OEB 140 Speciation

Allopatry, parapatry, and sympatry in speciation

Summary: It's less different than you think!

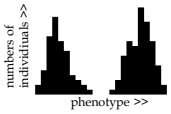
Maybe more interesting is whether speciation takes place in the presence of gene flow

1

SPECIATION

1.4 million described species
Maybe as many as 30 million species overall
How can we explain how all these species came to be?

How does speciation happen?
Regardless of species concept, two species form a *bimodal distribution* of phenotypes or genotypes (in sympatry)

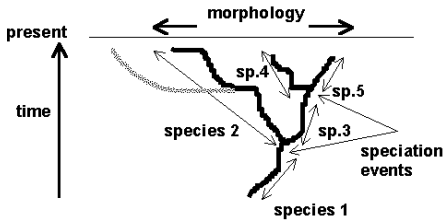


Even if they hybridise, two species can be distinguished by: morphology, ecology, behaviour, and/or genetics
[A single species has a unimodal distribution.]

How are these bimodal distributions of genotypes and phenotypes caused?

2

Anagenesis vs. cladogenesis



Anagenesis: phyletic evolution, change within a lineage (species)
Cladogenesis: splitting of species into two

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Splitting of species a/c Ernst Mayr (1963)

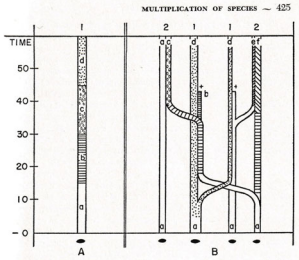

Fig. 15–1. A (on the left) designates a strongly isolated island on which a species *a* changes in the course of geological time through *b* and *c* to *d*. *B* (on the right) indicates an archipelago with four islands on which an originally monotypic species *a* breaks up into 5 species through geographic speciation and cross colonization. (From Mayr 1949a.)

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Table 15–1. Potential modes of origin of species a/c Ernst Mayr (1963)

I. Transformation of species (phyletic speciation)
  1. Autogenous transformation (owing to mutation, selection, etc.)
  2. Allogenous transformation (owing to introgression from other species) "introgression" = gene flow
II. Reduction in number of species (fusion of two species)
III. Multiplication of species (true speciation)
  A. Instantaneous speciation (through individuals)
    1. Genetically
      (*a*) Single mutation in asexual "species"
      (*b*) Macrogenesis ("macromutation")
    2. Cytologically, in partially or wholly sexual species
      (*a*) Chromosomal mutation (translocation, etc.)
      (*b*) Autopolyploidy
      (*c*) Amphiploidy ("allopolyploidy", hybrid speciation via polyploidy)
  B. Gradual speciation (through populations)
    1. Sympatric speciation (including hybrid speciation)
    2. Semigeographic speciation (see Chapter 17) (parapatric speciation)
    3. Geographic speciation (allopatric speciation)
      (*a*) Isolation of a colony, followed by acquisition of isolating mechanisms ("founder effect" speciation)
      (*b*) Extinction of the intermediate links in a chain of populations of which the terminal ones had already acquired reproductive isolation (vicariant speciation)

I2, II, and IIIA2(*c*) may lead to reticulate evolution

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How do all these species evolve?

***Causes of speciation*:**

random forces (like mutation and drift), or deterministic forces, i.e. natural selection?
(To be discussed later)

***Geographical milieu of speciation*:**

sympatric, parapatric, or allopatric?
(today)

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Geography of speciation

Until a few years ago, general rule believed: "Speciation only occurs in allopatry!"

Recent evidence: sympatric and parapatric speciation also possible.

Frenzied recent work on "ecological speciation"!

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Clues to the study of speciation

"D.S. Jordan's Law" (1905) of geographic isolation

David Starr Jordan, a proponent of gradualistic Darwinism at a time when it was under attack from the Mendelians, argued that:

"Given any species in any region, the nearest related species is not likely to be found in the same region nor in a remote region, but in a neighboring district separated from the first by a [geographic] barrier of some sort"

In a sense Jordan's law seems like almost the opposite of Wallace's law ("*Every species has come into existence coincident both in space and time with a pre-existing closely allied species*"), but by using "neighboring" he did not disagree strongly with Wallace.

