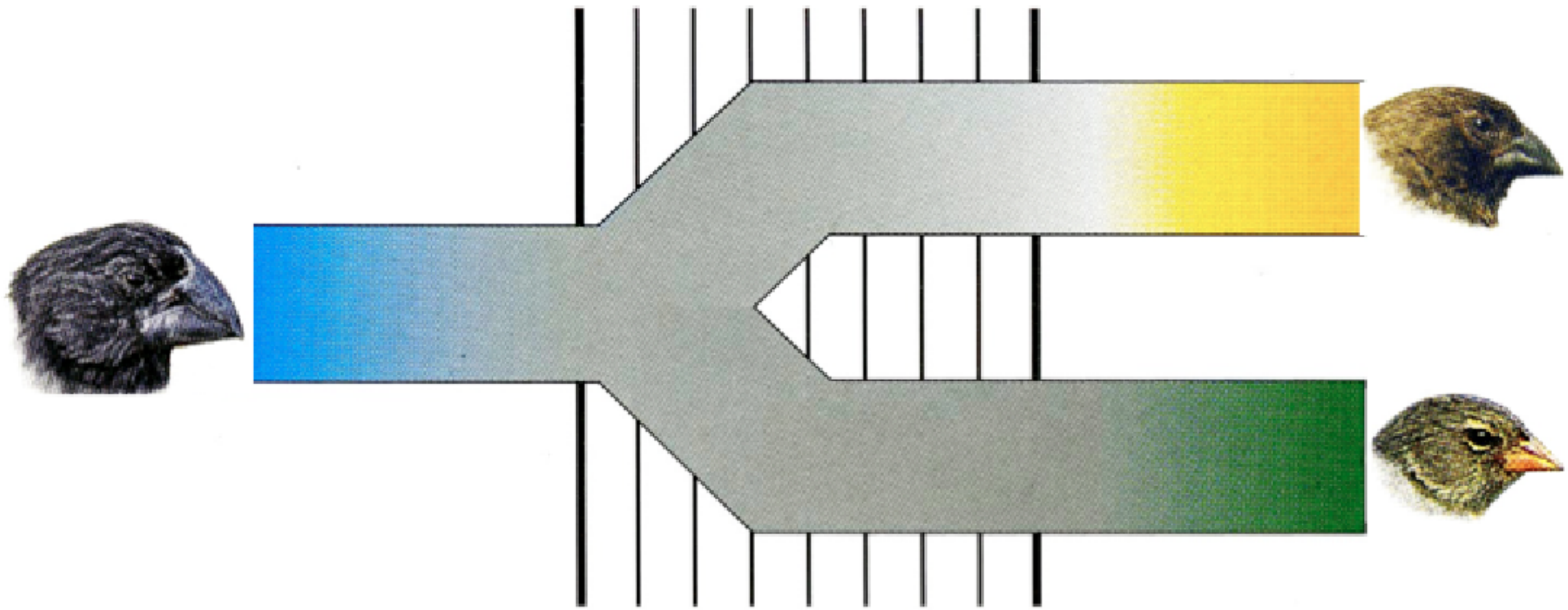
Speciation



Goals and Learning Objectives

1) Familiarize yourself with major species concepts (e.g., BSC, PSC) and the advantages or challenges in applying these to taxa
2) Understand how patterns of character displacement can arise, and relate this to cases of reinforcement. How have these cases been used to demonstrate the process of speciation?
3) Be able to identify and distinguish the different geographic modes of speciation and the role (or conditions) of gene flow/isolation in each of these
4) Consider the conditions and evidence one needs to demonstrate the geographic context of speciation and its modes (allopatric, peripatric, parapatric, sympatric)

Speciation

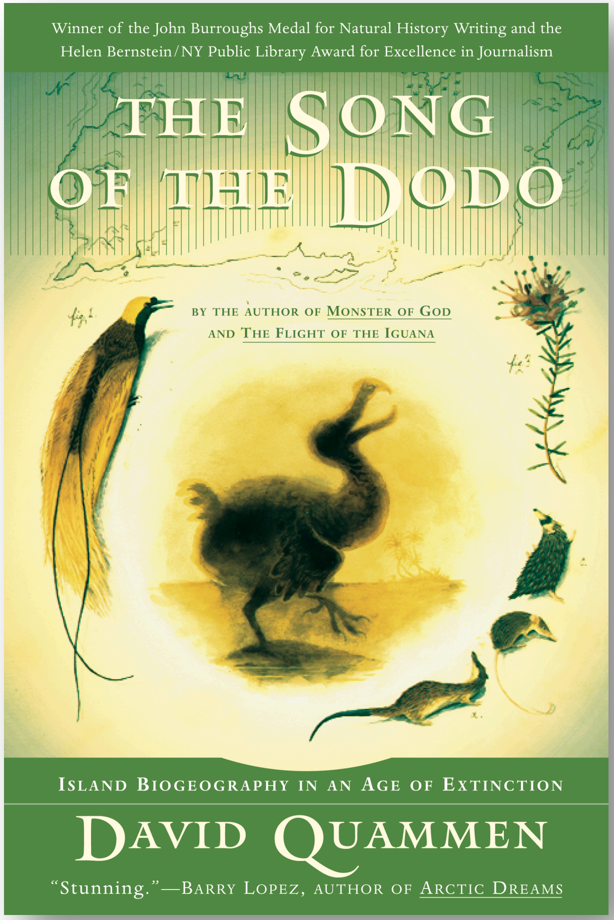
"Wallace and Darwin's great insight [natural selection as a factor in speciation] only began the era of asking. The 'mystery of mysteries' had been solved, at least in rough outline; then came the task of elaboration.

The colleagues and successors of Darwin and Wallace have now been at it for more than a century and a quarter, and throughout most of that effort biogeography has been their paramount tool.

The patterns of species distribution have provided clues about the ways in which species originate, change, and diverge, and the question how? has remained inseparable from the question where?....

The linkage between geographical circumstance and evolutionary development is embodied in the very word 'biogeography'."

- David Quammen -- *Song of the Dodo*



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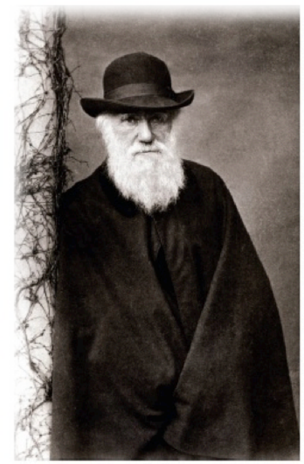
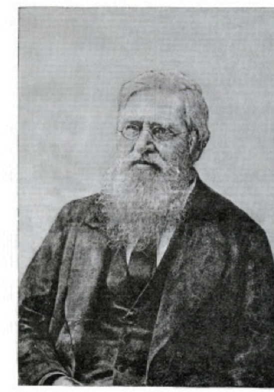


(a)



(b)

“The man who knew islands”

Alfred R. Wallace (1823-1913)

More than any other, Wallace compiled observations on distributions, diversity, extinction, disjunctions, and climate effects on distribution into a series of major works all between 1869 and 1880: “The Malay Archipelago”, “The Geographical Distribution of Animals”, and “Island Life”

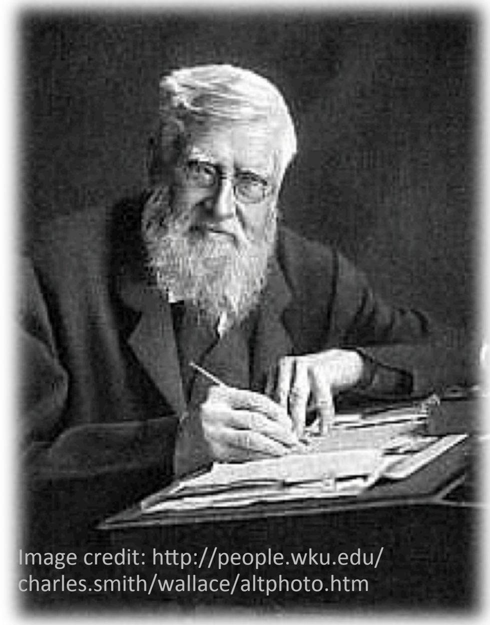


Image credit: http://people.wku.edu/charles.smith/wallace/altphoto.htm

“The man who knew islands”

Alfred R. Wallace (1823-1913)

Famous for recognizing *Wallace’s Line* which separates fauna of southeast Asian origin from those of Australian origin

http://evolution.berkeley.edu/evolibrary/article/_0_0/history_16

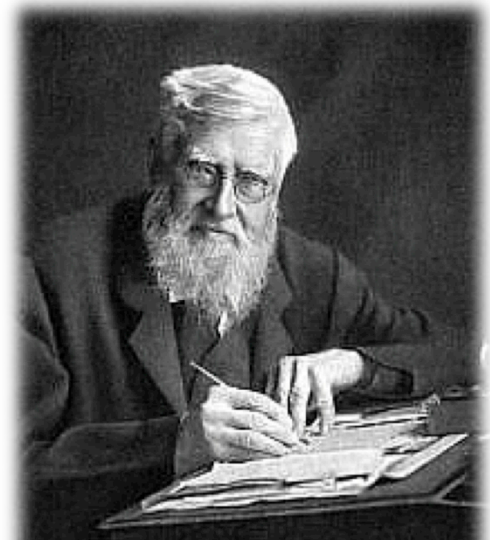


Image credit: http://people.wku.edu/charles.smith/wallace/altphoto.htm

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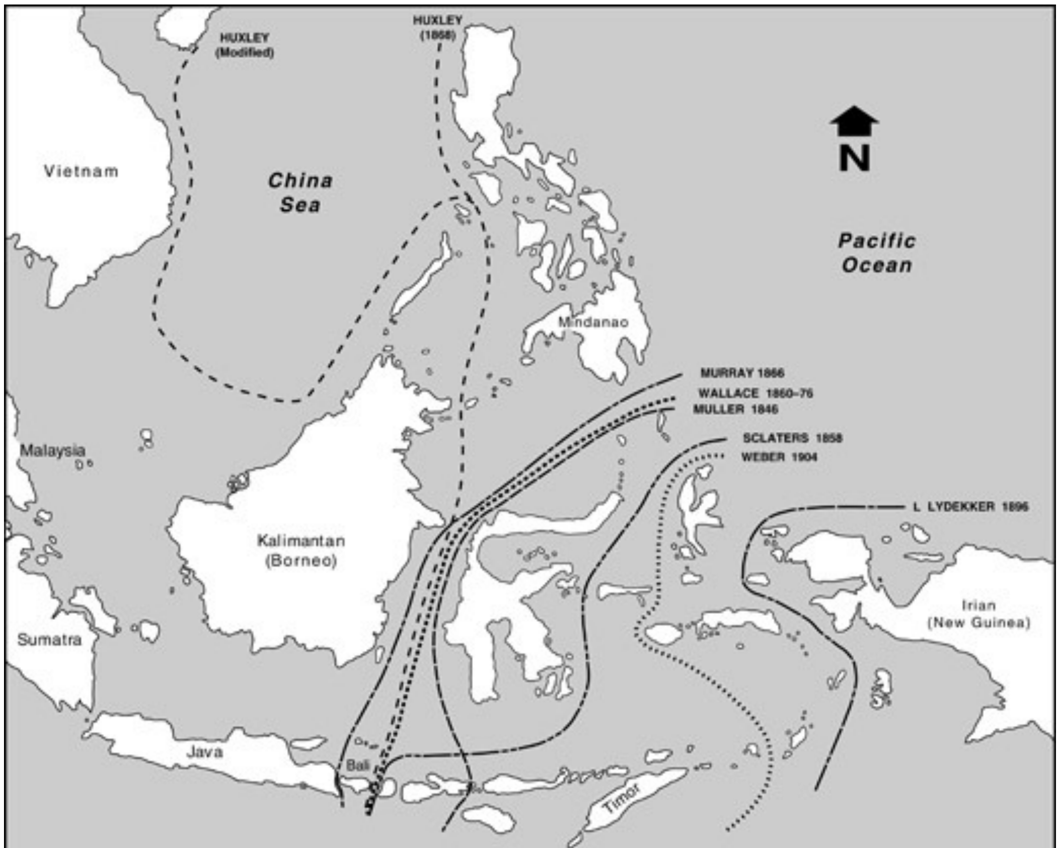

http://www.libraryindex.com/pages/3194/Biological-Realms.html

Image credit: http://people.wku.edu/charles.smith/wallace/altphoto.htm

Speciation

Why study species and speciation?

What constitutes a "species" and how they arise (speciation) is fundamental to biogeography:

1) Recall that the geographic distribution of species (and their attributes) is the fundamental unit of observation in biogeography. To collect and understand data on distributions, we must define what we mean by species.

2) The role of geography in speciation is still controversial and geographic aspects of species formation remain important areas of investigation.

3) The geographic distributions of species have played and continue to play important roles in understanding the process of speciation.

Speciation

Overview of this section:

1) Challenges to defining species

2) A note on species concepts

2) Mechanisms of speciation

3) Geography of speciation

Speciation

Overview of this section:

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Challenges in defining species

How distinct must a group of individuals be to be declared a species?

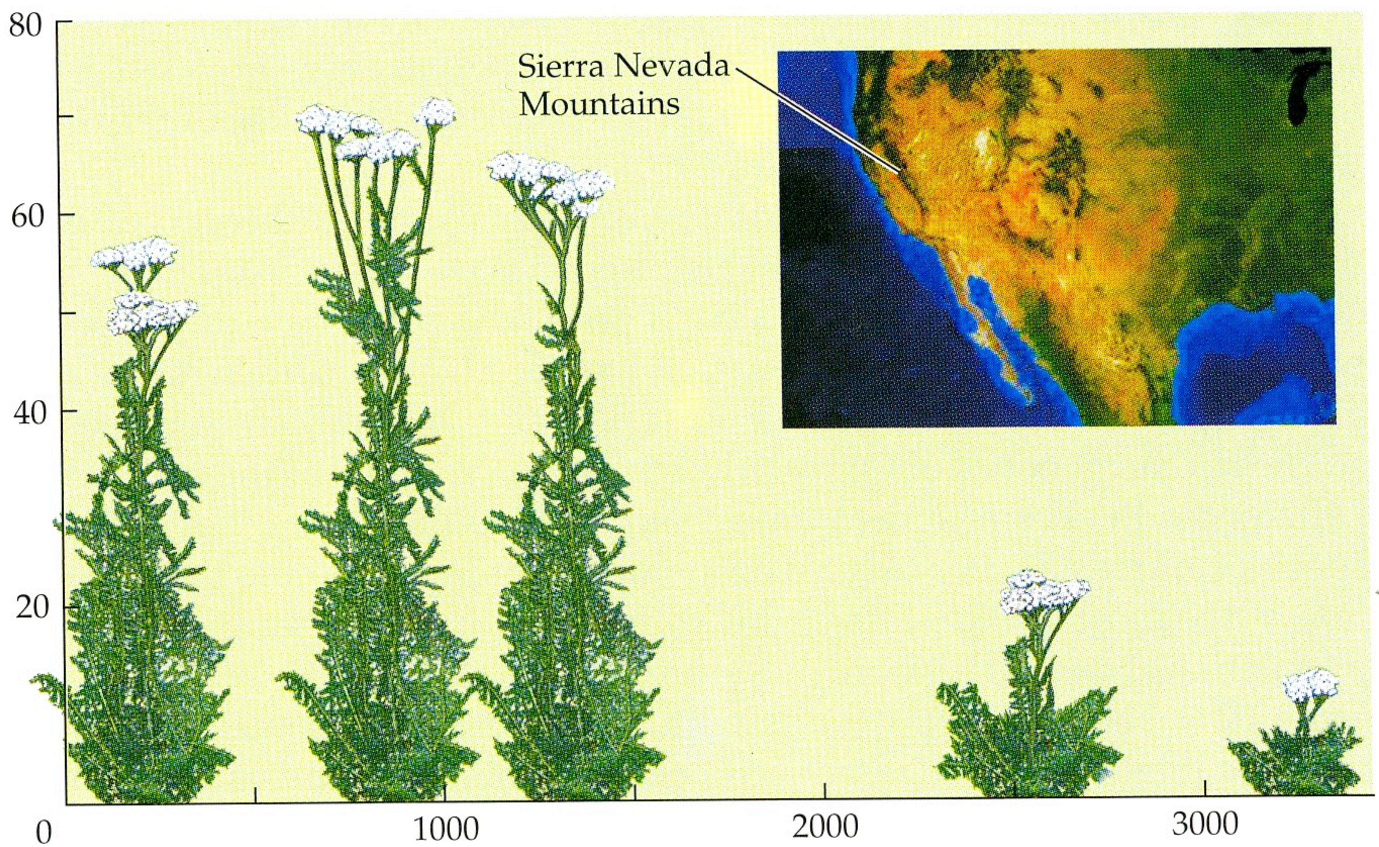
Some species have a tremendous amount of morphological and/or genetic diversity across their range.

Sometimes groups of individuals are identical morphologically, but genetically differentiated (cryptic species).

Challenges in defining species

Morphological differentiation of the yarrow (*Achillea millefolium*) along an elevational gradient in the Sierra Nevada mountains of California

Height of plants (cm)



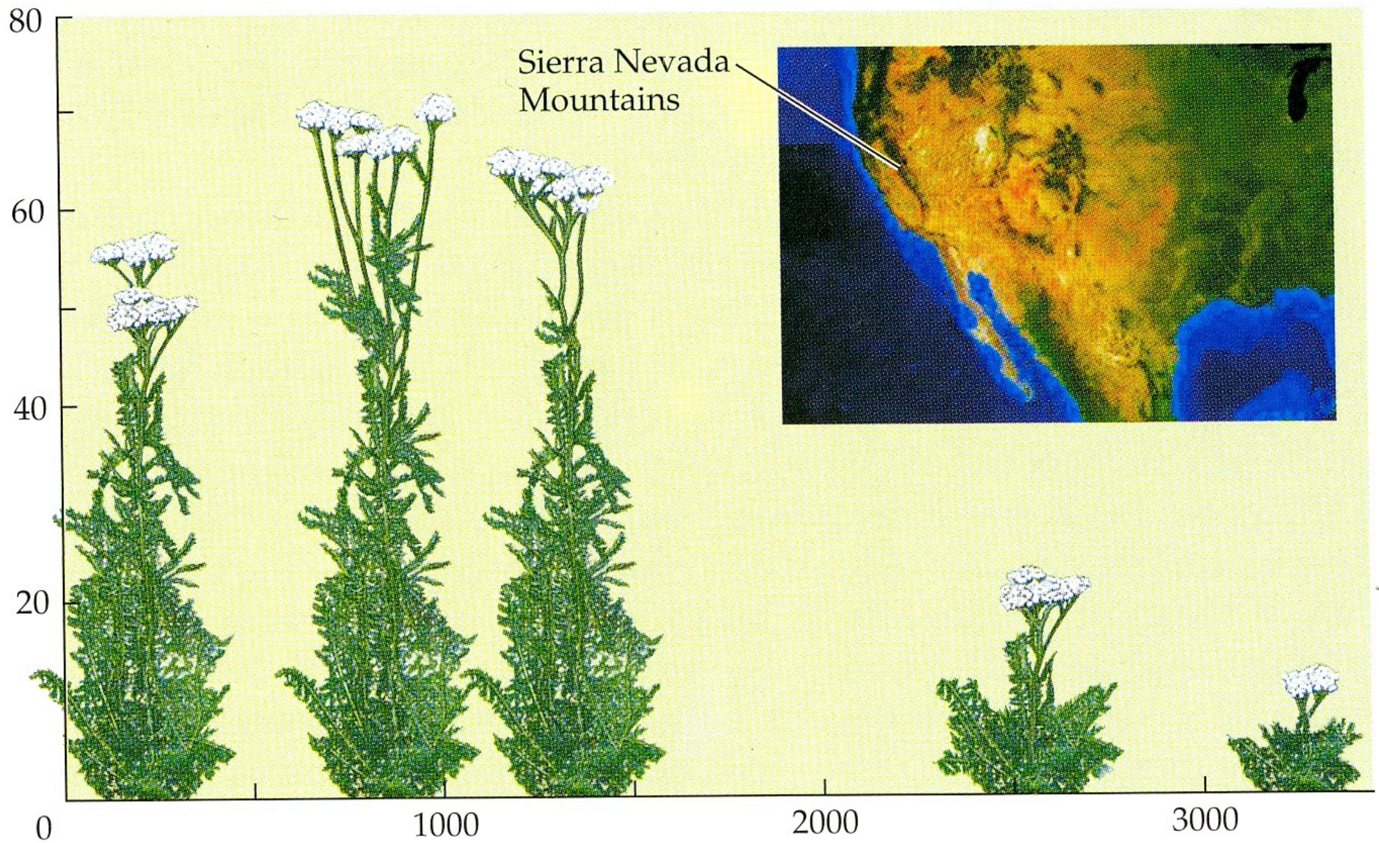
Elevation from which seed was collected (m)

Lomolino *et al.* 2010

Challenges in defining species

Demonstrated through common garden experiments that variation was result of adaptive (genetic) differentiation of a single population

Height of plants (cm)

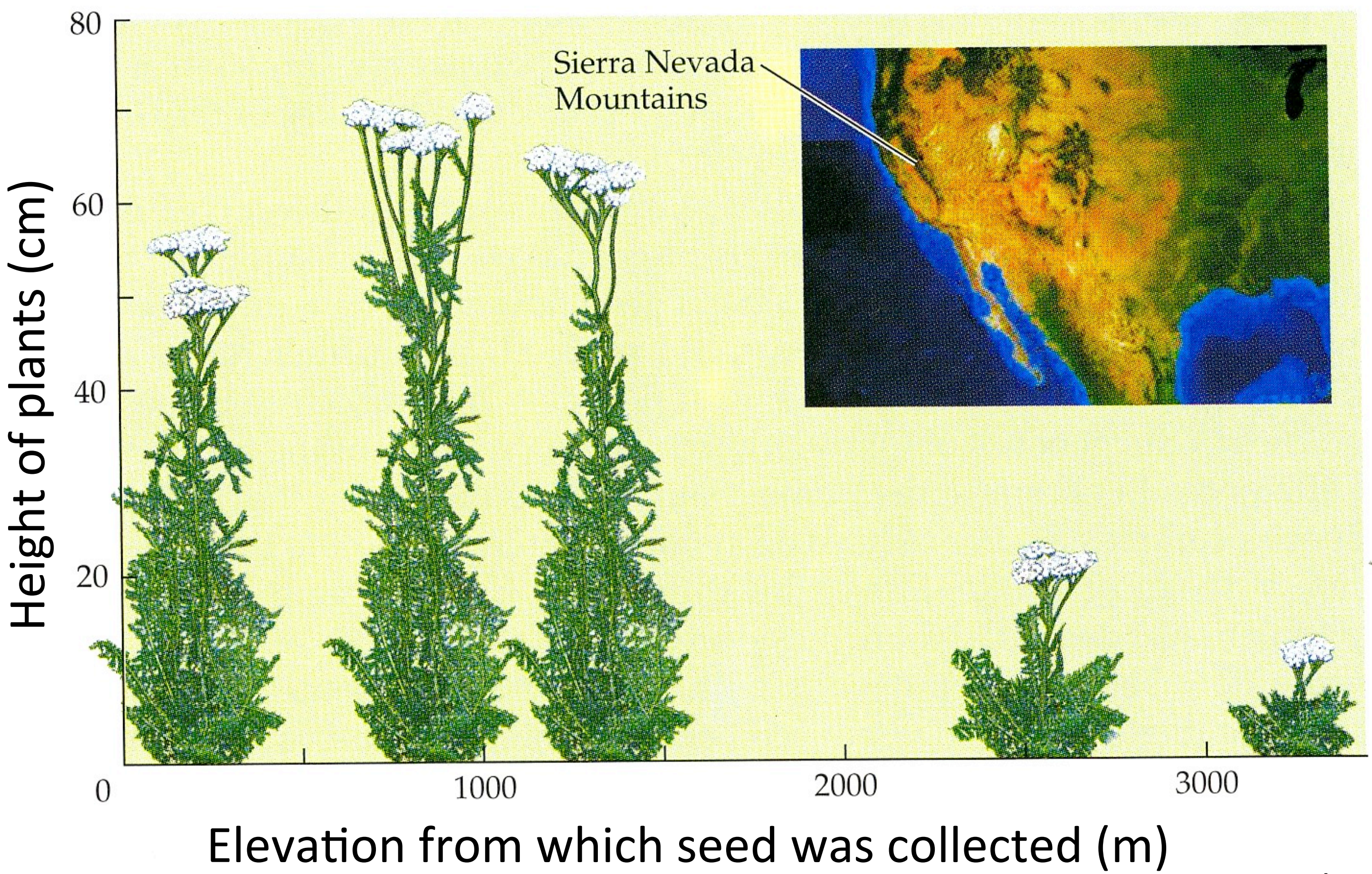


Elevation from which seed was collected (m)

Lomolino *et al.* 2010

Challenges in defining species

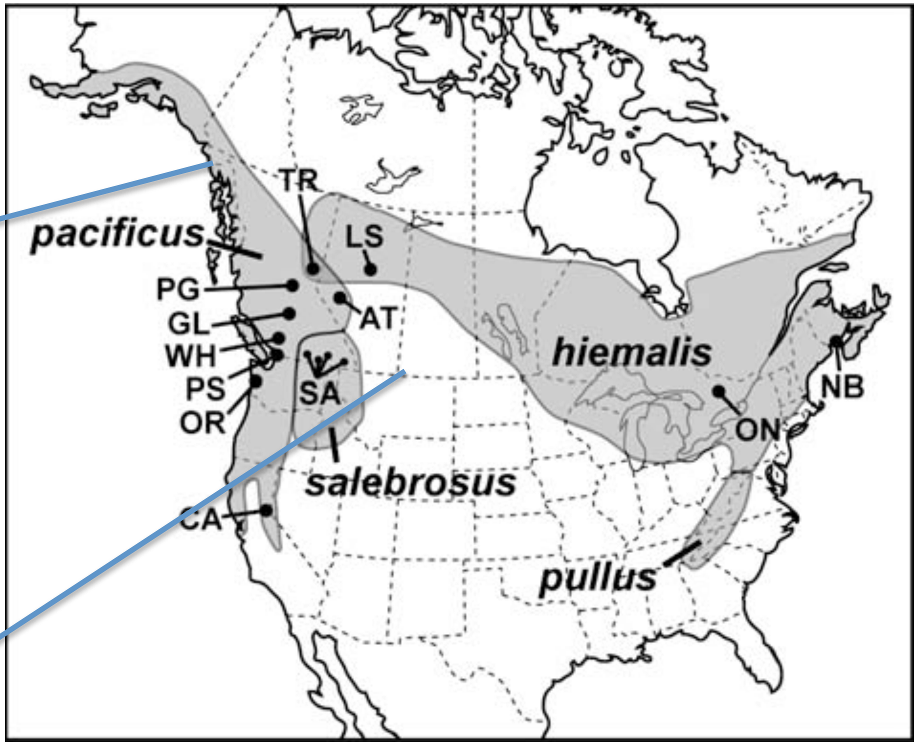
These differences reflect local adaptation, due to a combination of strong natural selection and limited gene flow.

