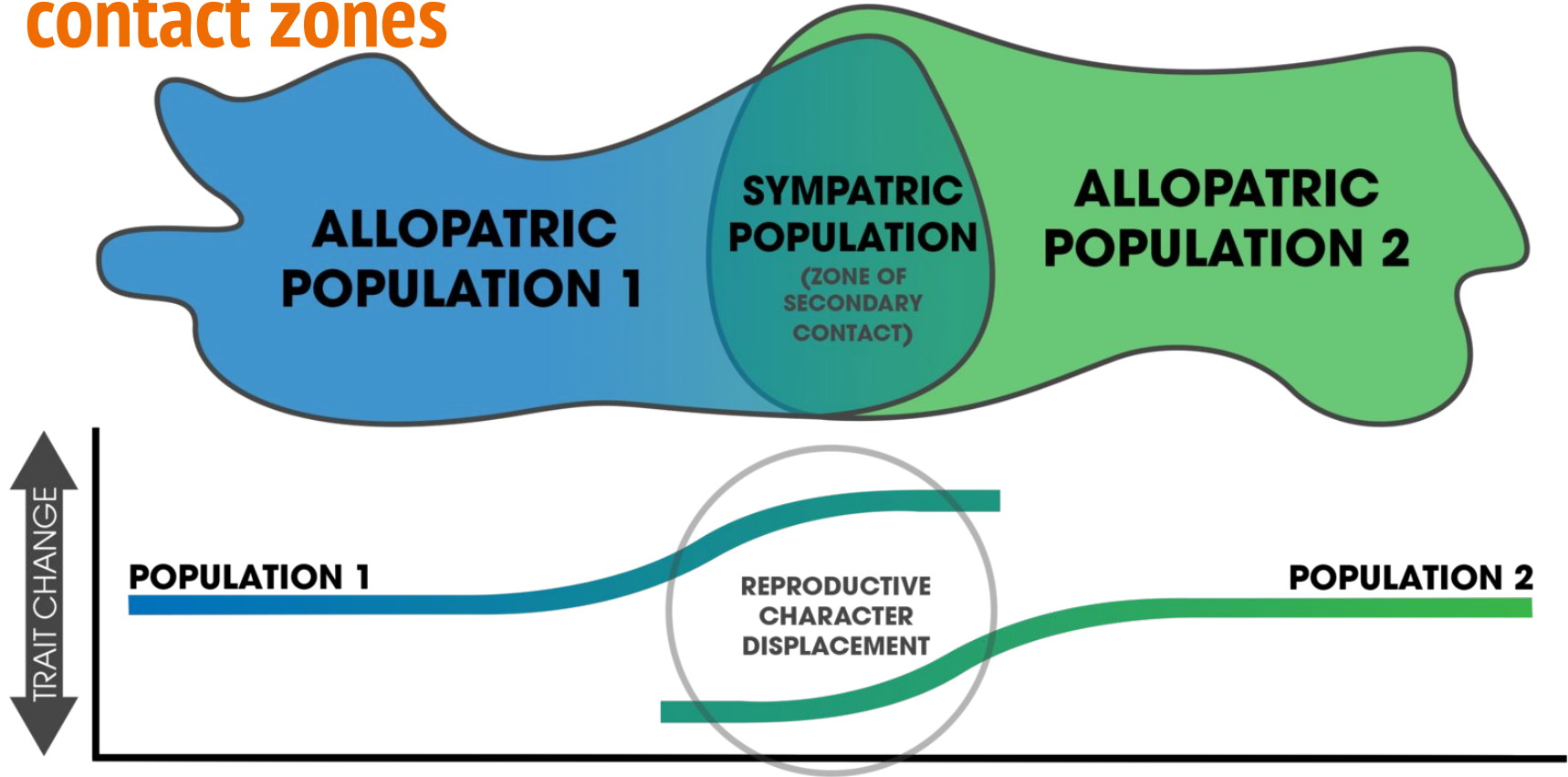


# Secondary contact can reinforce speciation

- Low fitness hybrids means incipient species will not merge back up
- This is analogous to disruptive selection:
  - Hybrids have lowest fitness ("heterozygotes" analogy)
  - Incipient species individuals have high fitness ("homozygotes" analogy)