Jordan knew of exceptions, but had fired the first shot in the debate over the importance of geographic isolation in speciation.

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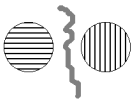
1) Allopatric speciation

a) Vicariance (range splitting)
Range of a species split in two. Divergent drift or selection in different environments. Could even be due to *similar* selection.



Eventually, barriers erode and there may be *secondary contact*. Three outcomes are possible:

1) Little divergence: broad or narrow hybrid zone.

2) Hybrid inviability/sterililty, then **reinforcement**? Parapatric speciation. (But if overlap narrow, not so likely)

3) May have already become separate species. Sympatry possible.

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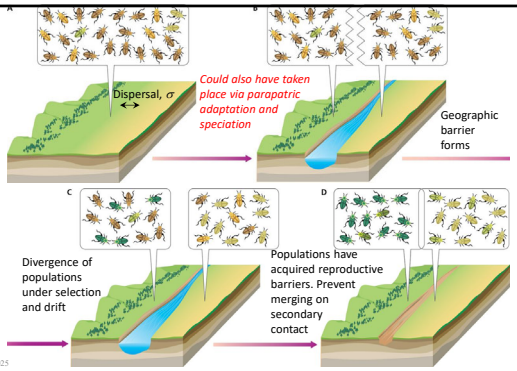

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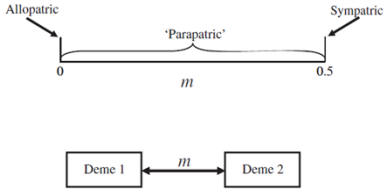
What is sympatric speciation? What is sympatry?



Gavrilets 2003; Mallet et al. 2009

Fig. 1 Demic view of sympatry and allopatry in the Gavrilets (2003) formulation.

However, this "demic" definition of sympatry was a change in definition compared to how Mayr, or Futuyma and Mayer had defined it! It gave "sympatric speciation" an infinitesimally small probability at the end of the spectrum!

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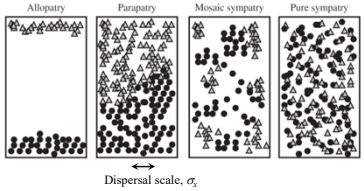
Sympatry, parapatry, allopatry



The allopatry/sympatry spectrum, using spatial definitions (after Mallet, 2008).

Sympatry is when individuals of two species are in each others' "cruising ranges," ~2σ. If they wanted to, they could mate with members of the other species.

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Argument for allopatric speciation

Coyne & Orr 2004: 84
"One can argue that allopatric speciation should be considered the "default" mode of speciation because it is supported by substantial evidence and occurs under a wider range of conditions than do other modes." Allopatry as a "null hypothesis," to be accepted if sympatric speciation is not disproved!

In sympatric and parapatric speciation, divergence into separate populations must overcome homogenization due to gene flow

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But a problem to demonstrate

Only when two new species are sympatric can you be sure they are really species, and reproductively isolated!

It's hard to test directly for allopatric species!

In captivity, many species form hybrid swarms but not in nature

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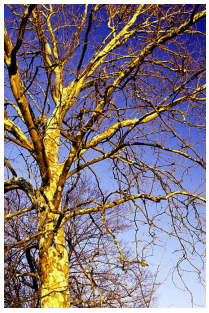

Vicariant speciation does eventually occur.
It clearly happens – *Reductio ad absurdum*: marsupials in Australia

However, allopatric speciation can be very slow: London plane tree *Platanus* = hybrid between *P. orientalis* (Asian) and *P. occidentalis* (American "sycamore")

No contact for > 20 My

Yet hybrid London plane has fertile seed, so the two have not really "speciated" at all.