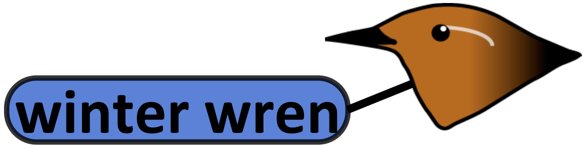


Lomolino *et al.* 2010

Challenges in defining species

Cryptic speciation in *Troglodytes* wrens, Tumbler Ridge (TR), Central BC





Toews and Irwin, *Molecular Ecology*, 2008

Challenges in defining species

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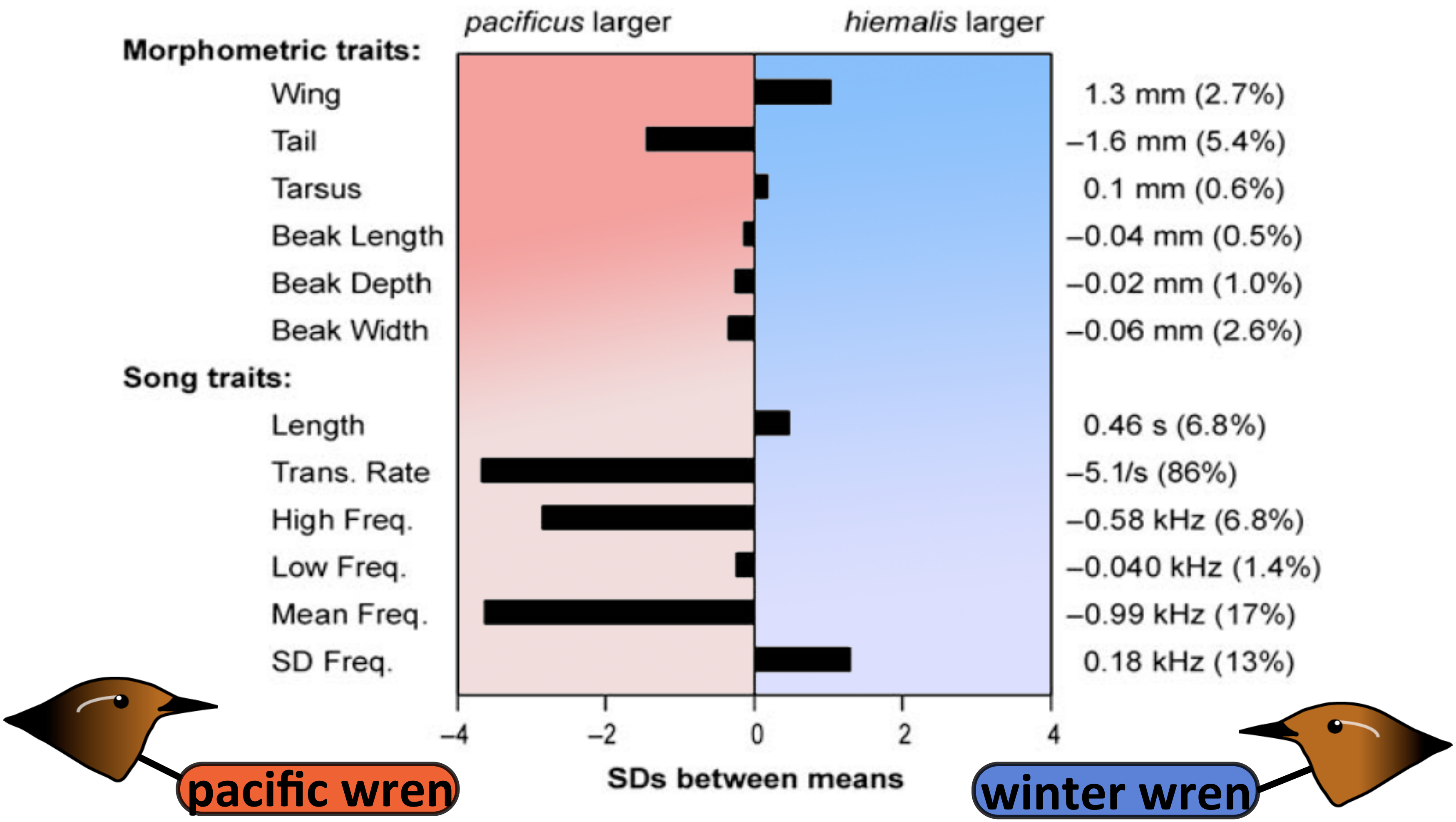


Toews and Irwin, *Molecular Ecology*, 2008

Speciation

Overview of this section:

1) Challenges to defining species

2) A note on species concepts

3) Mechanisms of Speciation

4) Geography of Speciation

Species Concepts

We won't cover alternative species concepts in detail…

There are at least 25 species concepts, concisely described by four groups (Coyne & Orr 2004)

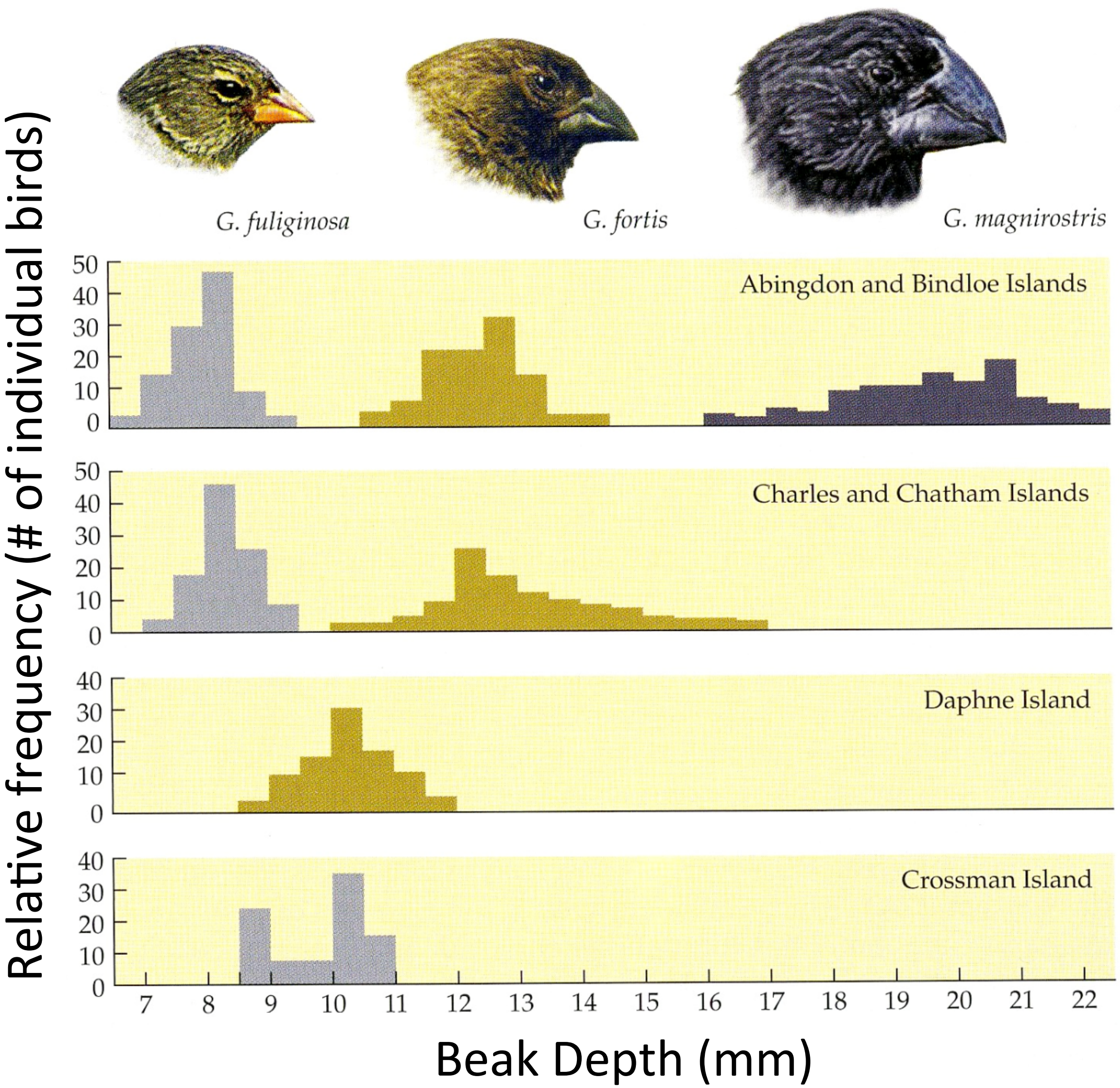
1) **Biological Species Concept (BSC)**
2) Phylogenetic Species Concepts (PSC)
3) [Genotypic or Phenotypic] Cohesion Species Concepts (CSC)
4) Ecological or Evolutionary Species Concepts (EcSC, EvSC)

Variation in most traits among individuals is **discontinuous**

Some individuals are very similar to one another, but differ greatly from other clumps of individuals – "clumpy-gappy" organization of biological diversity

Species concepts differ greatly in the sorts of clumps or groups they recognize…

Challenges in defining species



Character displacement in Darwin's finches

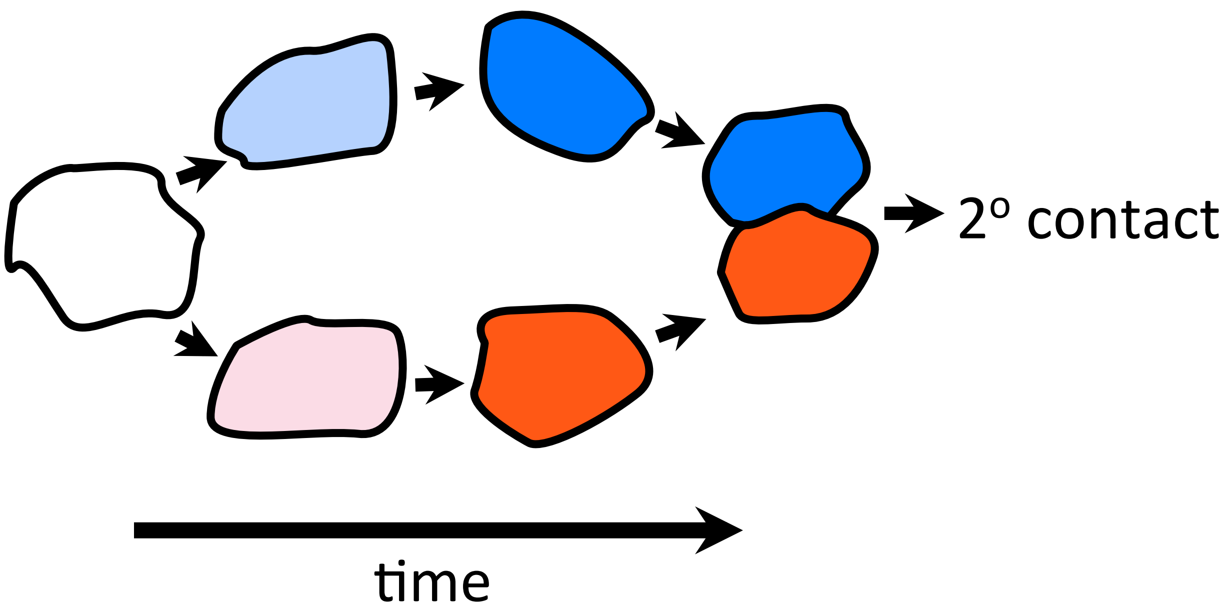
Morphology of species is influenced by co-occurring species and resource use

Discontinuous variation represents what most species concepts try to capture…

Lomolino *et al.* 2010

Species Concepts

Biological Species Concept: species are groups of interbreeding natural populations that are reproductively isolated from other groups (Mayr 1942, 1995). Most widely held concept for species delineation.



with time, reproductive isolation...

Species Concepts

Biological Species Concept: species are groups of interbreeding natural populations that are reproductively isolated from other groups (Mayr 1942, 1995). Most widely held concept for species delineation.

Issues:

How important is the distinction between *actually* or *potentially* interbreeding?

How can we apply the BSC to geographically isolated populations?

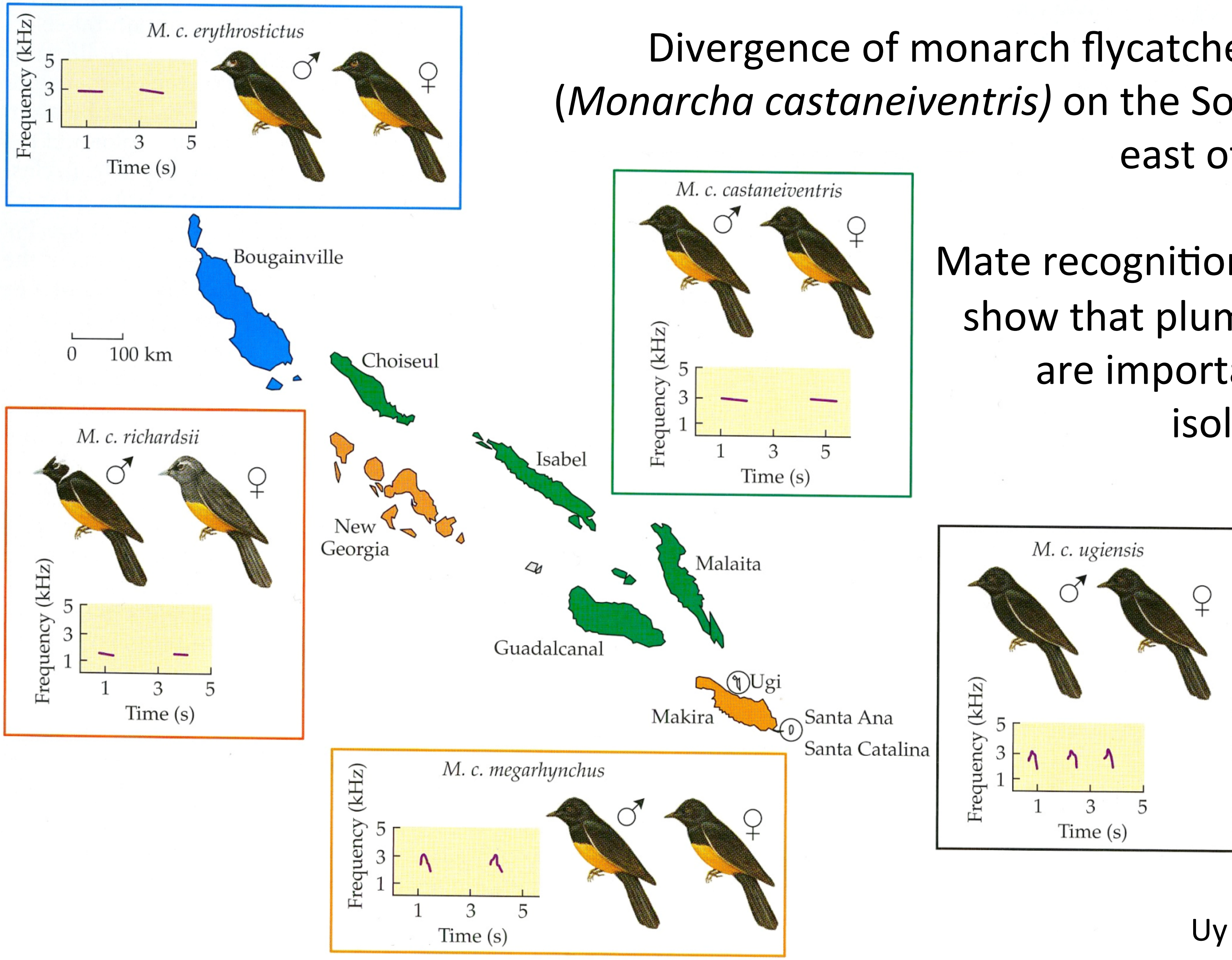
How can we apply the BSC to species known only from fossils?

How do we consider asexual species?

Species Concepts

Divergence of monarch flycatcher populations (*Monarcha castaneiventris)* on the Solomon Islands east of New Guinea.

Mate recognition experiments show that plumage and song are important premating isolating barriers.



Uy *et al*. 2009

Species Concepts

Phylogenetic Species Concept: a phylogenetic species is (1) a monophyletic lineage, (2) derived through an evolutionary process of descent from an ancestral lineage and (3) diagnosable through examination of character state transformations (McKitrick & Zink 1988; Cracraft 1989).

Issues:

Which derived diagnostic character states do we focus on?

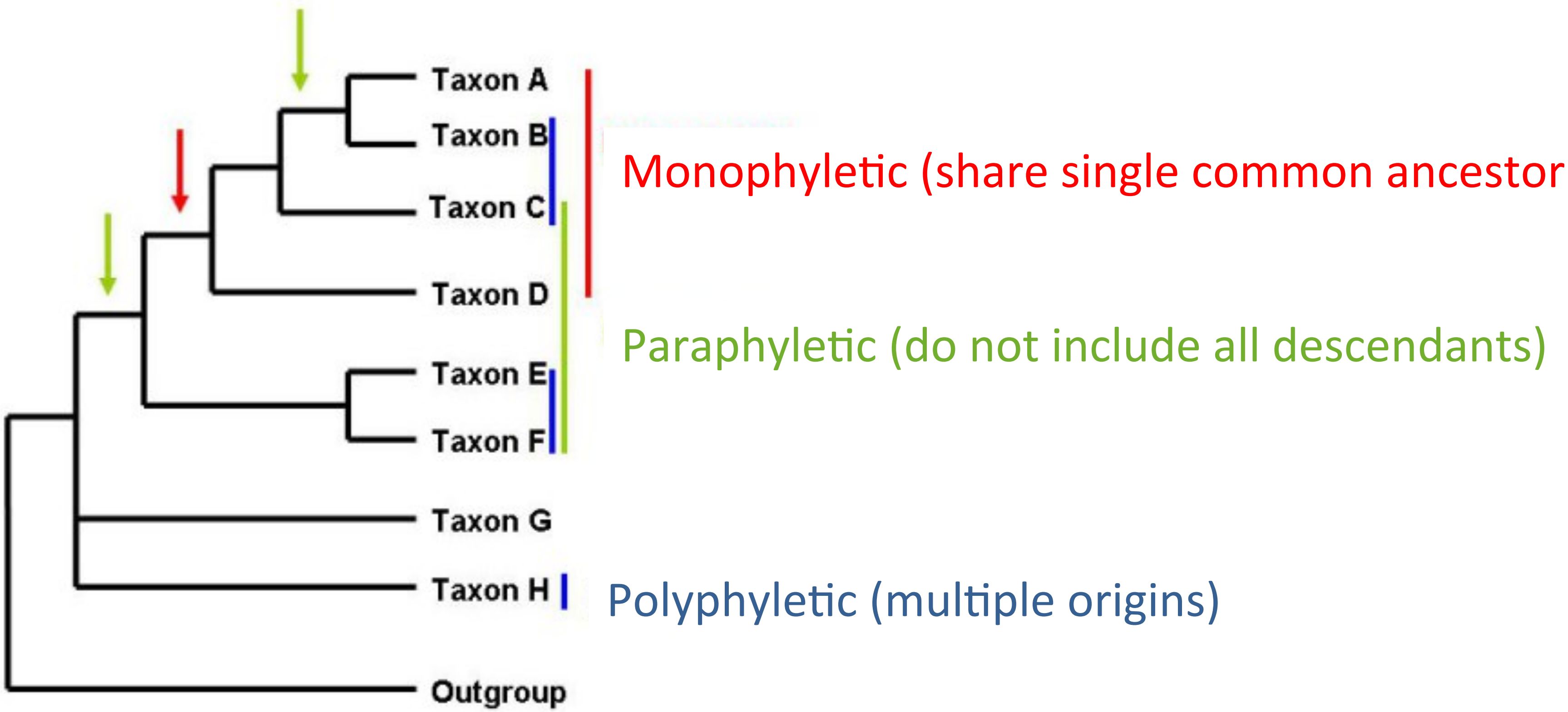
Requires reliable knowledge of evolutionary relationships of species.

Benefits:

Can apply to asexual and sexual reproducing species

Some terms in describing species relationships

Monophyletic group: Descendants from a single common ancestor
Paraphyletic group: Does not include all descendants from single common ancestor
Polyphyletic group: Descendants that have multiple origins, descended from more than one ancestor – an issue when species are described without genetic data



Speciation

Overview of this section:

1) Challenges to defining species

2) A note on species concepts and terms

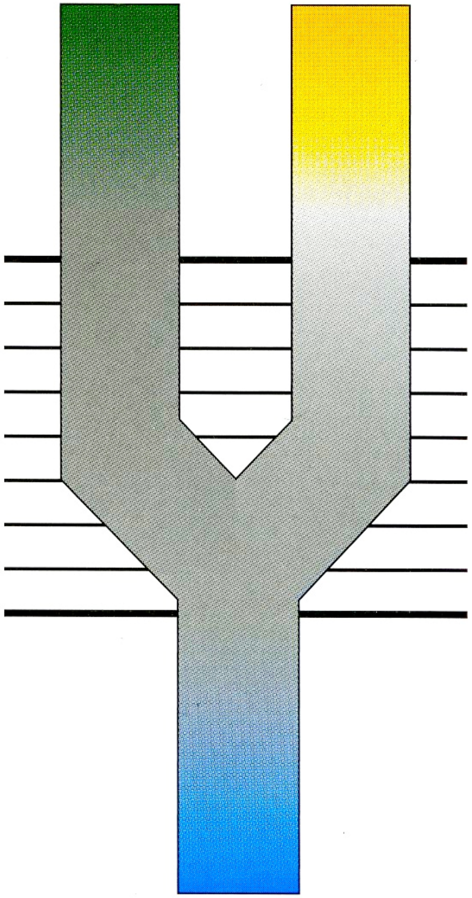
3) Mechanisms of Speciation

4) Geography of Speciation

Mechanisms that affect Speciation

What is Speciation?