# Character displacement is common in secondary contact zones

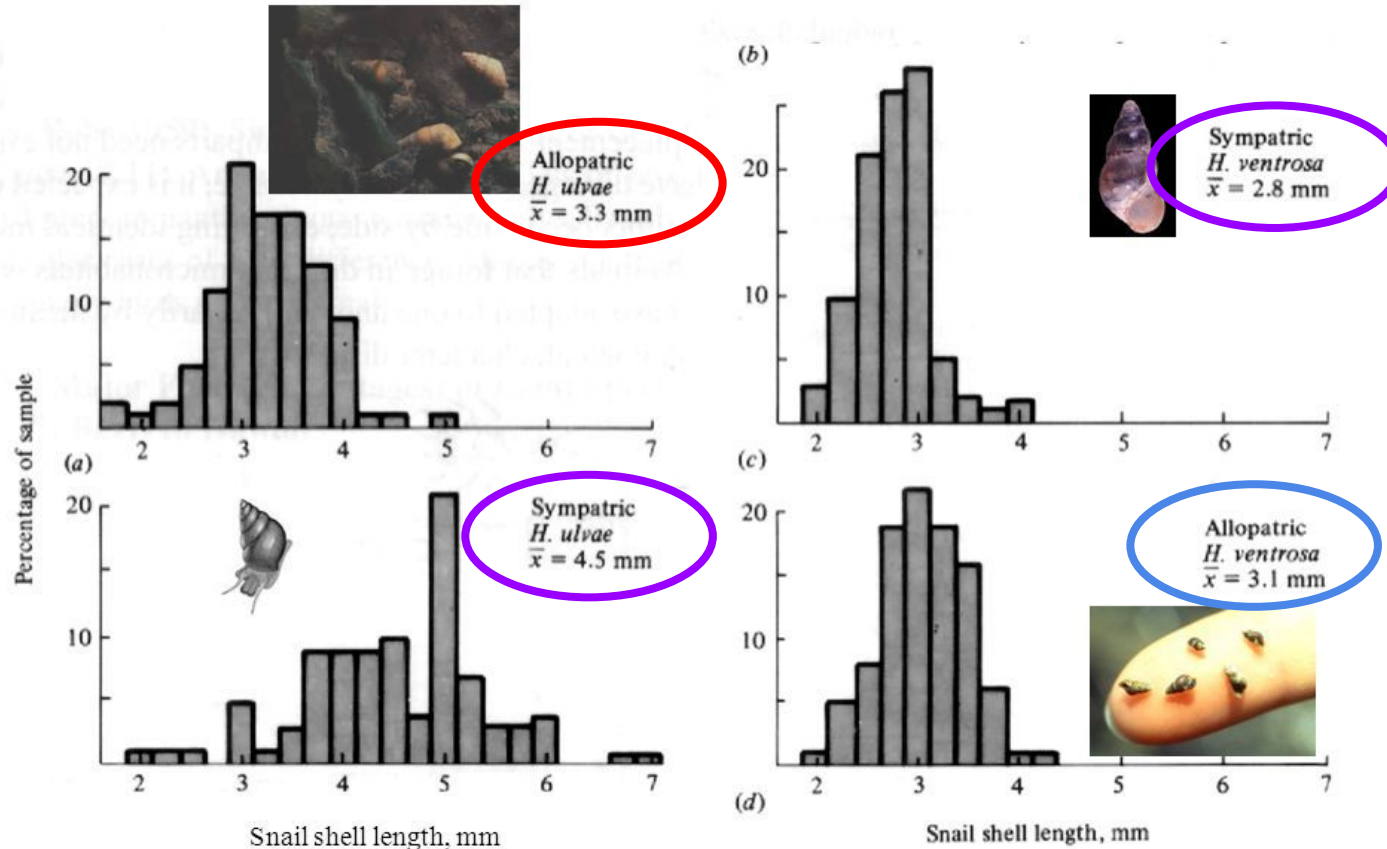


# Reproductive character displacement

- When sympatric and allopatric populations of a species, or two *very closely related species*\*, differ in traits crucial to reproduction
- Signifies that selection is acting to limit the extent of hybridization
  - Be careful with logic!!
  - When we observe **co-existing species/populations that are extremely similar**, it is likely due to character displacement "allowing" coexistence.
  - Without displacement, hybridization would occur and likely lead to reticulation
- This is one reason why hybrids may not be observed in secondary contact zones - "extra" selection prevents them from mating

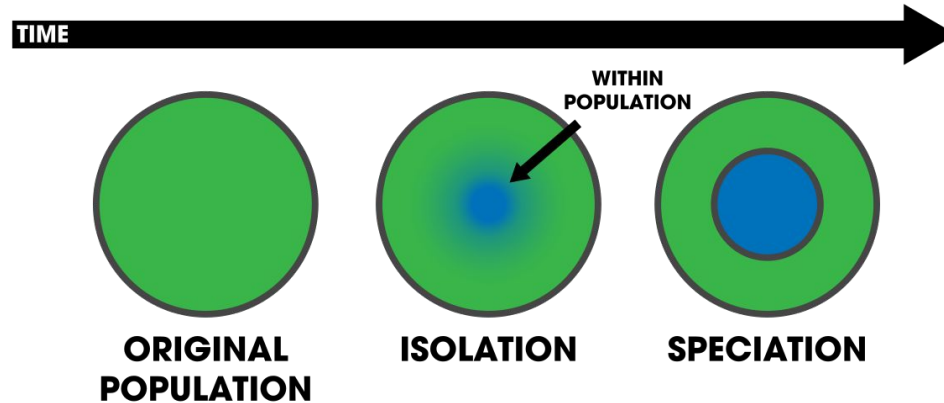
# Character Displacement in *Hydrobia* mud snails in Denmark