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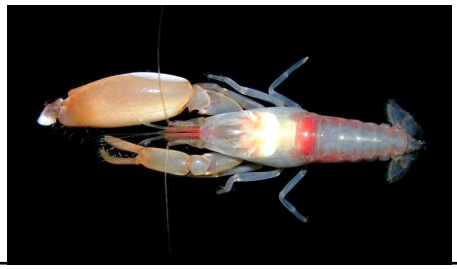
Evidence for allopatric speciation

Alpheus snapping shrimps

1. Concordance of species boundaries with existing dispersal barriers



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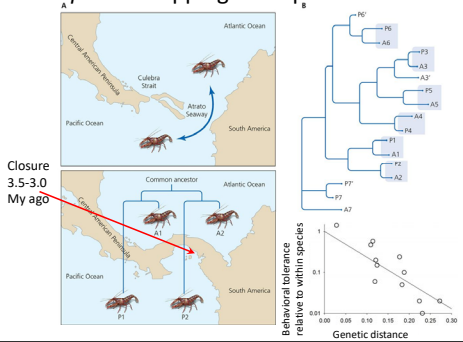
Alpheus snapping shrimps: Knowlton et al. 1993



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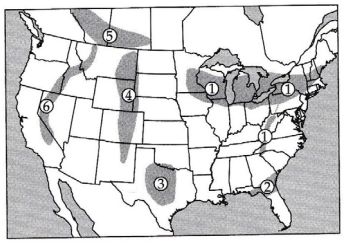
Evidence for allopatric speciation

2. Geographic coincidence of species borders/hybrid zones in multiple taxa



Remington (1968) "suture zones" -- contacts between multiple formerly isolated species

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John Avise 1992

(in Avise 1994, p. 243) "The striking concordance of geographic patterns ... strongly suggests an overriding influence of shared historical biogeographic forces"

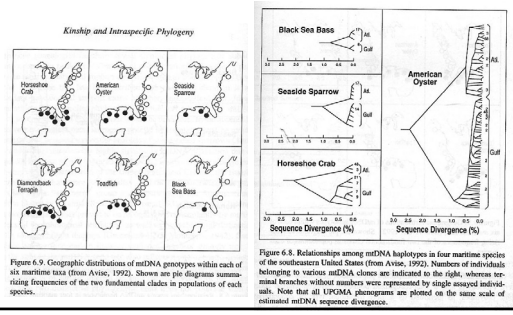

Figure 6.9. Geographic distributions of mtDNA genotypes within each of six maritime taxa (from Avise, 1992). Shown are pie diagrams summarizing frequencies of the two fundamental clades in populations of each species.

Figure 6.8. Relationships among mtDNA haplotypes in four maritime species of the southeastern United States (from Avise, 1992). Numbers of individuals belonging to various mtDNA clones are indicated to the right, whereas terminal branches without numbers were represented by single assayed individuals. Note that all UPGMA phenograms are plotted on the same scale of estimated mtDNA sequence divergence.

roughly similar ages

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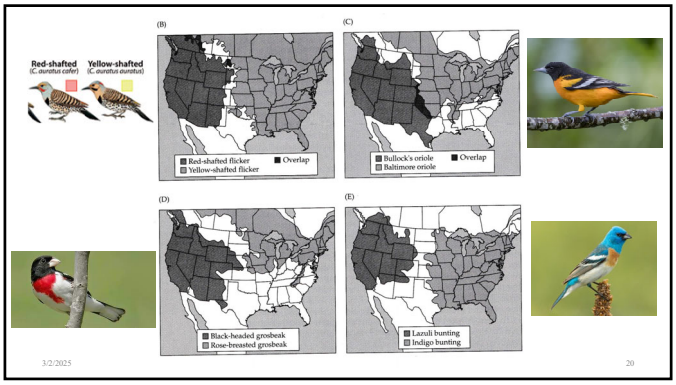

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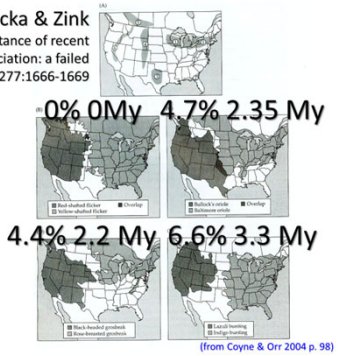
Klicka & Zink

1997. The importance of recent ice ages in speciation: a failed paradigm. Science 277:1666-1669



(from Coyne & Orr 2004 p. 98)