Speciation: the splitting of a single ancestral species into two or more descendant species.



Mechanisms that affect Speciation

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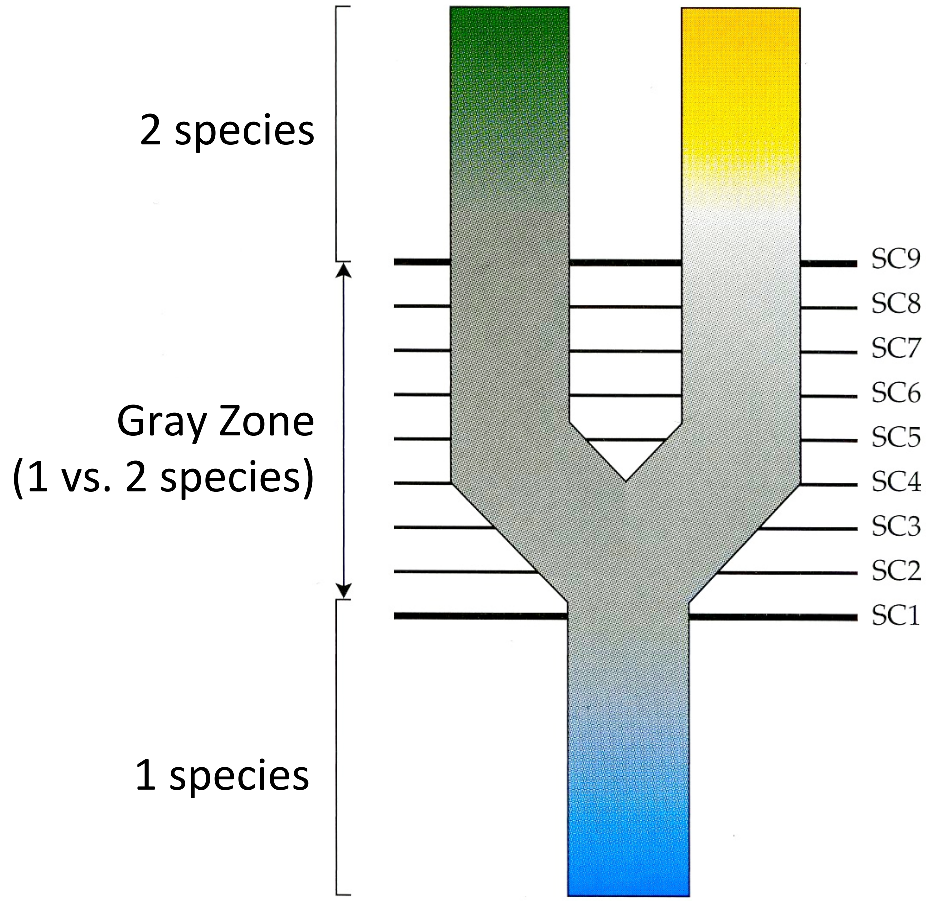


Different species concepts disagree on where 2 species should be recognized.

Morphological, mtDNA, multiple genes, reproductive isolation, ecological differentiation

Mechanisms that affect Speciation

We'll consider mechanisms that affect speciation as those that influence reproductive isolation.

Mechanisms of genetic differentiation:

- Mutation
- Genetic drift
- Natural selection
- Gene flow

And could also include:

- Physical isolation
- Sexual Selection
- Hybridization

Mechanisms that affect Speciation

The divergence of an ancestral species into two or more daughter species requires genetic changes among populations, ranging from those that are simply used to diagnose different species (e.g., under the PSC) to those that actually cause reproductive isolation between an ancestrally single reproductive community (e.g., under the BSC).

Mechanisms of genetic differentiation:

- Mutation
- Genetic drift
- Natural selection
- Gene flow

And could also include:

- Physical isolation
- Sexual Selection
- Hybridization

Lomolino *et al.* 2010

Mechanisms that affect Speciation

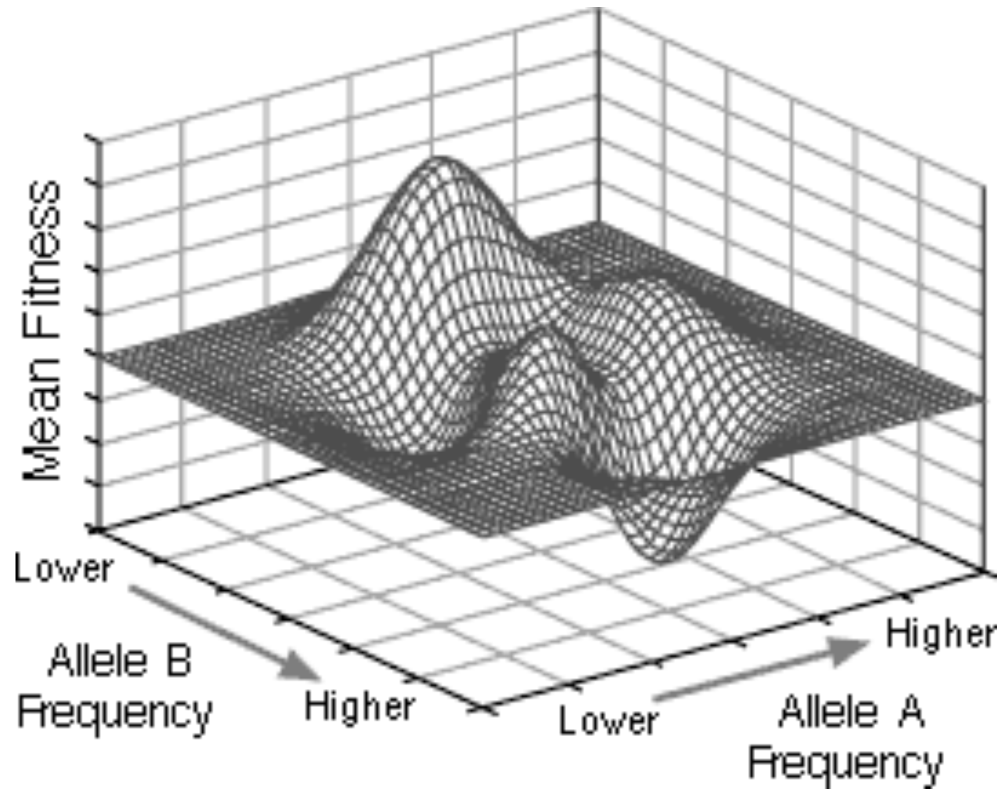
Selection vs. Drift in Speciation

(a very quick note)

Peak shift speciation

Natural selection pushes populations towards fitness peaks

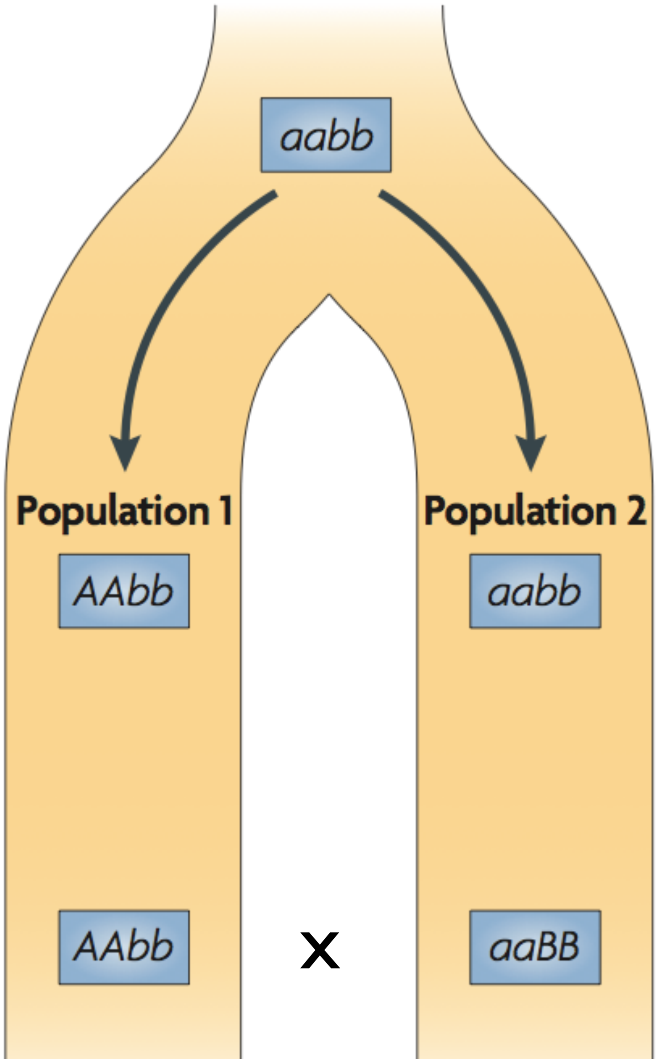
Peak shifts are more likely with genetic drift, where small population size allows populations (by chance) to cross "fitness valleys"



An adaptive landscape which shows fitness peaks for allele frequencies, separated by adaptive valleys

from Coyne & Orr 2004

Mechanisms that affect Speciation

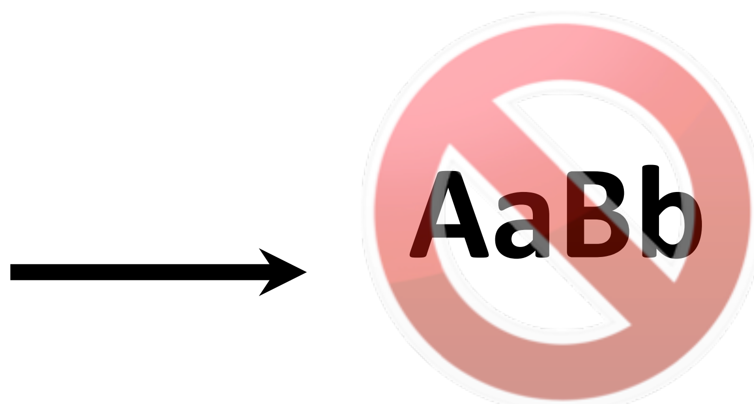


Presgraves 2010

"Dobzhansky-Muller Model"

As populations diverge, different alleles may become fixed in each by **natural selection** or (less likely) **genetic drift**

If those two populations meet again and interbreed, they could bring together alleles that are incompatible, and their offspring may have lower fitness.



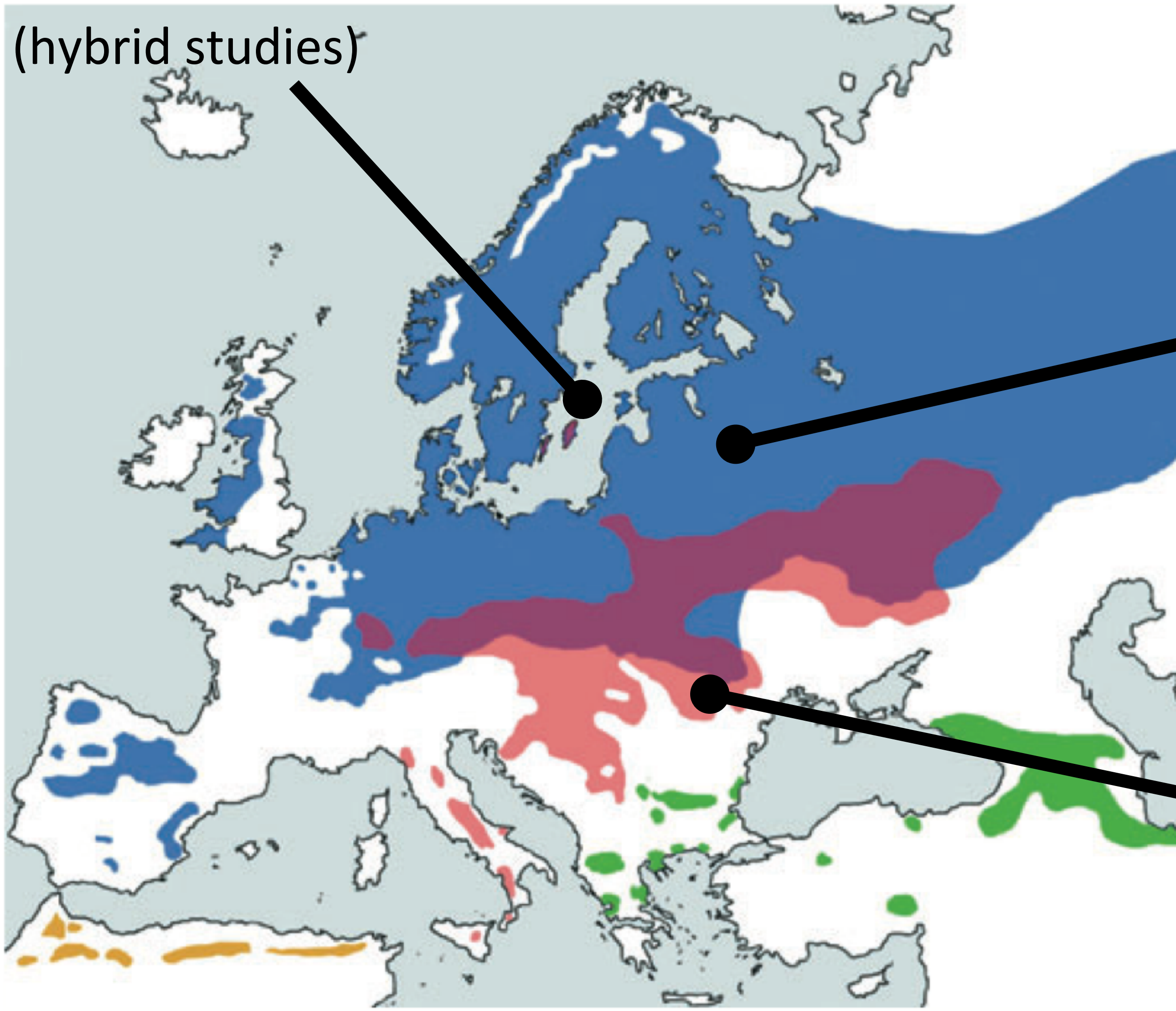
hybrids

Mechanisms that affect Speciation

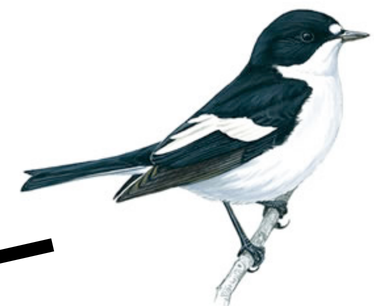
Islands of Gotland and **Öland**

(hybrid studies)

Hybridization and post-mating isolation



Sætre and Saether 2010



pied flycatcher

(*Ficedula hypoleuca*)

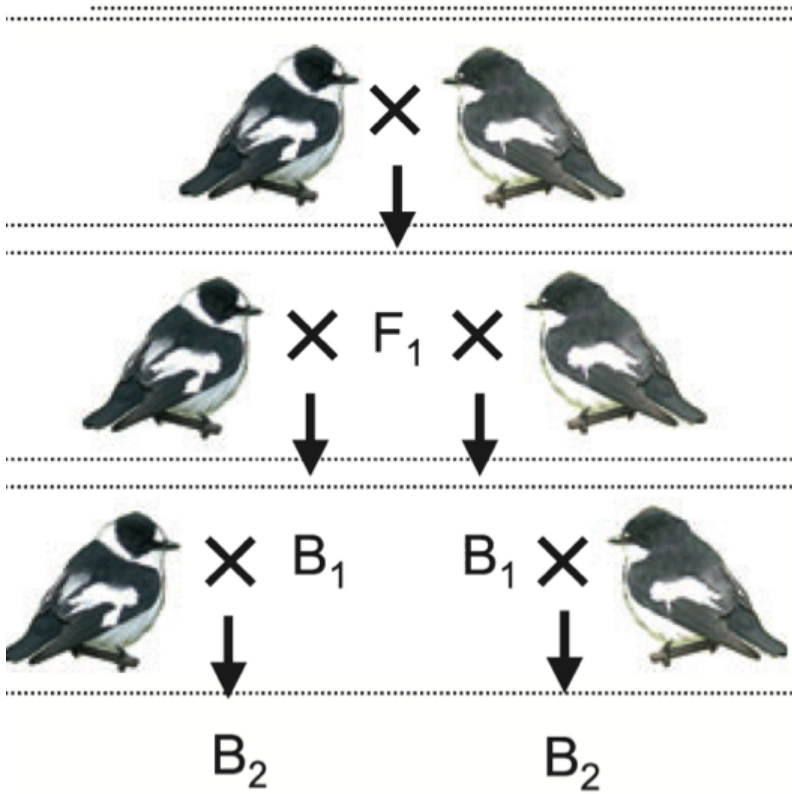
collared flycatcher

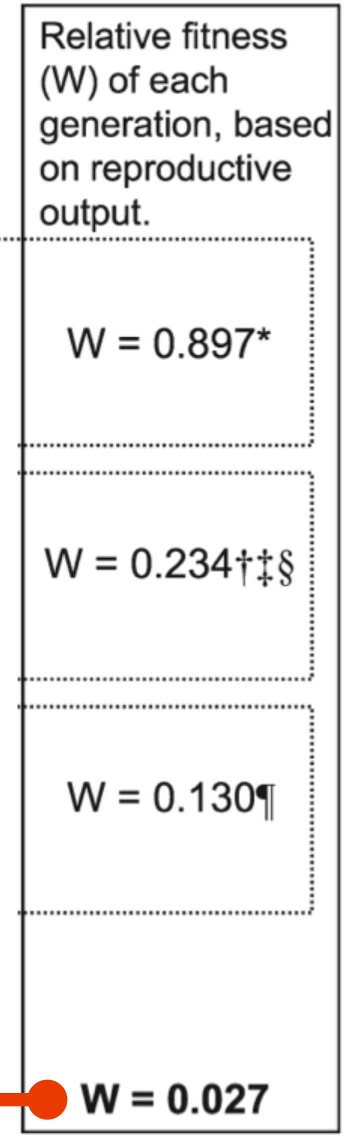
(*Ficedula albicollis*)

Mechanisms that affect Speciation

Reduction in hybrid fitness

further backcrosses





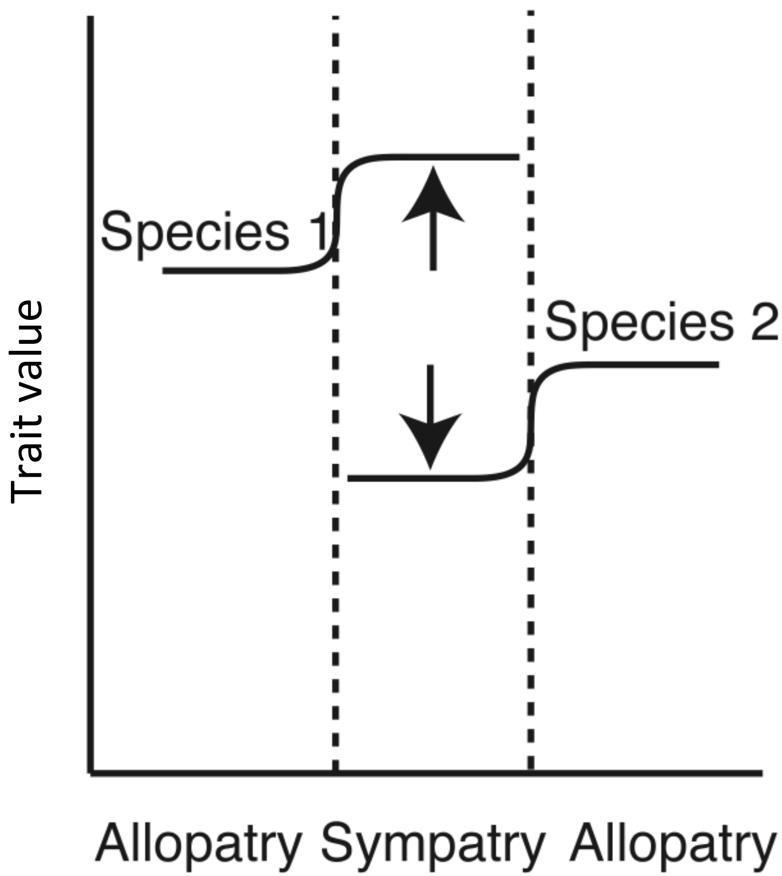
hybridizing individuals have **2.7%** fitness compared to non-hybridizing (fitness = # eggs surviving to hatch)

Sætre and Saether 2010

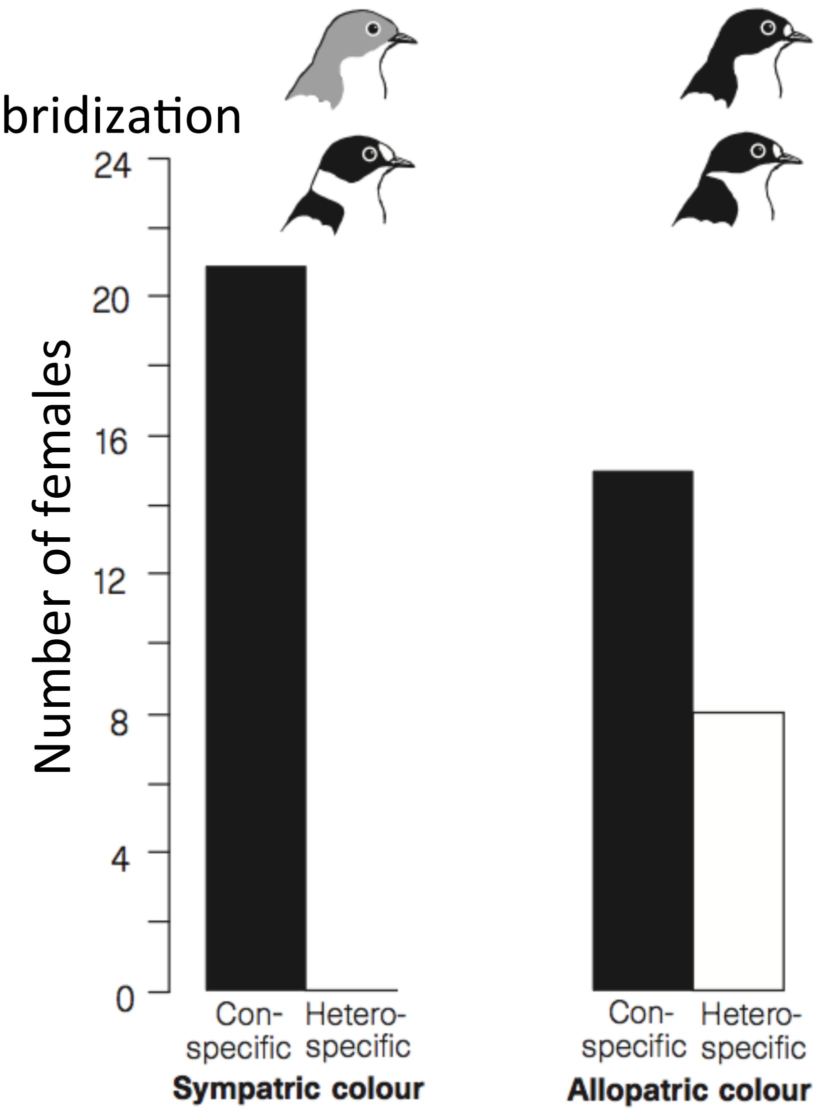
Mechanisms that affect Speciation

Reinforcement

natural selection against maladaptive hybridization



Kirschel et al. 2009



Sætre et al. 1997

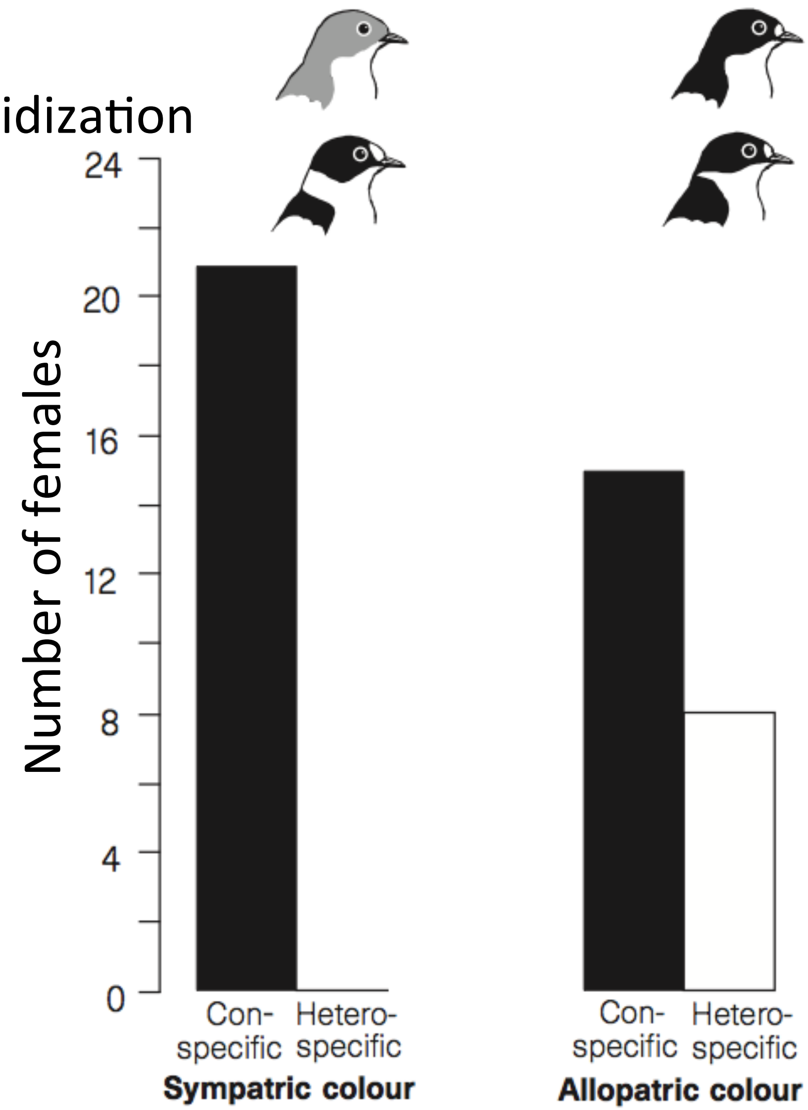
Mechanisms that affect Speciation

Reinforcement
natural selection against maladaptive hybridization

Male pied and collared flycatchers from allopatric populations have similar black & white plumage