Shell length is used  
for **MATE**  
**RECOGNITION!**



# Sympatric speciation

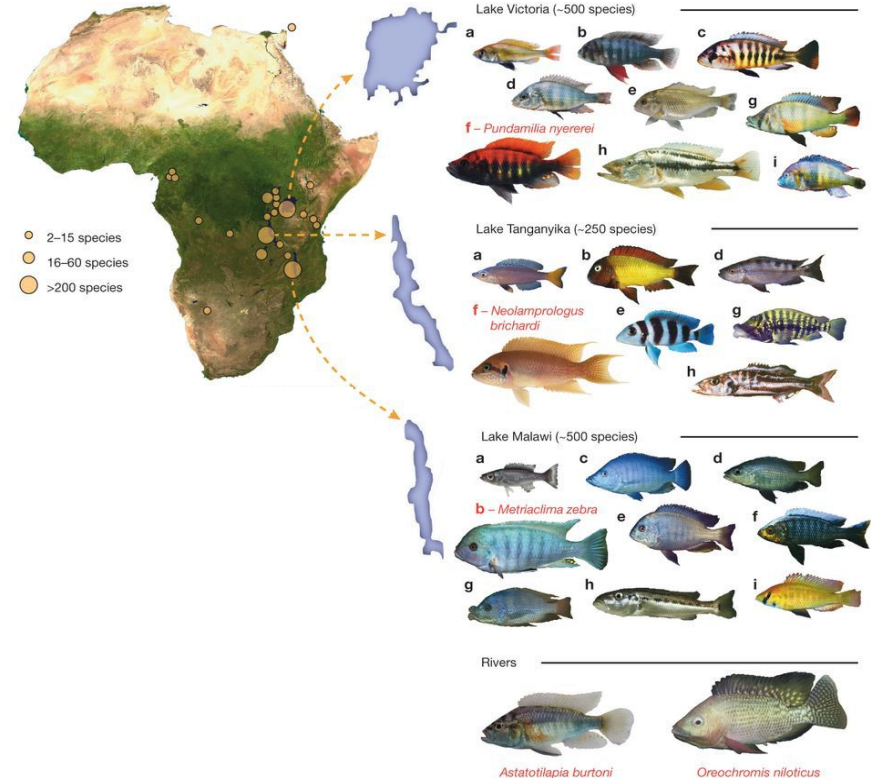
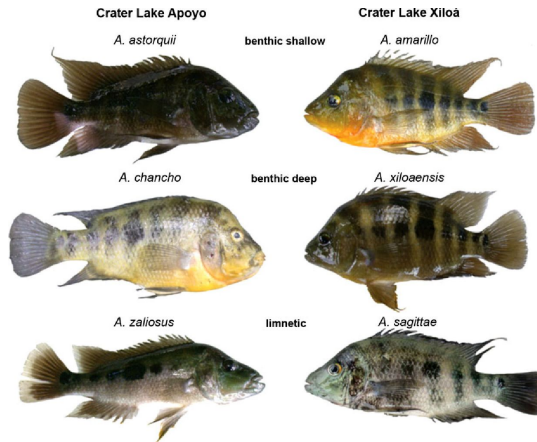
Speciation WITHOUT a geographic barrier



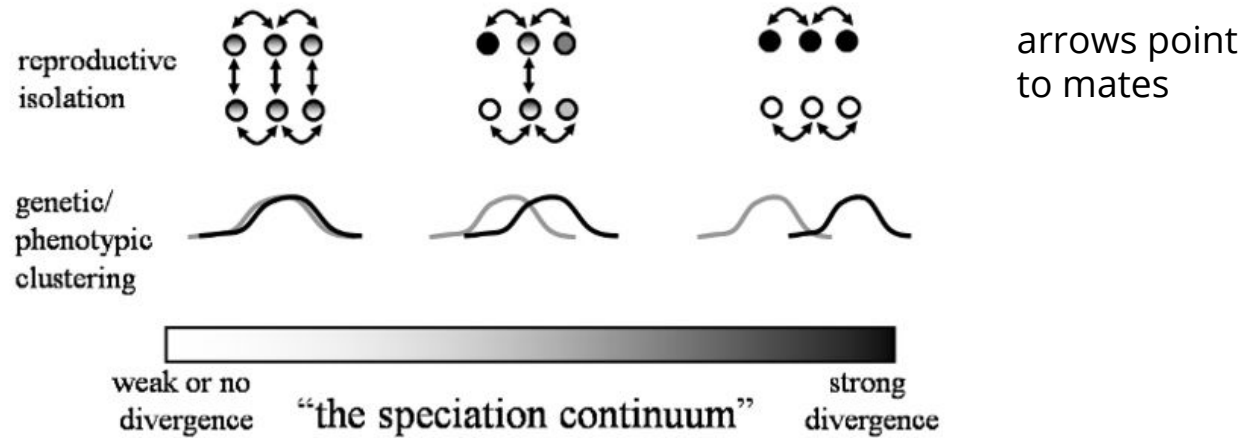
**QUESTION:** Do you expect isolation mechanisms to be stronger in allopatric or sympatric speciation?

# Sympatric speciation is very rarely observed

- One clear example is speciation in **cichlid fish**



# Species and speciation as a continuum



divergence = genetic change