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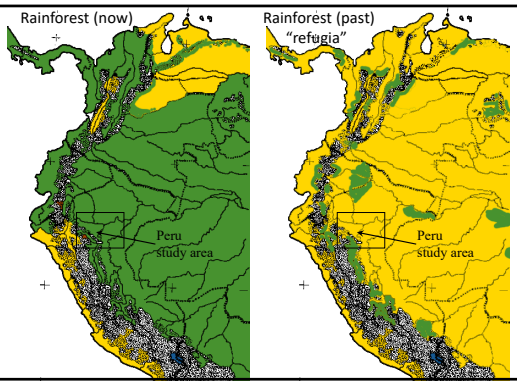

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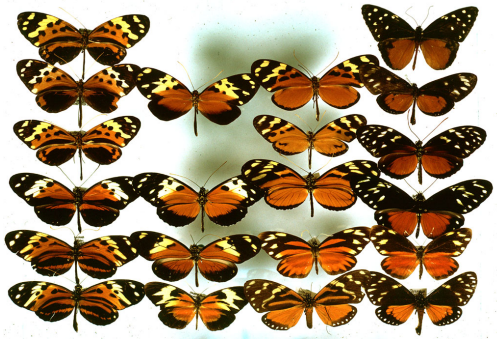

Geographic variation in Mimicry 'rings': Pleistocene refugia?

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Ithomiine mimicry contact zones

Orange tip transparent, and

Black and white transparent mimicry rings

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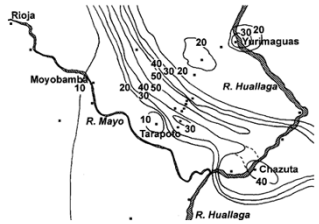
Butterfly suture zone in Peru



Contours represent % of species hybridizing

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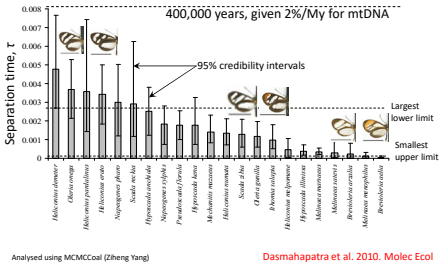
Genetic data rejects simultaneous divergence

(22 pairs of taxa , 4 loci, 5 Kbp)



Analysed using MCMCCoal (Ziheng Yang)

Dasmahapatra et al. 2010. Molec Ecol

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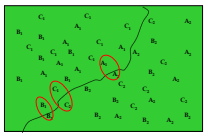
Evidence against simple vicariance

Hypothesis tests:

1. 'Suture zones' √
2. Some forms are recent √
3. Ages are concordant X

Prediction 3 not met
Divergence rate depends on lineage not geology.
Ecology important?



Dasmahapatra et al. 2010. Molec Ecol

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Evolution, 54(6), 2000, pp. 2166–2171

LITTLE EVIDENCE FOR SYMPATRIC SPECIATION IN ISLAND BIRDS

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Documented endemic, congeneric species on small isolated islands, area 0.8 - 3500 km^2
46 islands & small archipelagos -- at least 1 endemic land bird spp.; 147 endemic spp.
7 pairs of endemic congeners (excluding flightless rails)
Of the 7, only 4 pairs are potentially sister species and possibly sympatric origin
3 of these 4 pairs always been considered results of double invasion from mainland
The one remaining pair may have speciated allopatrically on a small archipelago.

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Evidence for allopatric speciation

Absence of sister species where geographic isolation unlikely

Endemic bird species on islands, studied by Coyne & Price (2000)

46 islands with endemic bird species
8 pairs of endemic species inhabiting the same island
- 4 are clearly not sister species – so must be double invasion
- 2 might be sisters, but likely due to "double invasion" (one of a pair resembles a mainland species)
- 1 pair of flightless rails (extinct) on Chatham Is. are sisters – but double invasion likely
- 1 pair: 2 species of bunting endemic to Tristan da Cunha -- may involve speciation on nearby island