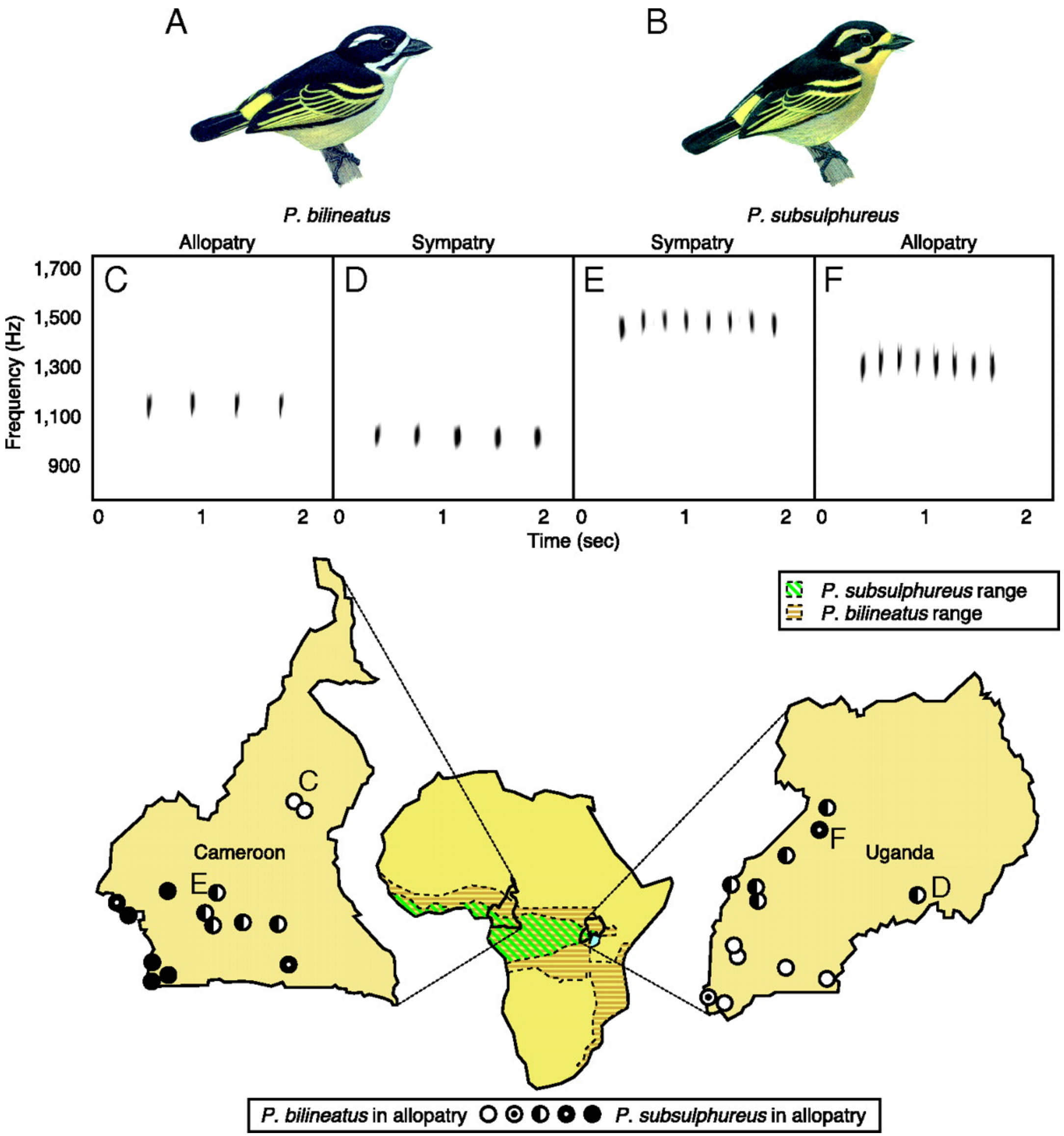
Where ranges of the species overlap, male pied flycatchers are dull brown (collared's have a larger white patch)

Plumage differences in sympatric males reduce hybridization…Females never make a mistake for the other species when males have the sympatric plumage pattern



Sætre et al. 1997

Mechanisms that affect Speciation

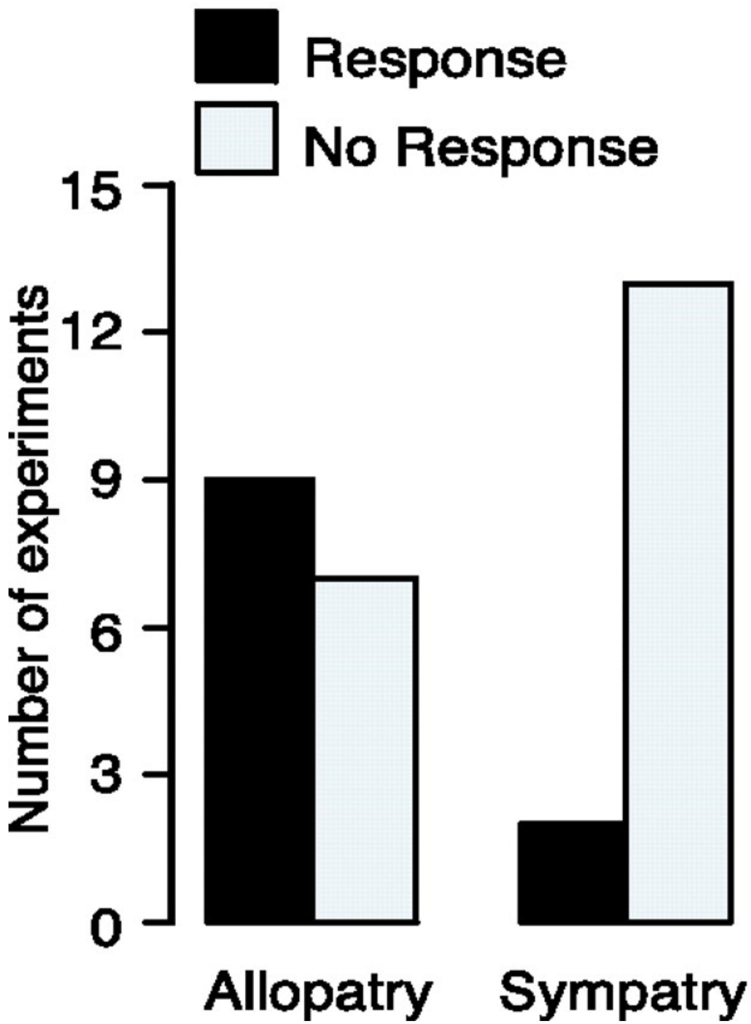


African Tinkerbirds:

Songs in sympatric populations differ more compared to songs in allopatric populations

Kirschel et al. 2009

Mechanisms that affect Speciation



Allopatric tinkerbirds respond significantly more than sympatric tinkerbirds to heterospecific playback.

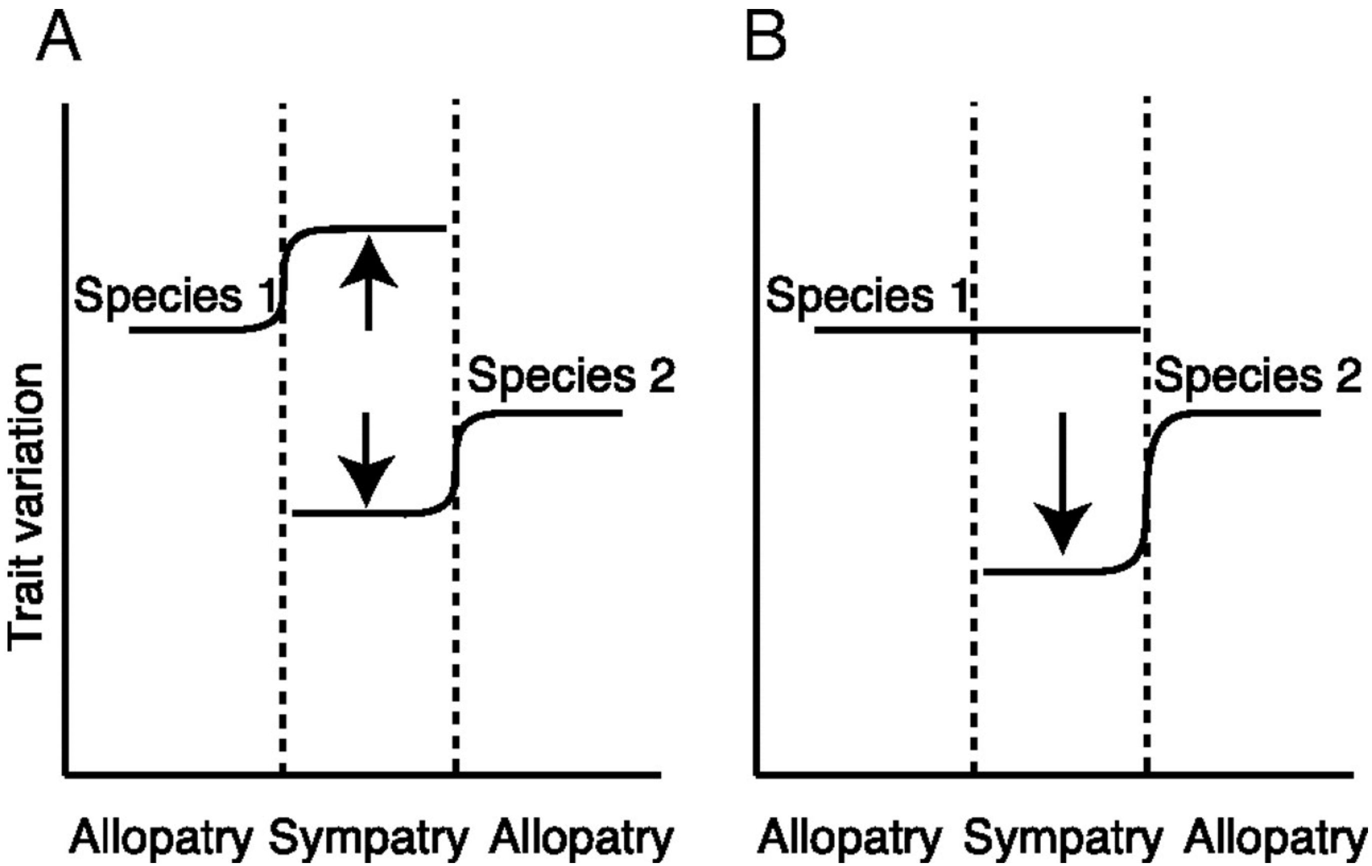
Songs become more distinct in sympatric populations, which enables species recognition.

Kirschel et al. 2009

Mechanisms that affect Speciation

Character displacement can be symmetric or asymmetric in sympatry

When species 1 is common, but species 2 is rare, species 1 is not influenced by the rare presence of species 2 in sympatry



Kirschel et al. 2009

Geography of Speciation

Models of speciation have traditionally been organized based on geography

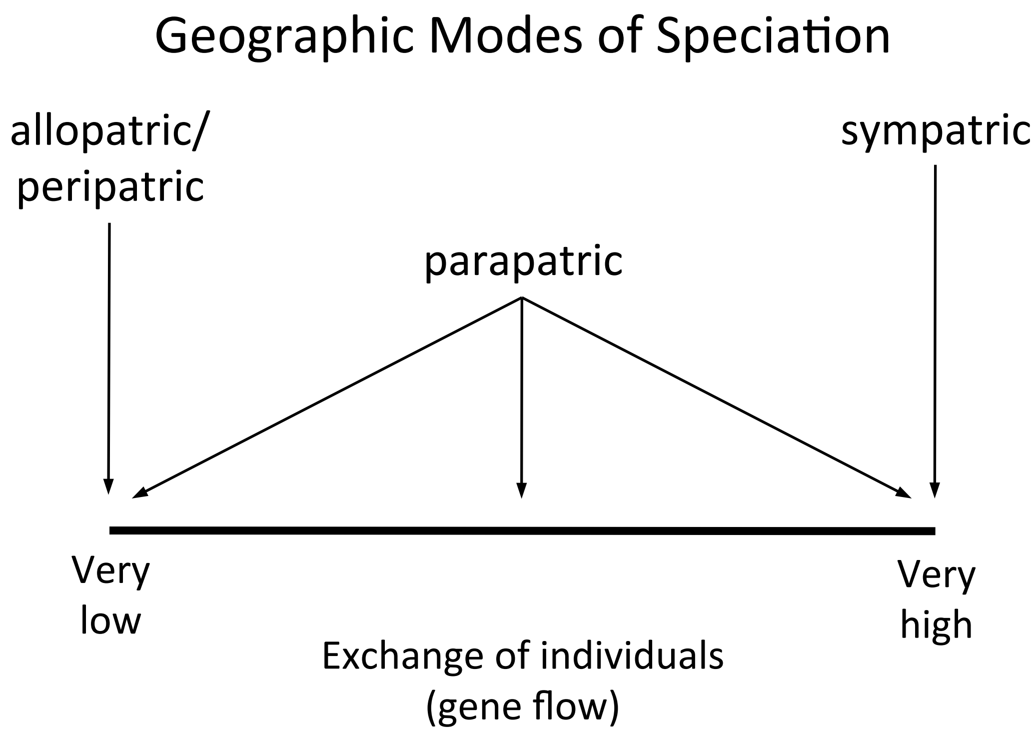
- Allopatric speciation
  - Vicariant speciation
  - Peripatric speciation
- Parapatric speciation
- Sympatric speciation

The geography of speciation has been hotly debated:

Does speciation require complete geographic isolation, or can it occur in populations that exchange genes to a limited extent (parapatric) or freely (sympatric)?

Geography of Speciation

Major modes of geographic speciation can be viewed along a continuum of gene flow

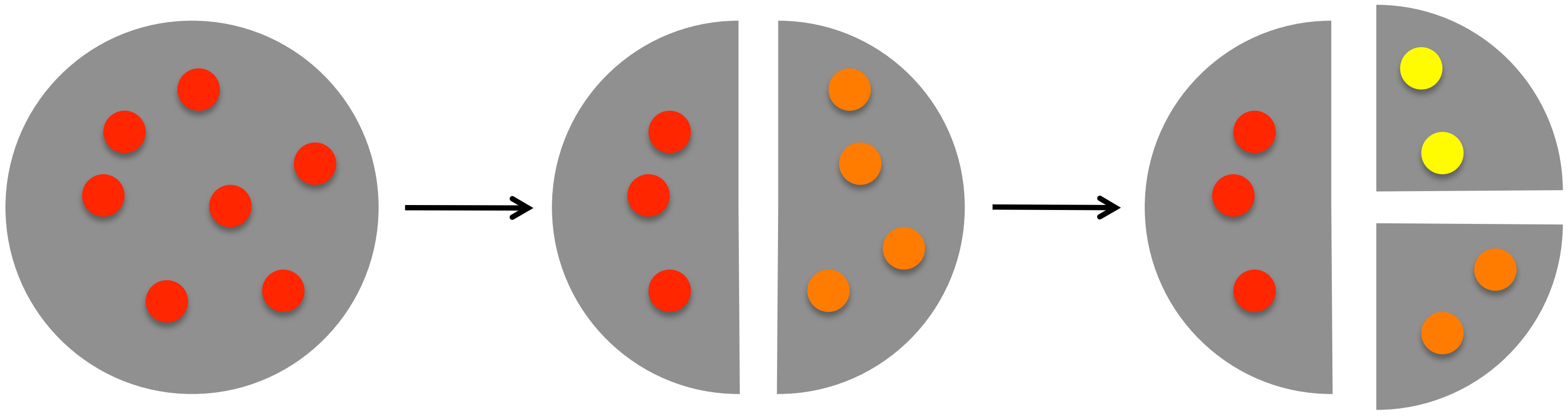


Geography of Speciation

1. Allopatric Speciation – Vicariant speciation

The evolution of reproductive isolation during geographic isolation

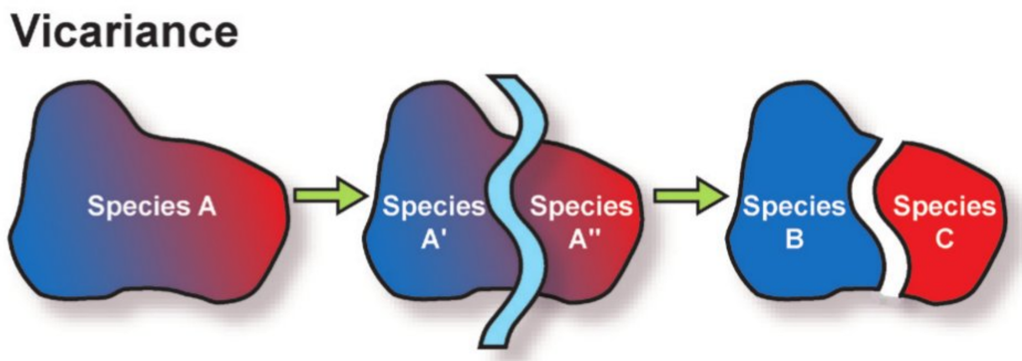
Has long been recognized as a principle mechanism of speciation, but championed by Ernst Mayr (e.g., Mayr 1963).



Geography of Speciation

1. Allopatric Speciation – Vicariant speciation

Vicariance: establishment of a barrier separating populations that were already present



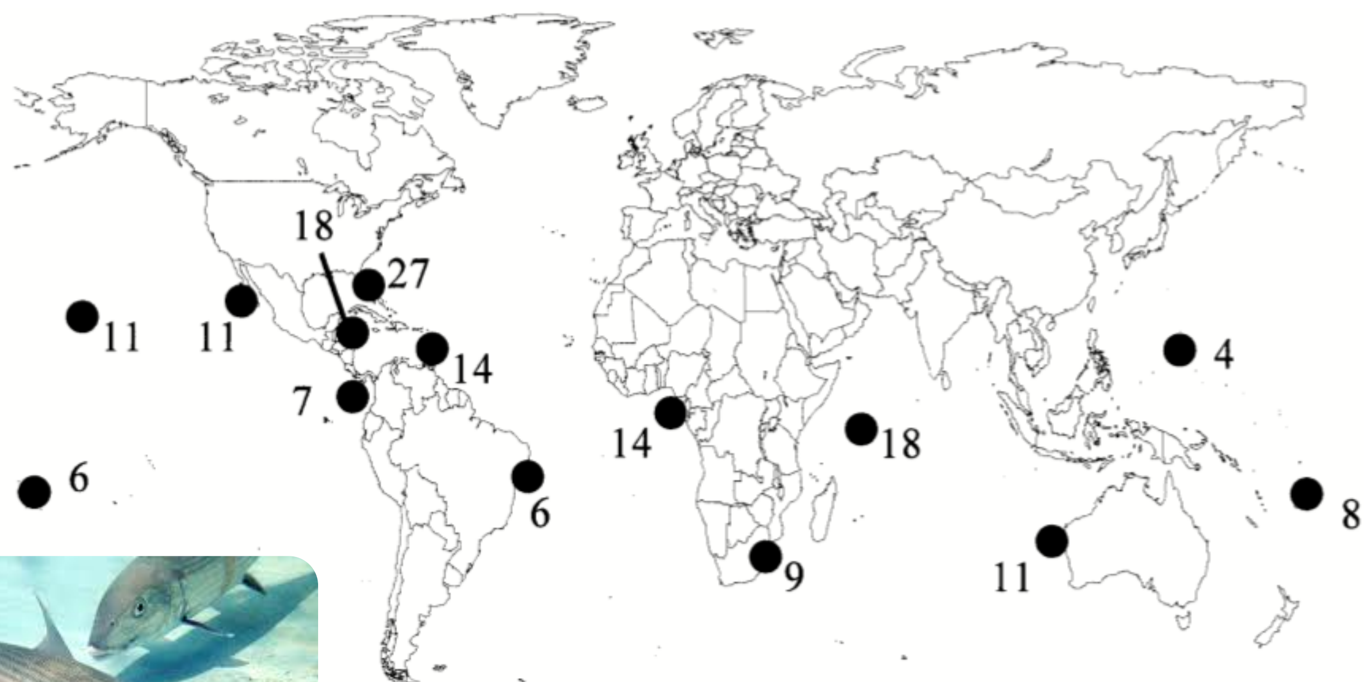
Geographic separation of populations can occur through climatic or geological events (e.g., elevation of land bridges, glaciation, formation of mountains, continental drift)

Geography of Speciation

1. Allopatric Speciation

Biogeographic observations:

1) Allopatry of sister species



Bonefishes occur in tropical sandflats across the globe

Once classified as a single pantropical species, based on conserved morphological/ecological traits

Geography of Speciation

1. Allopatric Speciation

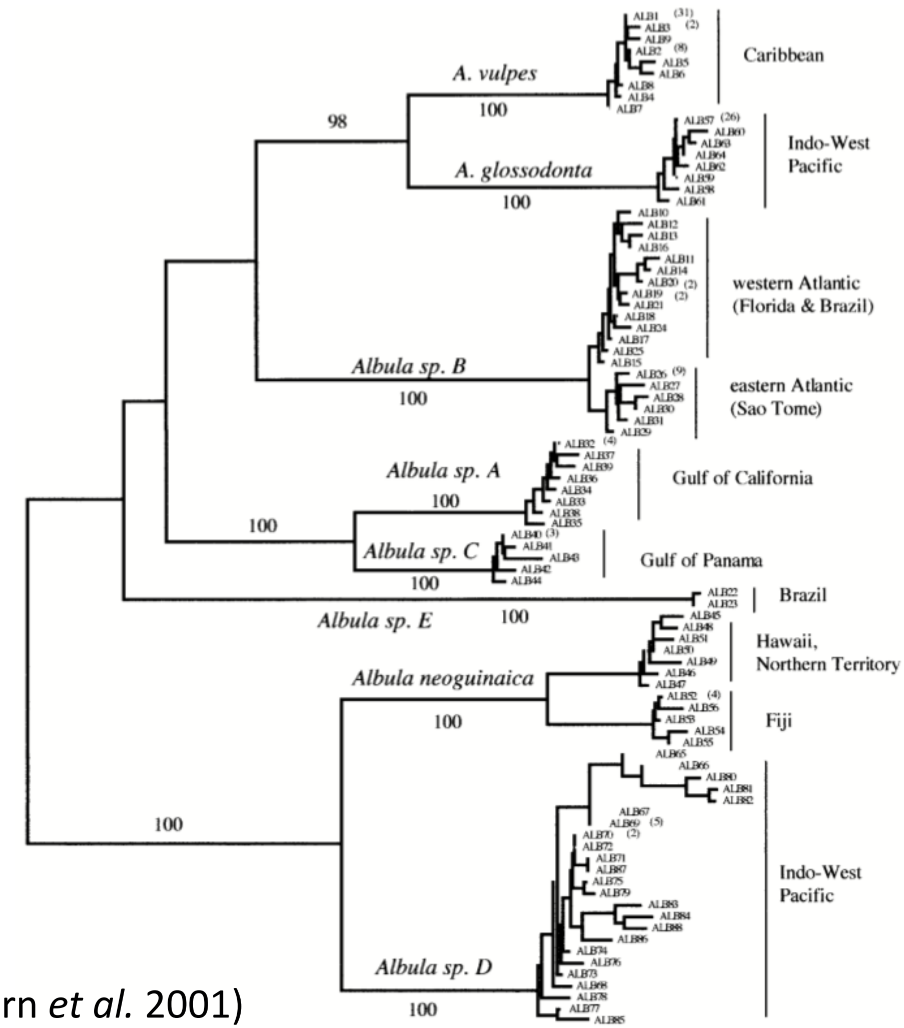
Biogeographic observations:

1) Allopatry of sister species

Sister species and clades are allopatric

Most divisions attributed to geological and oceanographic boundaries (e.g., mid-Atlantic expanse, Sunda Shelf)

Phylogeny of Albula mtDNA haplotypes



(Colborn *et al.* 2001)

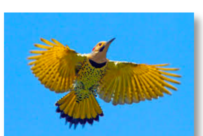
Geography of Speciation

1. Allopatric Speciation

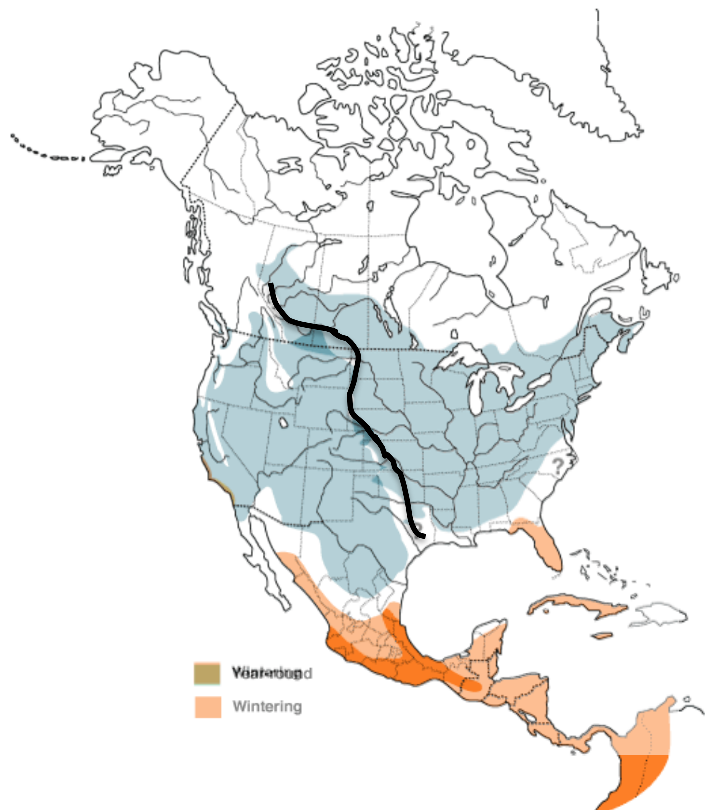
Biogeographic observations:

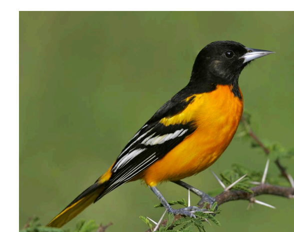
2) Geographic concordance of species range boundaries (and hybrid zones)

red-shafted flicker (west)
yellow-shafted flicker (east)



Bullock's oriole (west)
Baltimore oriole (east)

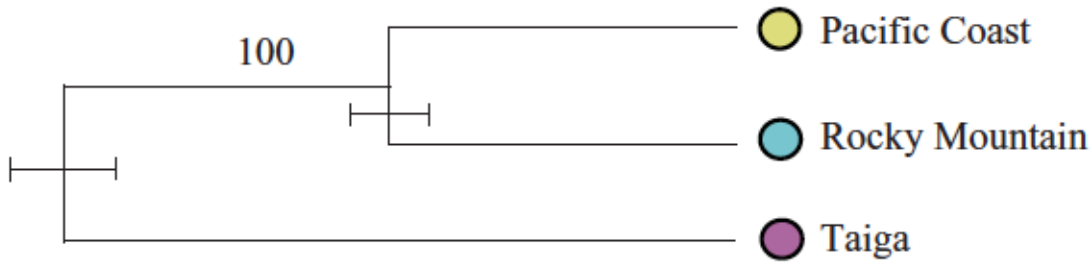


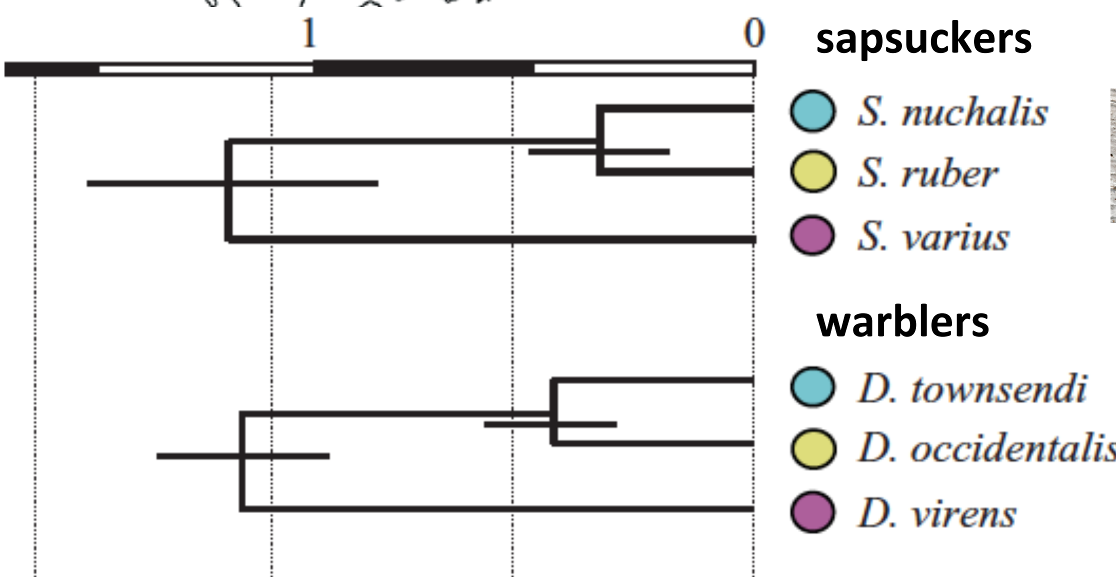


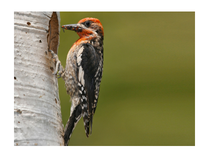
Geography of Speciation

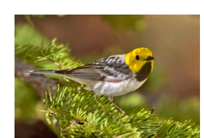
1. Allopatric Speciation

At least ten "superspecies" show this pattern in birds, likely due to isolation of populations during glacial advance and divergence in allopatry









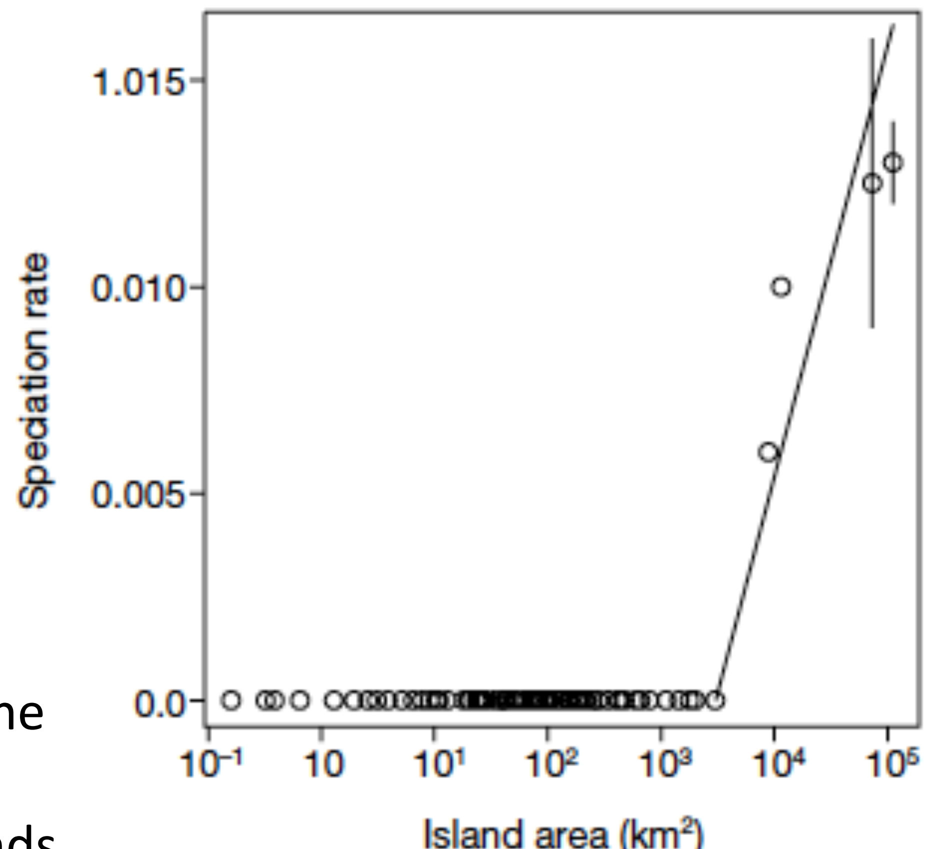
Geography of Speciation

1. Allopatric Speciation

Biogeographic observations:

3) The absence of sister species where isolation is unlikely

No sister lizard species on the smallest islands (< 3000 km^2) in the Caribbean although intra-island speciation occurred on large islands



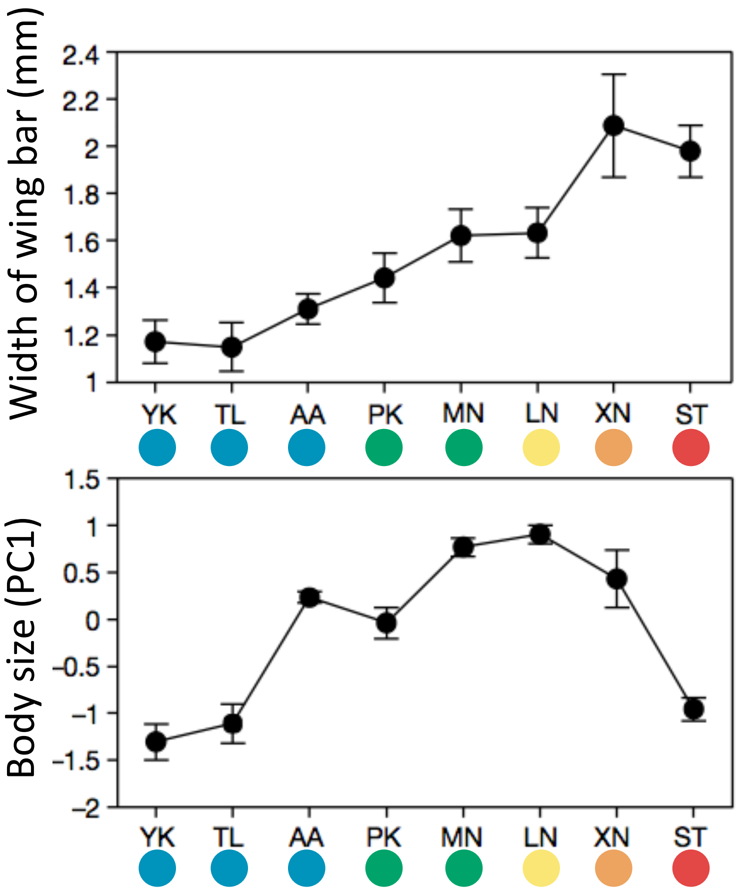
(Losos & Schluter 2000)

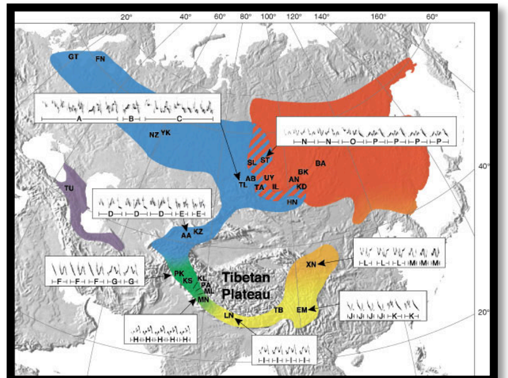
Geography of Speciation

1. Allopatric Speciation

Biogeographic observations:

4) Increased reproductive isolation with increased geographic distance





Siberian populations of greenish warbler (YK and ST) are among the most divergent in plumage (i.e., wing bar width) and genetics, not shown, but similar in body size

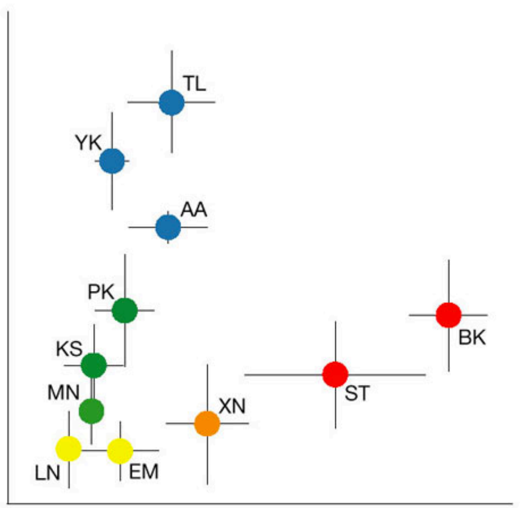
(Irwin *et al.* 2001)

Geography of Speciation

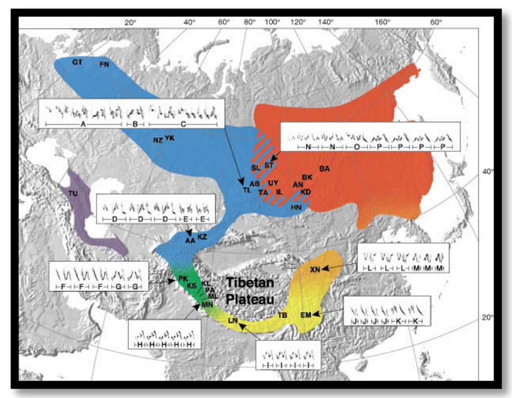
1. Allopatric Speciation

Biogeographic observations:

4) Increased reproductive isolation with increased geographic distance



PC1 - Increasing length of song, number of units and types

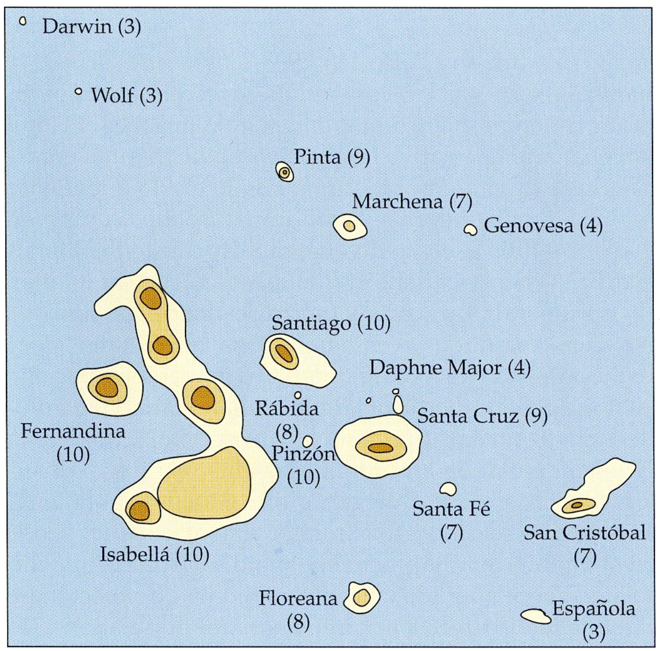


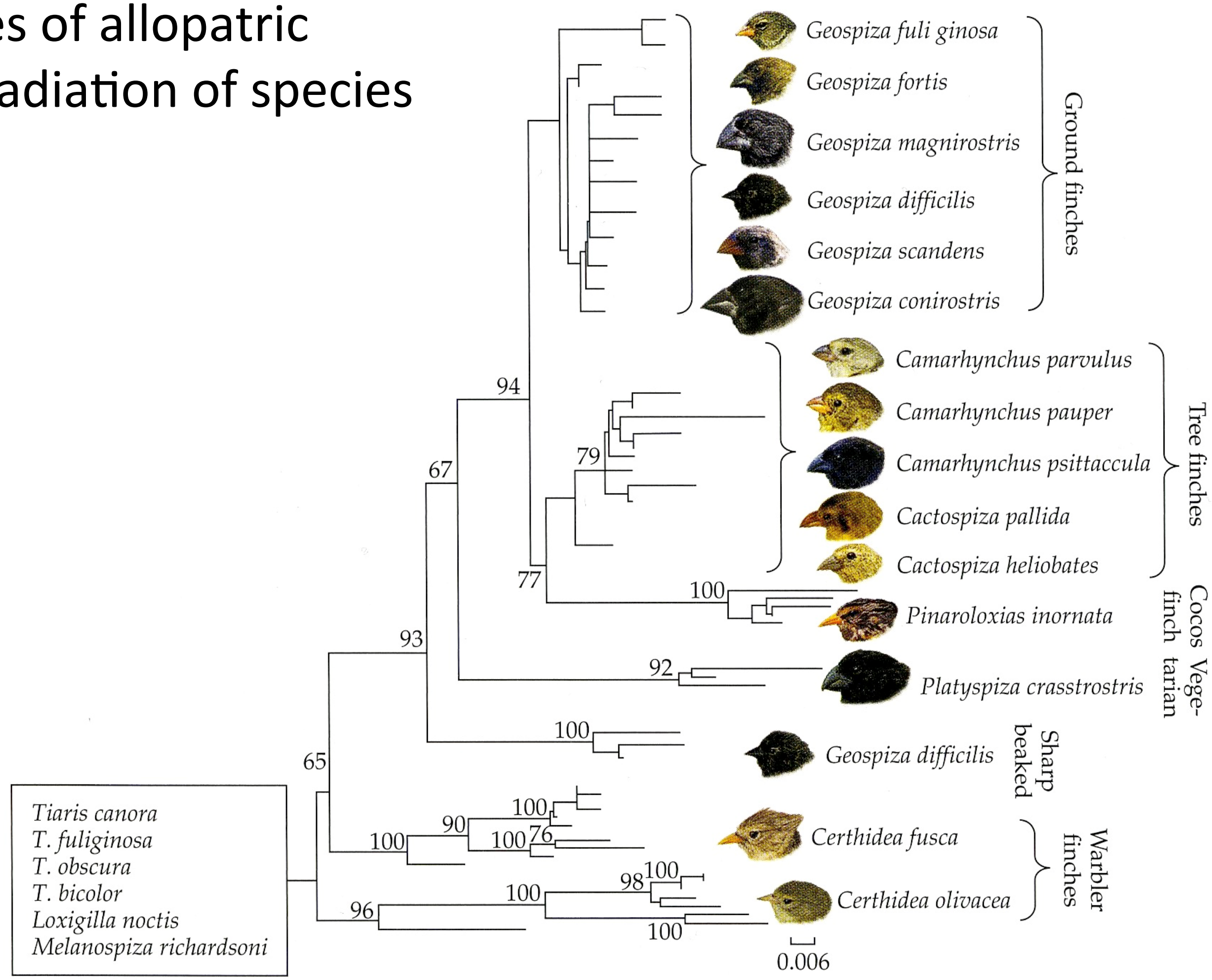
Siberian populations of greenish warbler (TL and BK) are among the most divergent in songs (more complex), Himalayan populations have similar songs (simplest)

(Irwin *et al.* 2001)

Geography of Speciation

Some of the best examples of allopatric speciation are shown by radiation of species on island archipelagos…

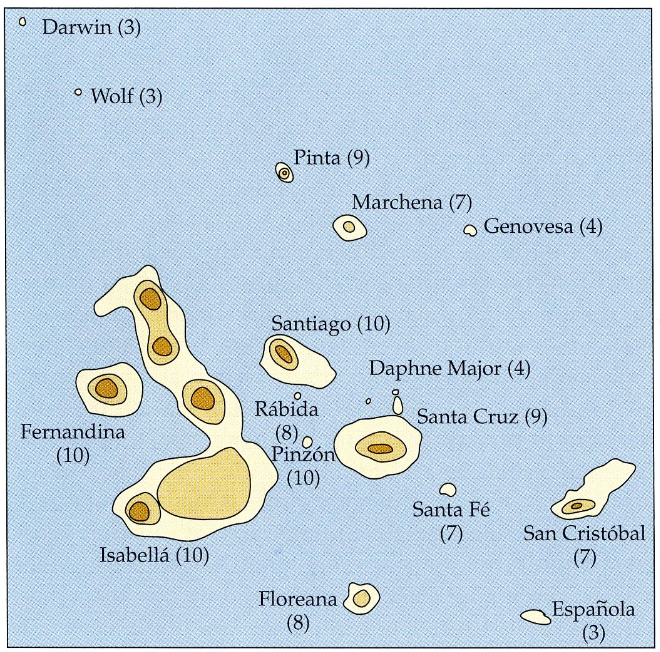


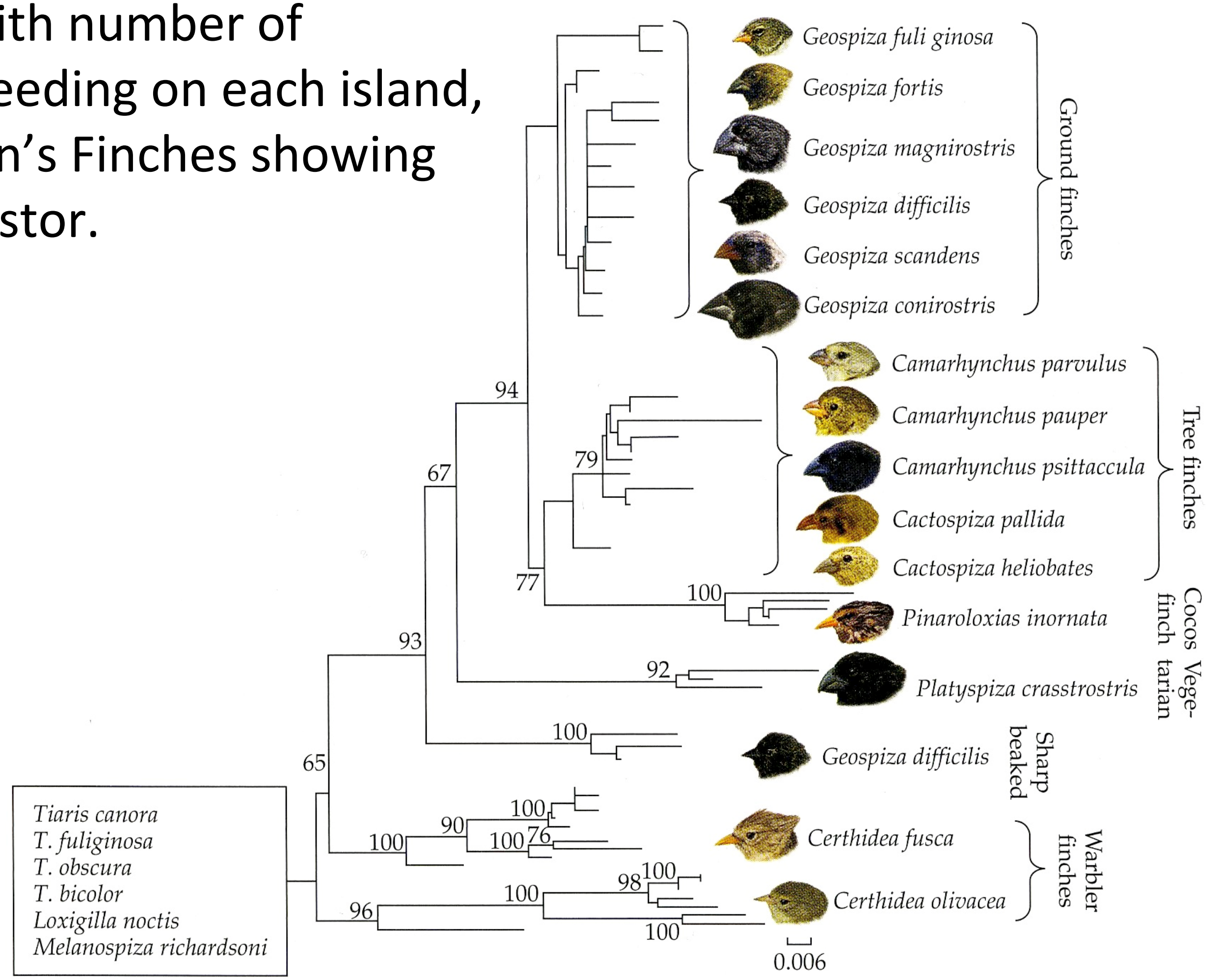


(Lomolino *et al.* 2010)

Geography of Speciation

Galapagos archipelago, with number of Darwin's Finch species breeding on each island, and a phylogeny of Darwin's Finches showing relation to mainland ancestor.



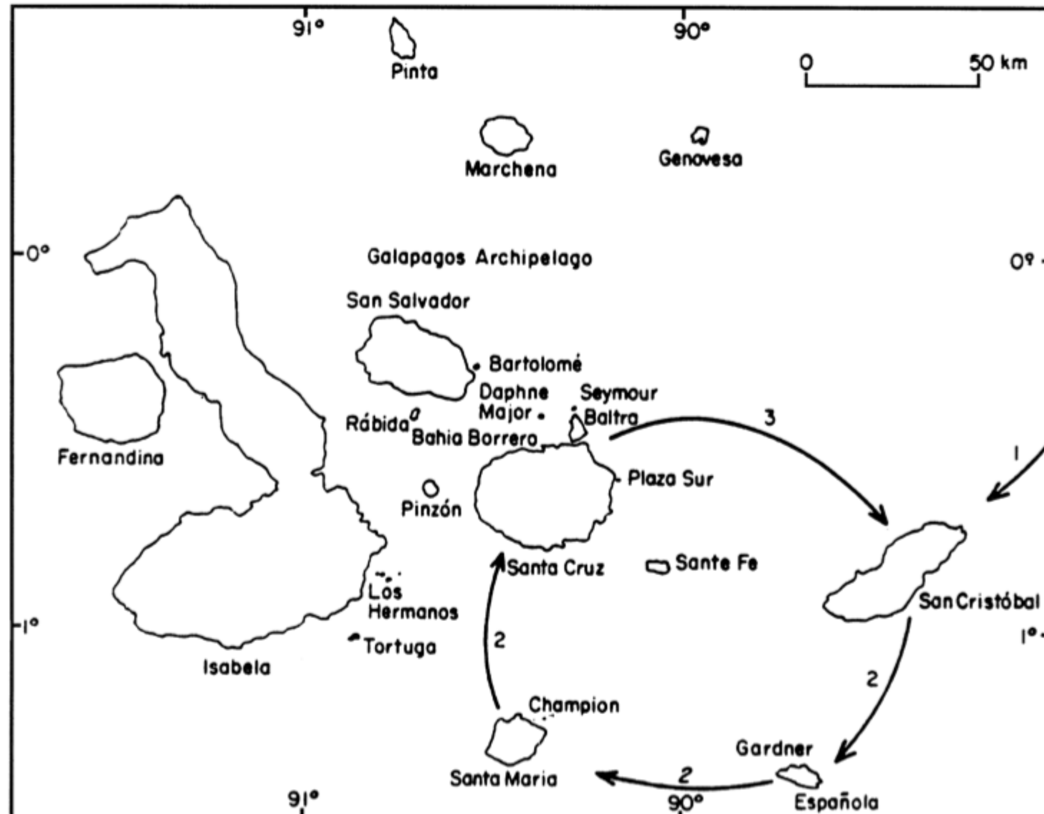


(Lomolino *et al.* 2010)

Geography of Speciation

Speciation cycle in Darwin's Finches comprises three steps:

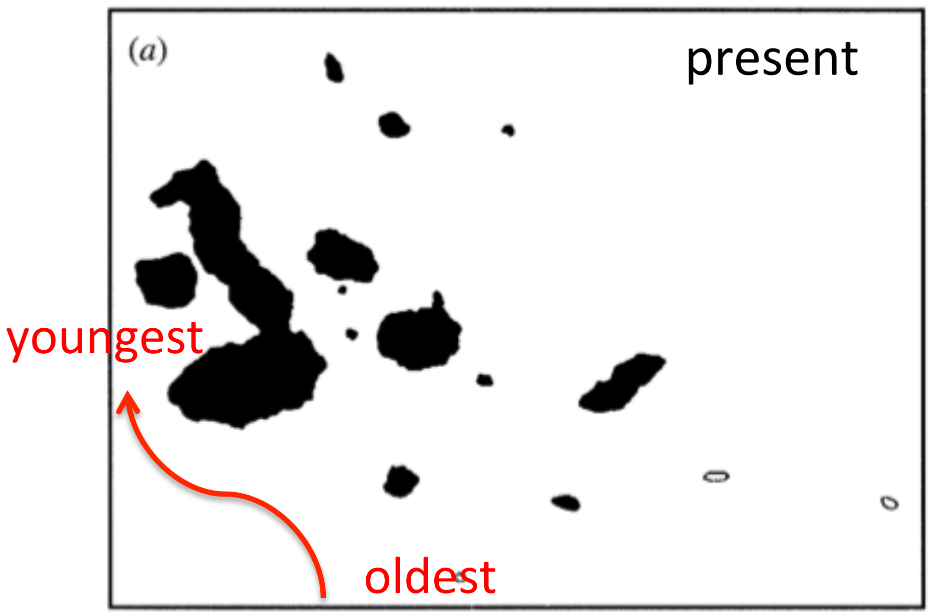
1) Colonization of the archipelago
2) Establishment of allopatric populations
3) Establishment of sympatry



(Grant *et al.* 1996)

Geography of Speciation

Geological history of the Galapagos archipelago over the last 3 Ma, since the time they were colonized by ancestral Darwin's Finches



The Galapagos islands are located on the northern part of the Nazca plate, which is slowly drifting over a volcanic hotspot towards the southeast (at 5cm/yr)

As the plate moves, the hotspot remains stationary, so islands are formed and slowly drift away, allowing the creation of new islands.

(Grant *et al.* 1996)

Geography of Speciation

Geological history of the Galapagos archipelago over the last 3 Ma, since the time they were colonized by ancestral Darwin's Finches

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Geography of Speciation

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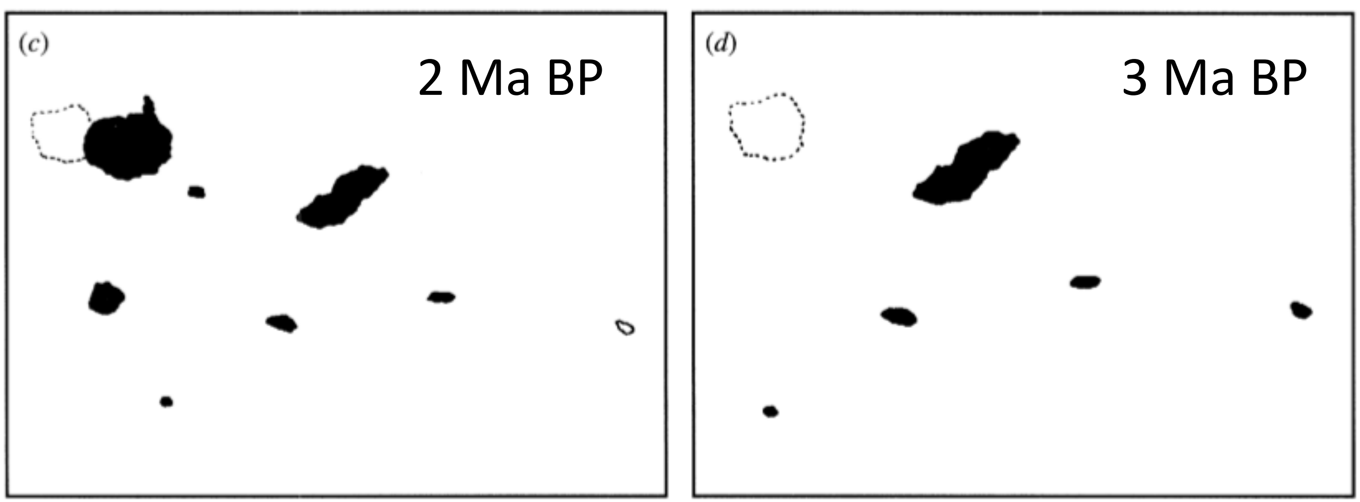

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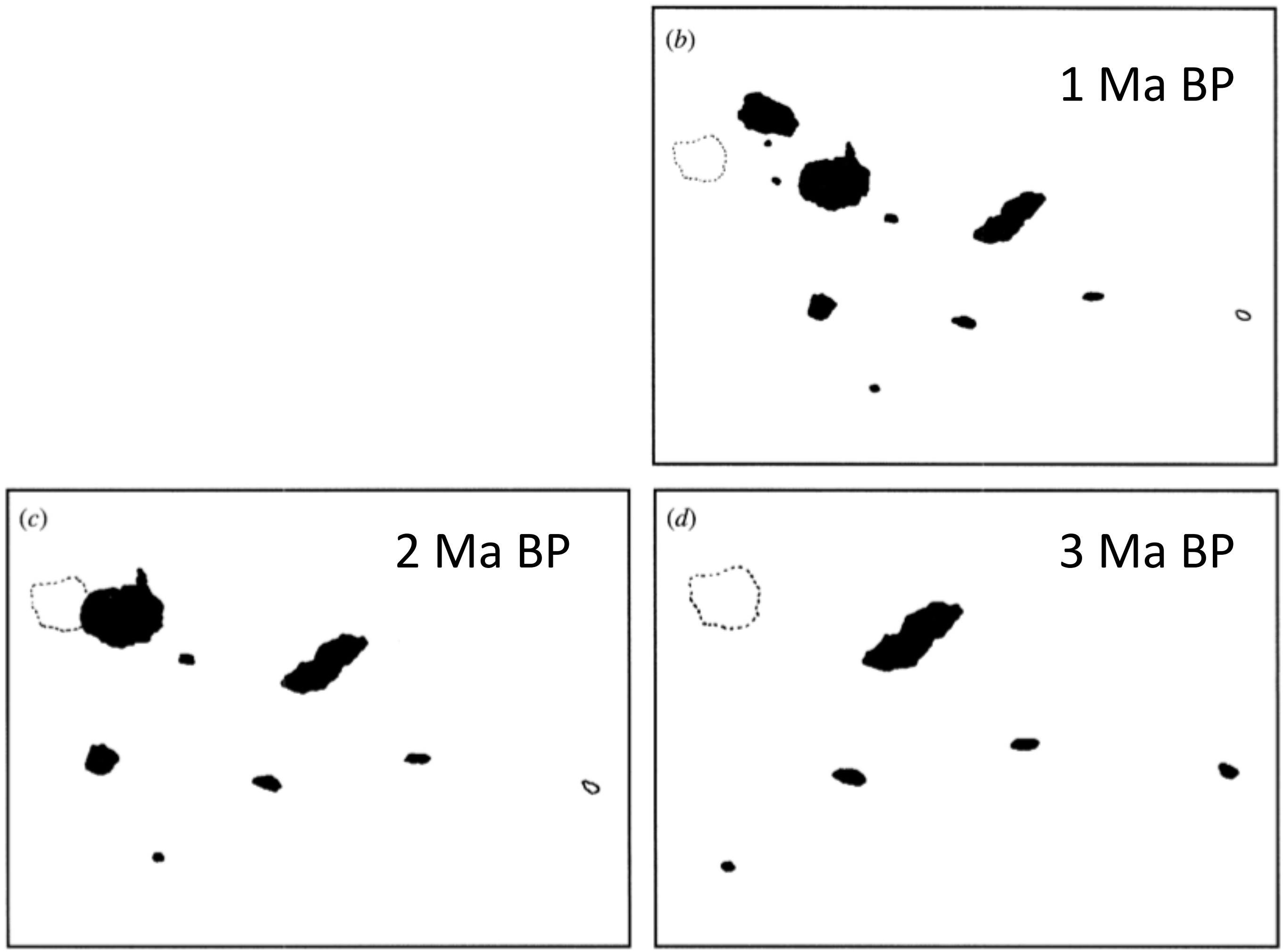

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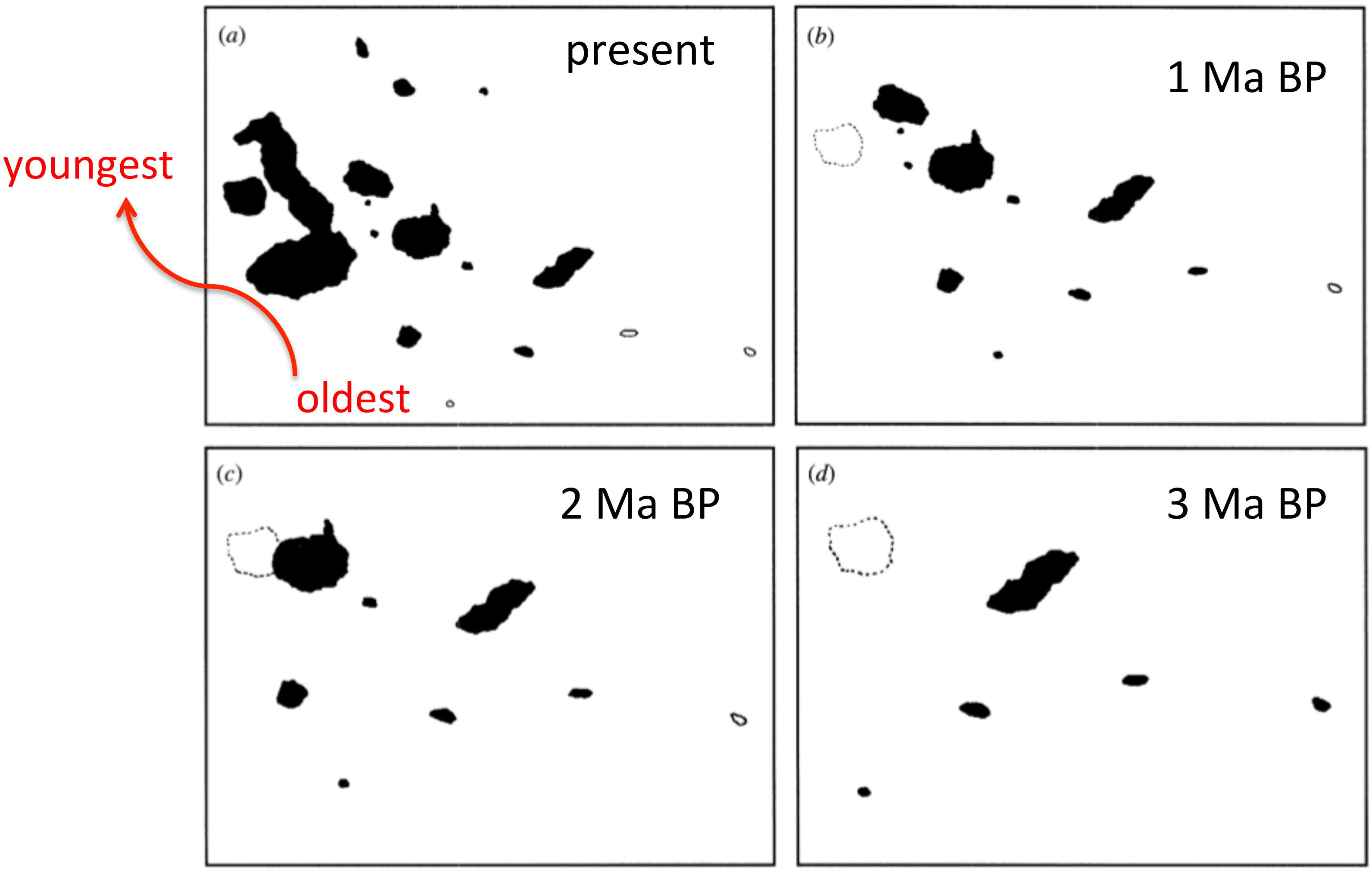
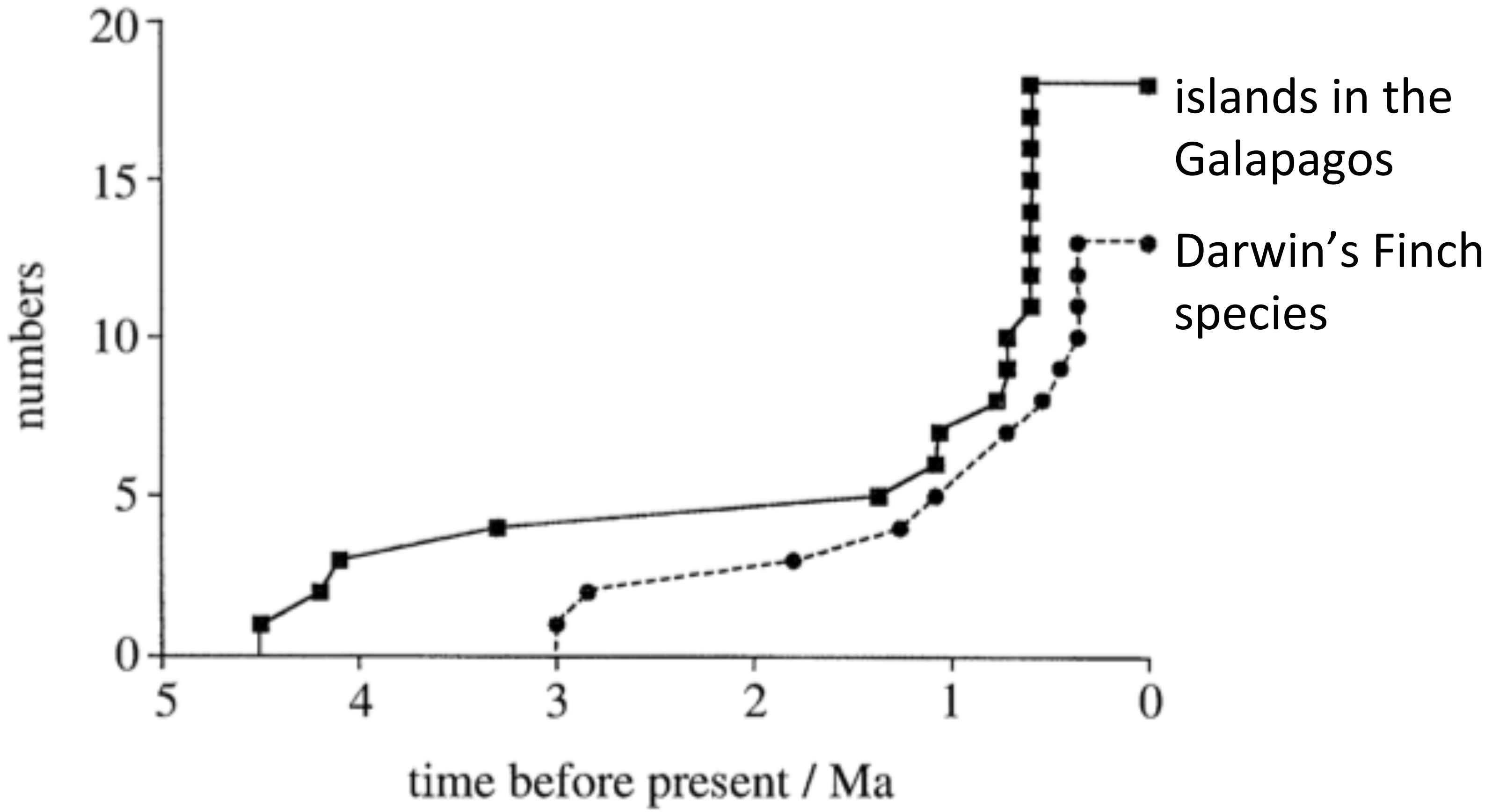


(Grant *et al.* 1996)

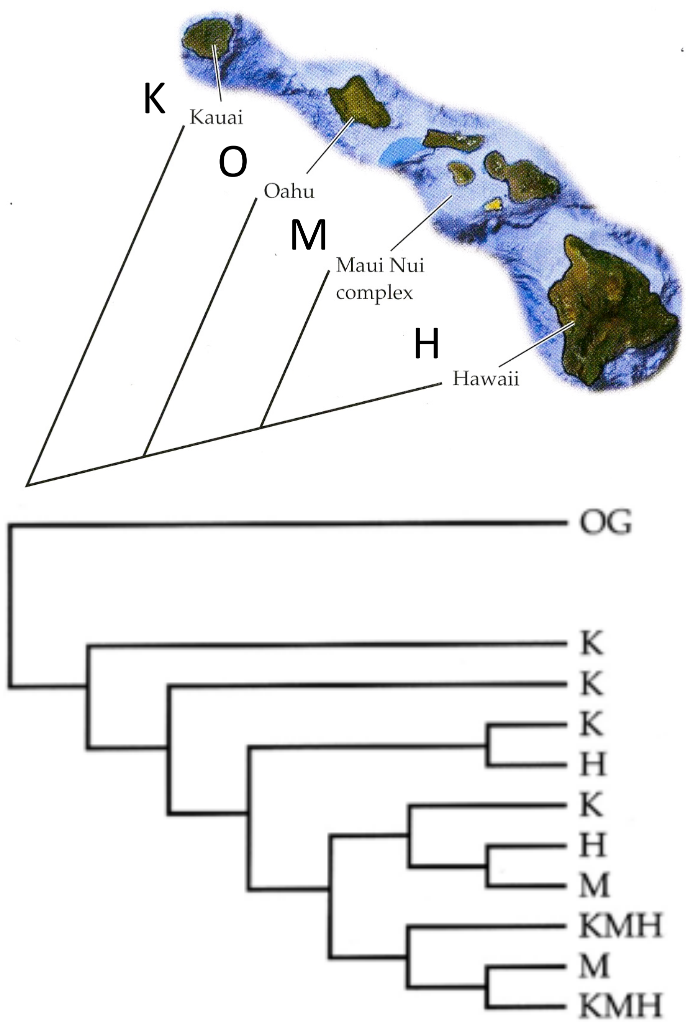
Geography of Speciation

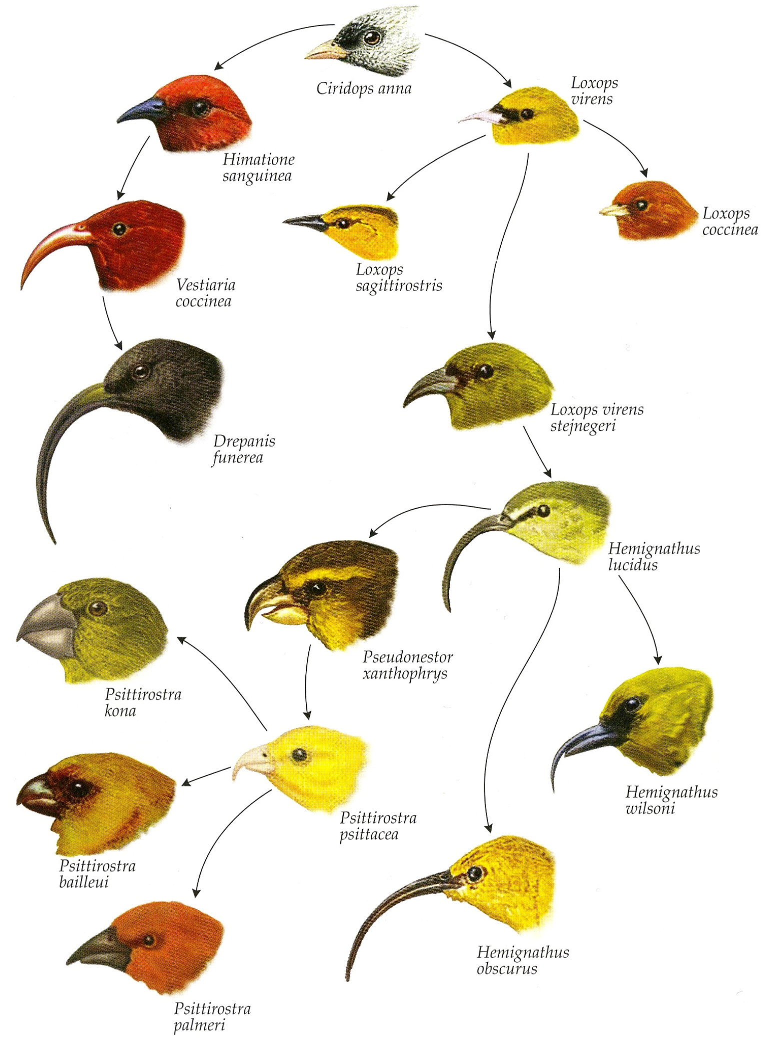
Accumulation of Darwin's Finch species in relation to the increase in number of Galapagos islands



Geography of Speciation

Honeycreepers on the Hawaiian archipelago



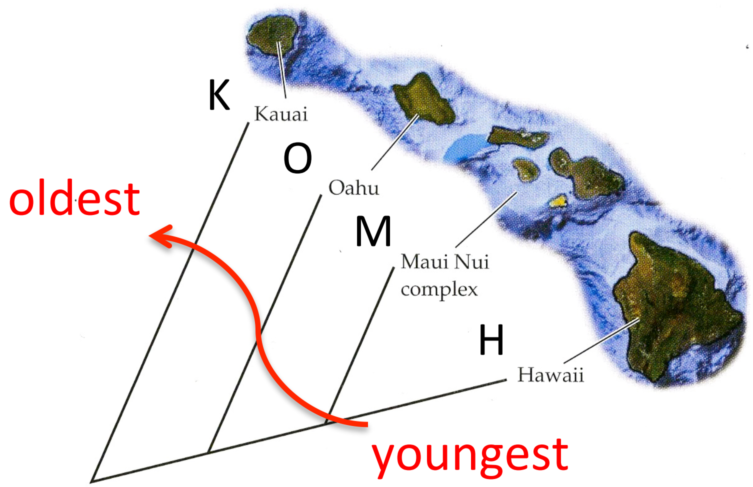


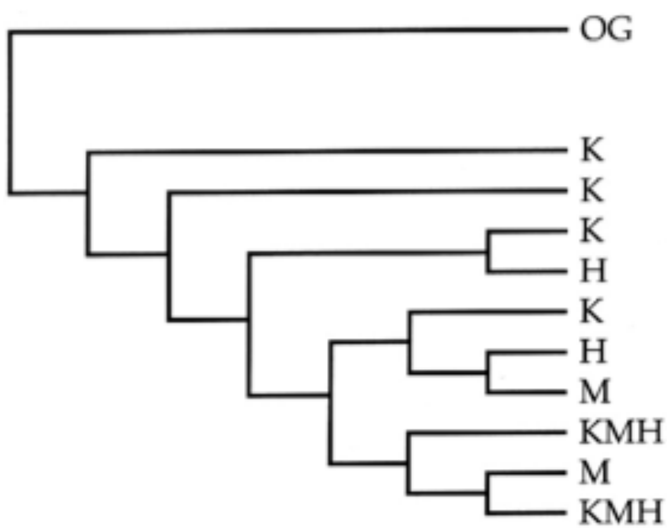
OG = Out Group

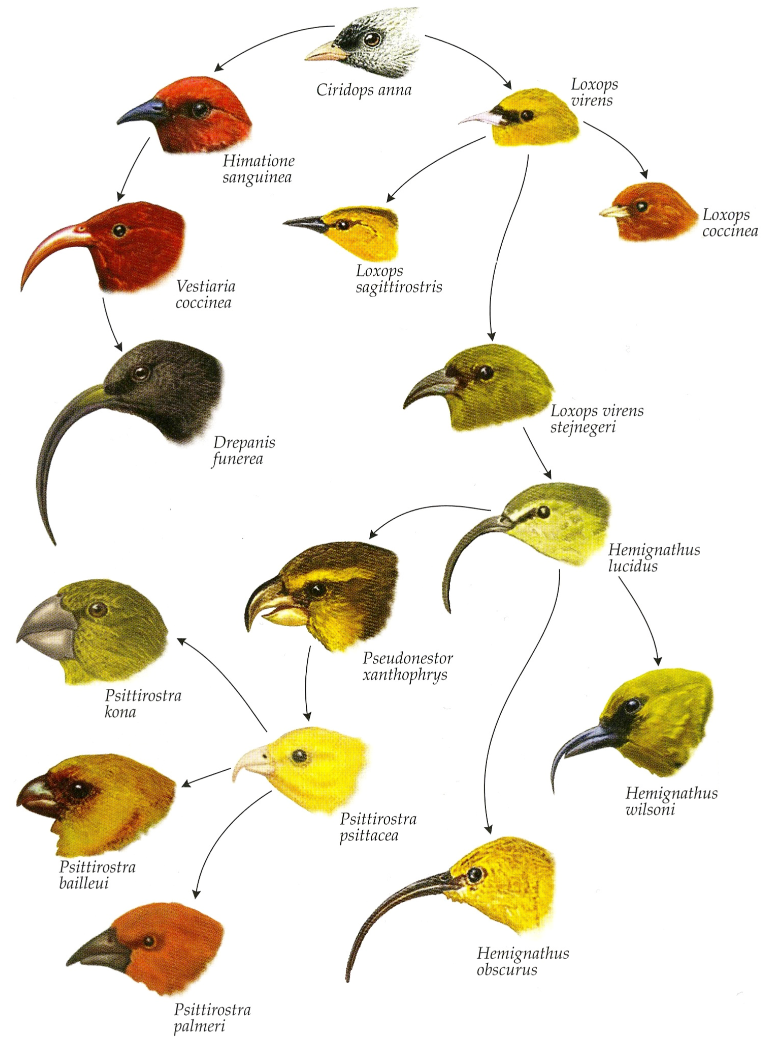
(Lomolino *et al.* 2010)

Geography of Speciation

For Darwin's finches and Hawaiian honeycreepers, ecological differentiation to exploit different niches (i.e., food resources) led to radiation







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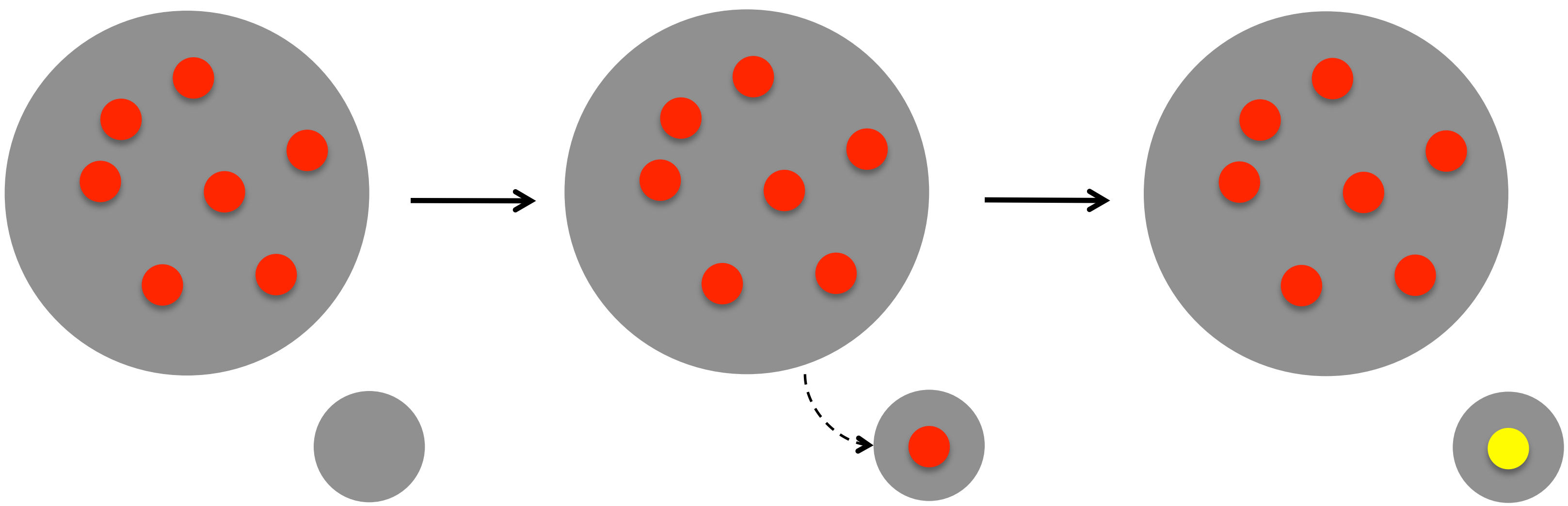
Geography of Speciation

2. **Peripatric Speciation** – a special kind of allopatric speciation, usually due to "founder effect" and high genetic drift



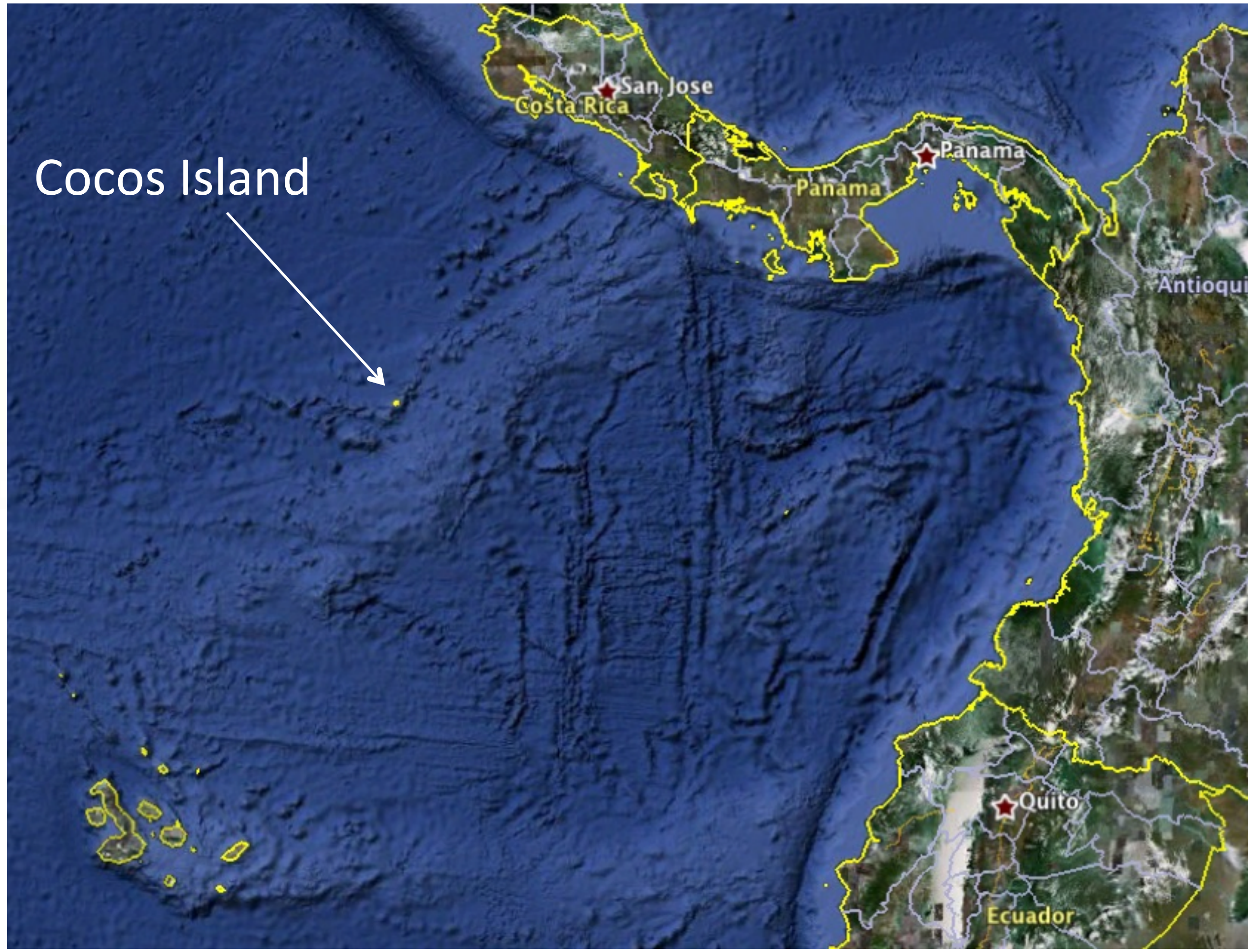
…one difference between vicariant and peripatric speciation is that in the latter case, one population is very small and involves invasion of novel habitats that exert strong selection and/or high genetic drift

Geography of Speciation

2. Peripatric Speciation

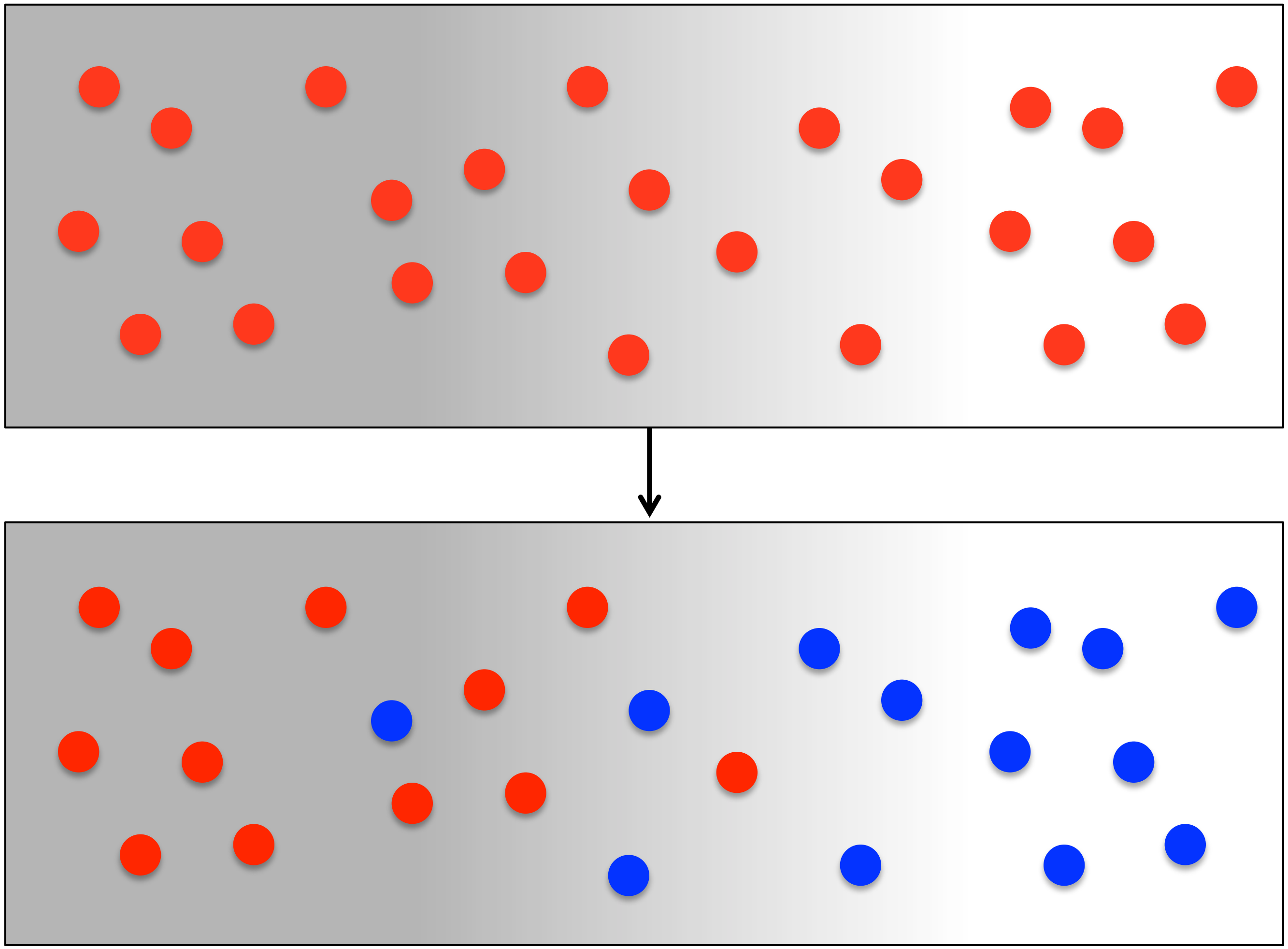
Cocos Finch
(*Pinaroloxias inornata*)

Most closely related to clade of tree finches in Galapagos – a peripheral isolate related to Galapagos Darwin's finches



Geography of Speciation

3. Parapatric Speciation – variable populations diverge along selective gradient



…in parapatric speciation, selection on opposite ends of a gradient must favor strong differentiation in the face of gene flow where ranges remain in contact

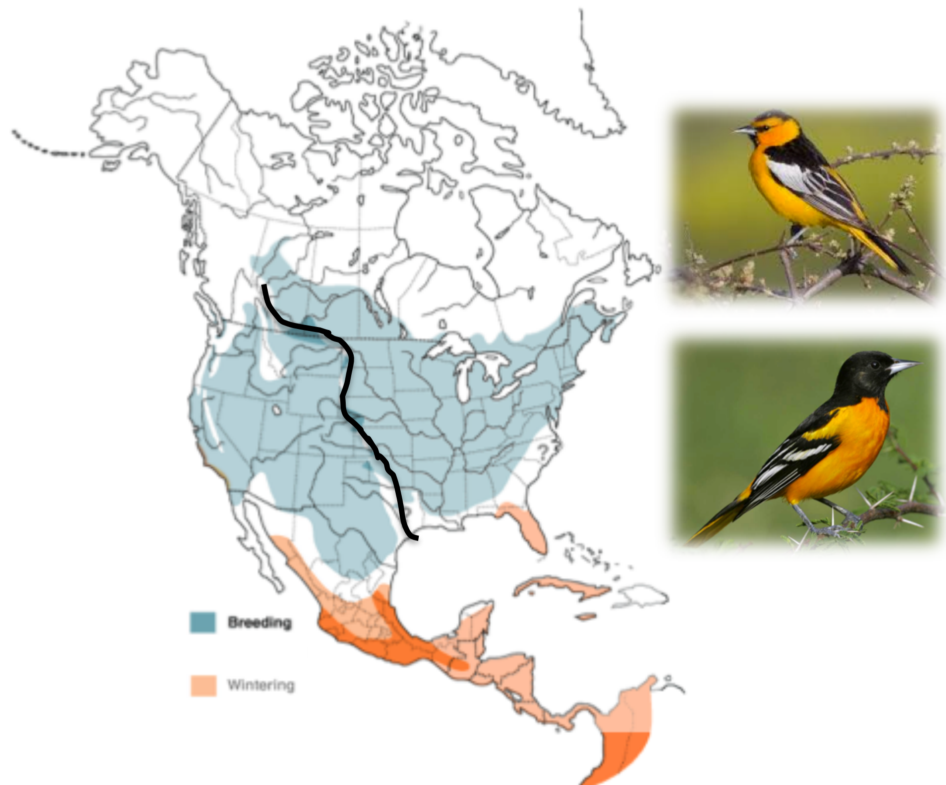
Geography of Speciation

3. Parapatric Speciation

How do we know this is allopatric and not parapatric speciation?

red-shafted flicker (west)
yellow-shafted flicker (east)

Bullock's oriole (west)
Baltimore oriole (east)



Geography of Speciation

3. Parapatric Speciation

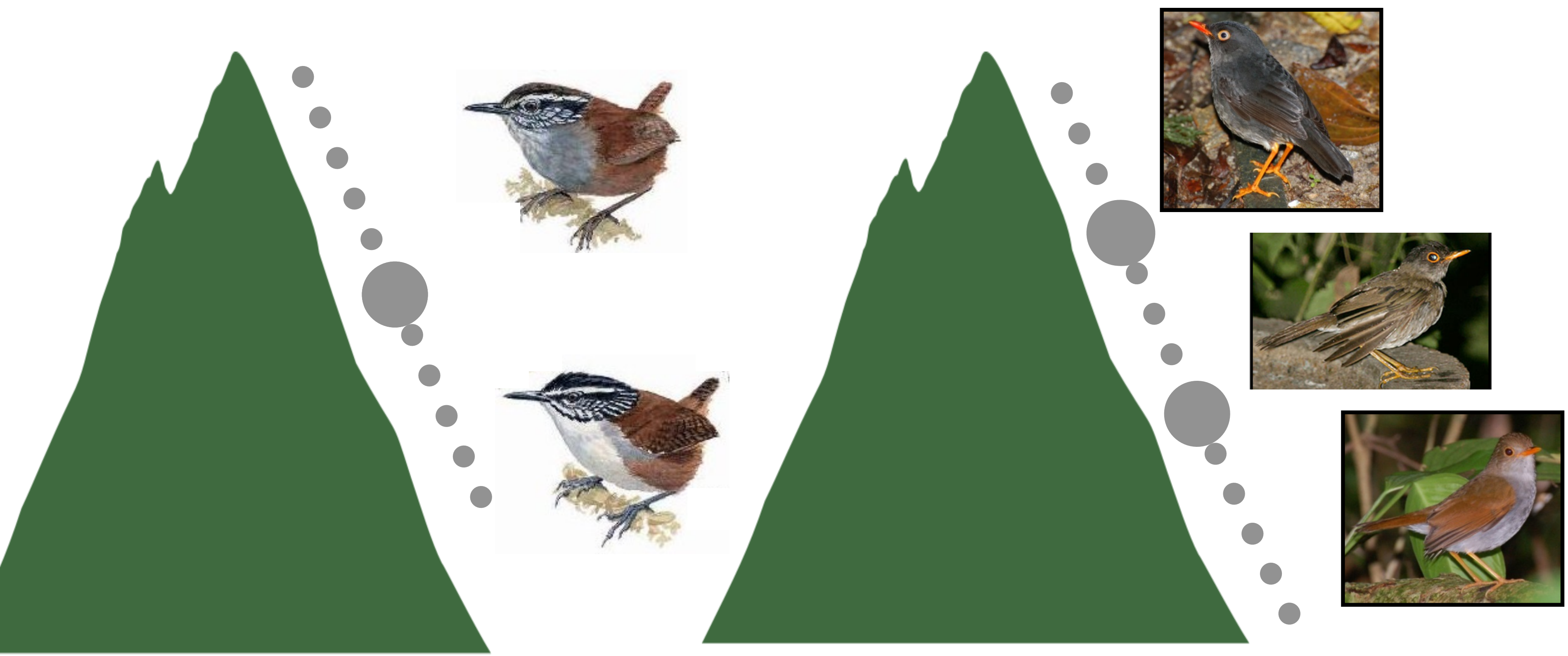
How do we know this is allopatric and not parapatric speciation?

This possibility is unlikely since the ecotone did not exist over most of the period when the species diverged (the Pleistocene glacial cycles).
But, the ecological transition may play a role in maintaining the hybrid zones

Geography of Speciation

3. Parapatric Speciation (?)

Recall elevational replacements in congeners along mountainsides
Ecological determinants of distribution are likely competition…
But how did these patterns arise? Were they generated by parapatric speciation?



Geography of Speciation

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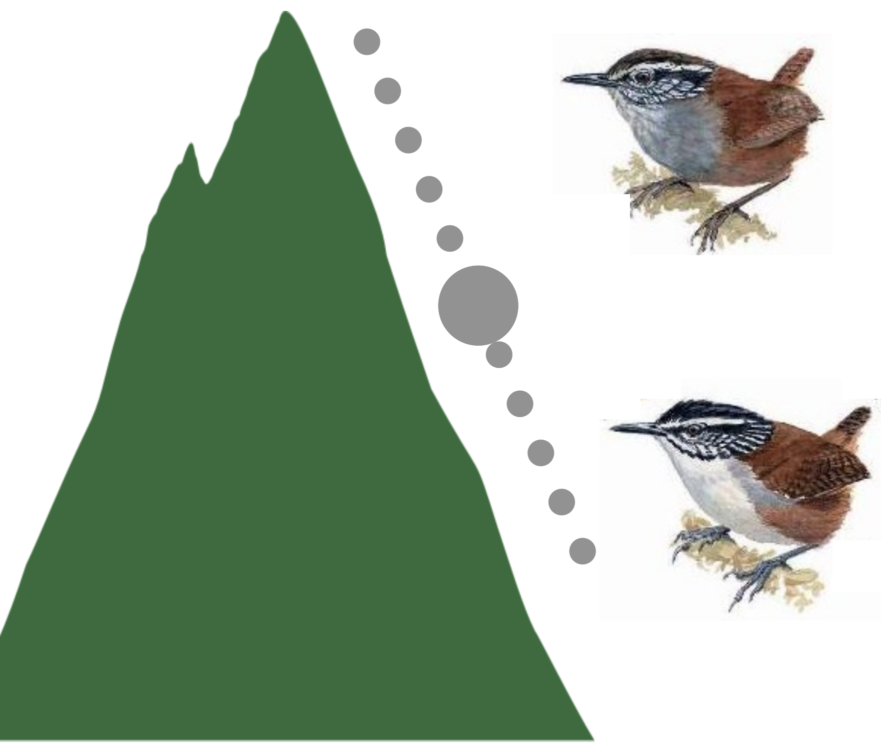
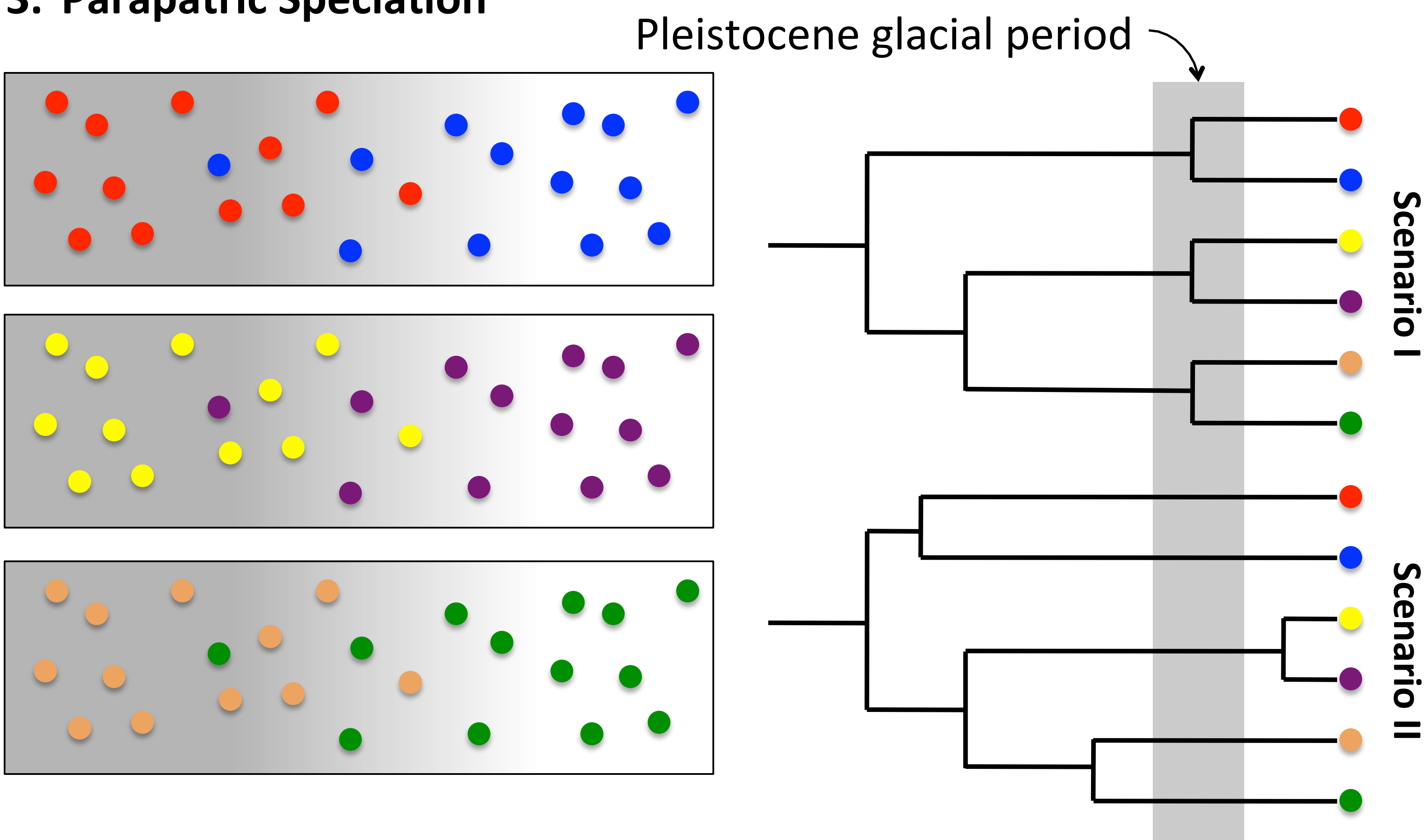


To demonstrate parapatric speciation we would have to answer the following:

1) Are the species sister taxa?
2) Is there divergence in phenotypic or signaling traits associated with elevation?
3) Is there reproductive isolation between forms replacing each other?
4) Is divergence in signals associated with assortative mating?

Geography of Speciation

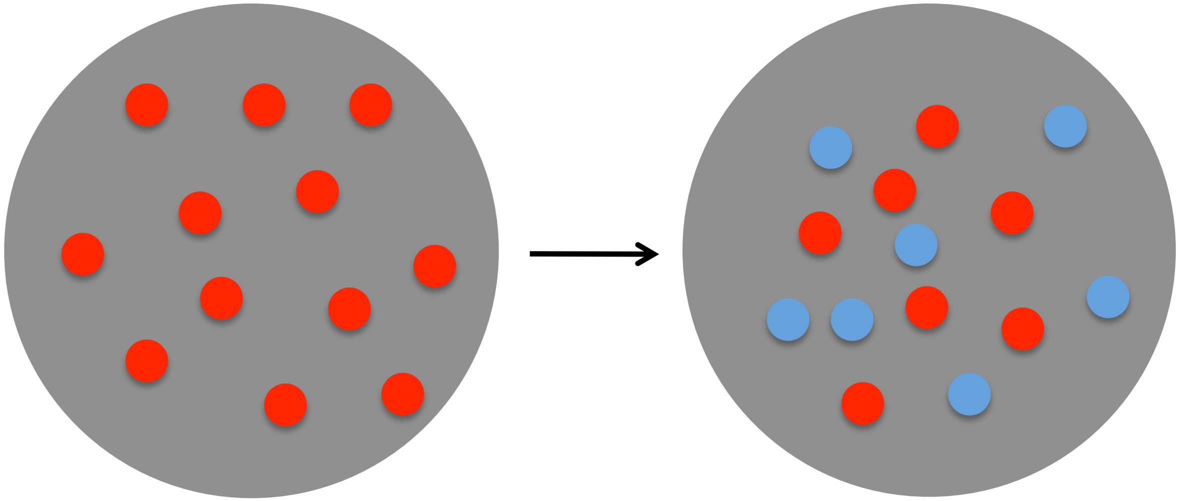
3. Parapatric Speciation



In some cases we can map different geological events onto a phylogeny, giving us inference of the timing of diversification with respect to historical events.

Geography of Speciation

4. Sympatric Speciation



Geography of Speciation

4. Sympatric Speciation

Criteria for concluding that speciation occurred in sympatry
(from Coyne & Orr 2004):

1. Species must be largely or completely sympatric
2. The species must have substantial (genetically-based) reproductive isolation
3. The sympatric species must be sister species
4. The biogeographic history of the species must make an allopatric phase very unlikely

Geography of Speciation

4. Sympatric Speciation

Cases of sympatric speciation?

- ~~Darwin's Finches~~
- ~~Hawaiian Honeycreepers~~
- Cichlid fish in African lakes
- African Indigobirds

Note: Sympatric speciation is easiest when one trait has multiple functions…

Geography of Speciation

4. Sympatric Speciation – cichlid fishes in Africa. Here, distribution and phylogeny combine to suggest sympatric speciation

Cichlid fish in African lakes

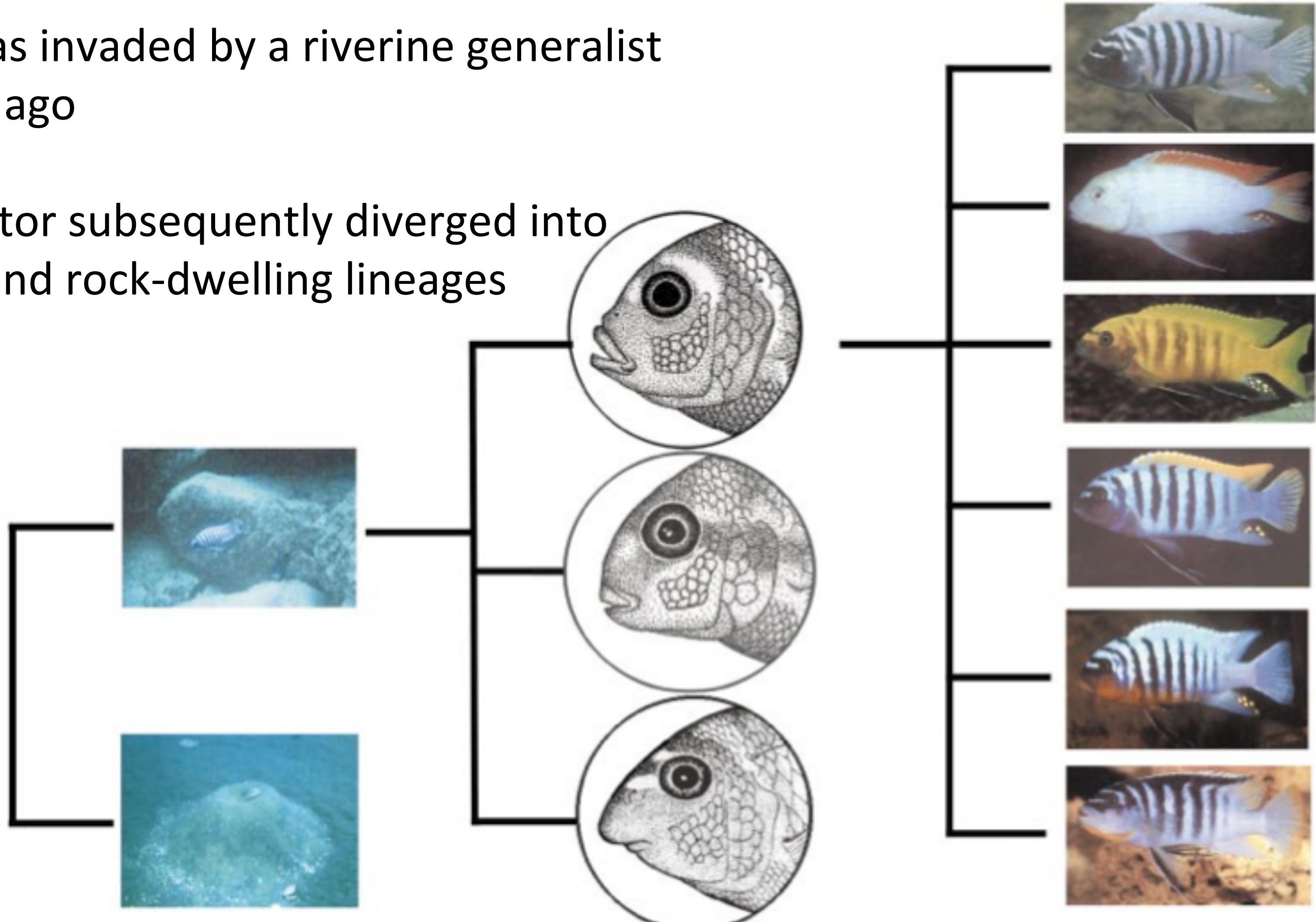
Lake	Area (km^2)	Endemic cichlid species	Maximum age of lake	Major fish lineage
Victoria	68 635	~ 500	0.75 myr	Haplochromine
Malawi	29 604	659-1000	2 myr	Haplochromine
Tanganyika	32 893	170-250	12 myr	Several
Nabugabo	29	5	0.004 myr	Haplochromine
Barombi Mbo	4	11	1 myr	Tilapiine
Bermin	0.6	9	2.5 myr	Tilapiine

Geography of Speciation

4. Sympatric Speciation

Lake Malawi was invaded by a riverine generalist ~700 000 years ago

Common ancestor subsequently diverged into sand-dwelling and rock-dwelling lineages



(Lomolino *et al.* 2010)

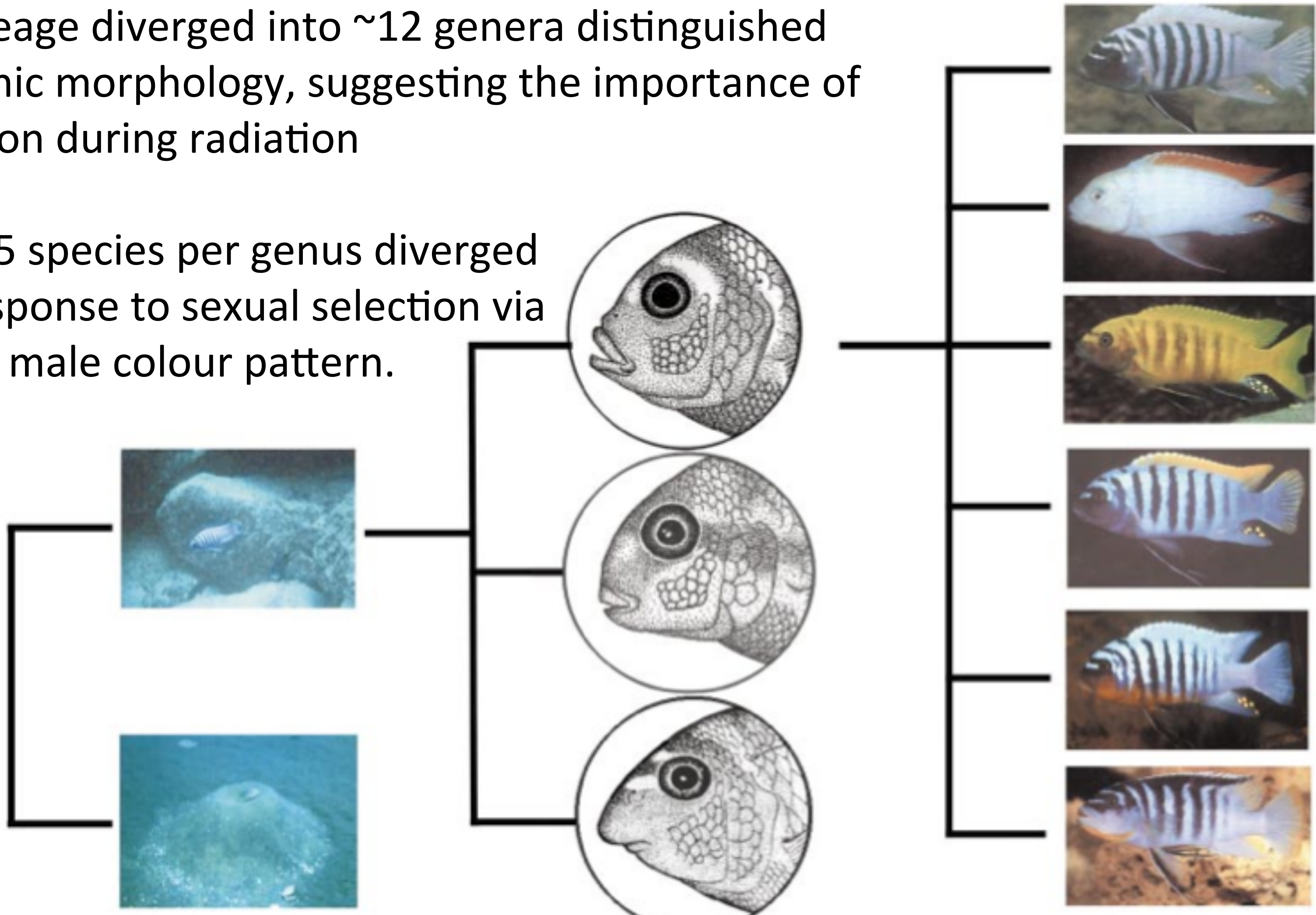
(from Danley & Kocher 2001)

Geography of Speciation

4. Sympatric Speciation

Rock-dwelling lineage diverged into ~12 genera distinguished primarily on trophic morphology, suggesting the importance of trophic competition during radiation

Subsequently, ~25 species per genus diverged presumably in response to sexual selection via female choice for male colour pattern.



(Lomolino *et al.* 2010)

(from Danley & Kocher 2001)

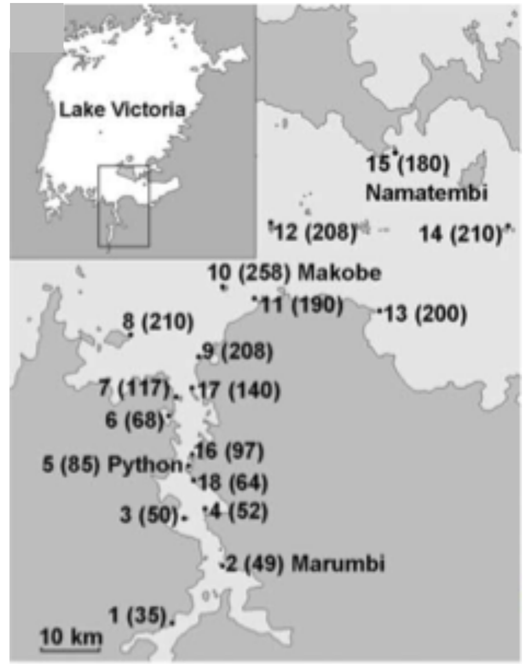
Geography of Speciation

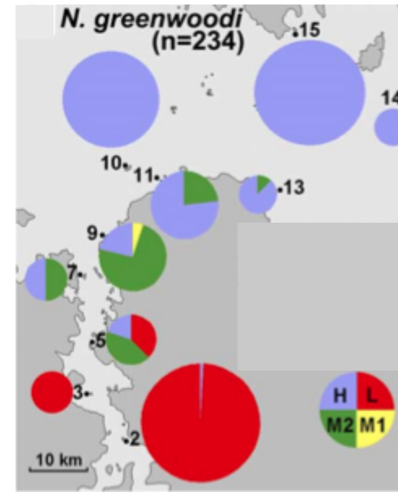
4. Sympatric Speciation

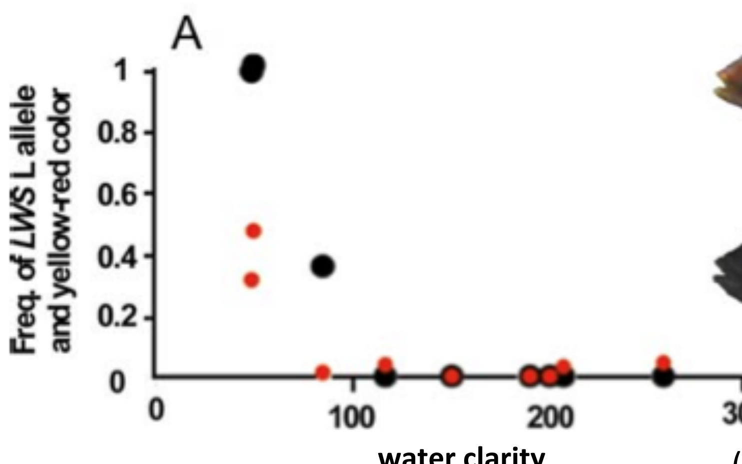
Selection fixed opsin proteins with different light absorbance properties

Divergent visual system coincides with divergent male breeding coloration

Divergent natural selection acting on ecological traits, which also affect mate choice







(from Terai *et al.* 2006)

Geography of Speciation

4. Sympatric Speciation

Indigobirds (*Vidua sp.*)

Host-specific brood parasites

Male indigobirds mimic host songs

Females use these songs to choose both their mates and the nests they parasitize

Host specificity provides mechanism for reproductive isolation after a new host is colonized

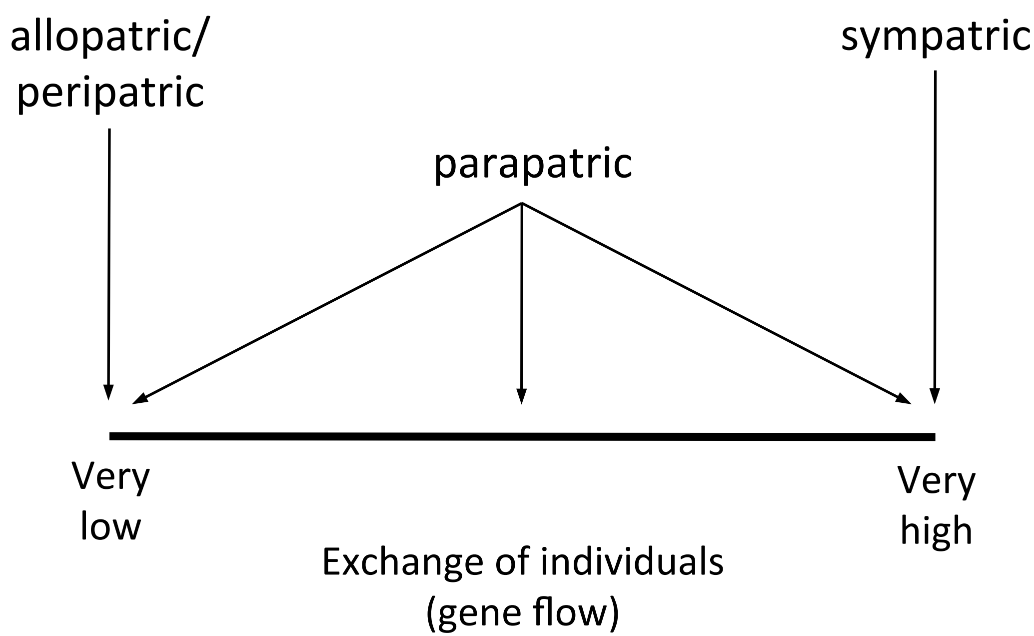
(Host switches lead to speciation because both males and females imprint on their hosts)

Sorensen et al. 2003

Geography of Speciation

Remember: We can view modes of speciation along a continuum of how much genes are exchanged between diverging populations

Geographic Modes of Speciation



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