Dieffenbach's Rail

Chatham Is. Rail

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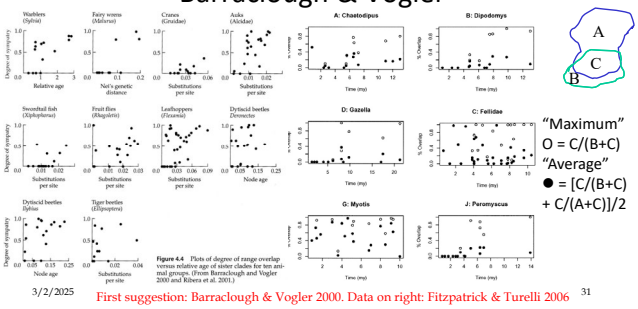
Age-range correlations: overlap
Barraclough & Vogler



"Maximum"
O = C/(B+C)
"Average"
● = [C/(B+C) + C/(A+C)]/2

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First suggestion: Barraclough & Vogler 2000. Data on right: Fitzpatrick & Turelli 2006

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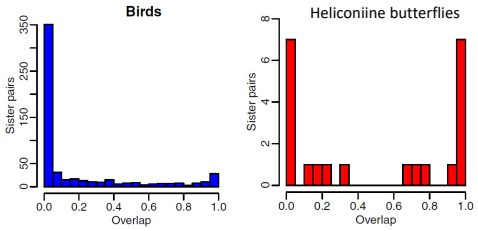
Evidence for allopatric speciation

4. Comparative method and degree of overlap – of *sister* species only



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Rosser, Phillimore, & Mallet 2015

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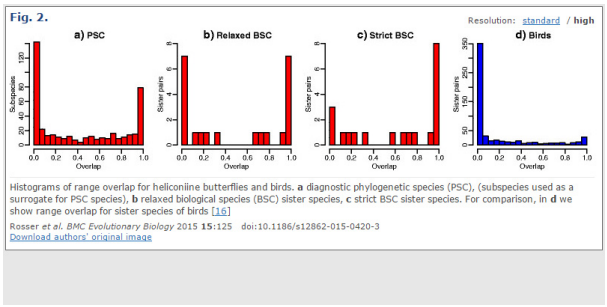

Histograms of range overlap for heliconiine butterflies and birds. **a** diagnostic phylogenetic species (PSC), (subspecies used as a surrogate for PSC species), **b** relaxed biological species (BSC) sister species, **c** strict BSC sister species. For comparison, in **d** we show range overlap for sister species of birds [16]

Rosser *et al. BMC Evolutionary Biology* 2015 **15**:125 doi:10.1186/s12862-015-0420-3

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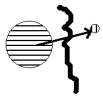
b) Allopatric speciation - the founder effect



A speedier allopatric mechanism was suggested: "founder effect"
Mayr (1954): founders, take small fraction of available genetic variation (genetic drift as in shifting balance Phase I).

Population undergoes "genetic revolution"; reorganizes genome (selection as in shifting balance Phase II).

Strong selection, leading to genetic revolution due to (a) genes being unused to low diversity, and (b) different ecological conditions in new home.

→ Secondary contact etc., as for vicariance

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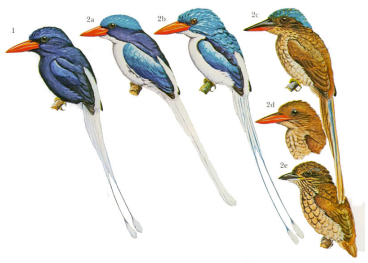
Evidence

Spectacular New Guinea birds called the racket-tailed kingfishers, genus *Tanysiptera*.



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That mutation, recombination, selection and isolation are the four cornerstones of evolution is now generally acknowledged. The way in which these factors interact in the various evolutionary processes and the role played by diverse subsidiary factors are, however, by no means fully clarified. In particular, the role of one factor, a sudden change in the genetic environment, seems never to have been properly considered. That this factor might be exceedingly important in the evolutionary process occurred to me when studying a puzzling phenomenon, frequently encountered by the systematist, the conspicuous difference of most peripherally isolated populations of species.

Let us look, for instance, at the range of the Papuan kingfishers of the *Tanysiptera hydrocharis-galatea* group (Fig. 1). It is typical for

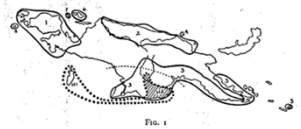

Fig. 1

hundreds of similar cases. On the mainland of New Guinea three subspecies occur which are very similar to each other.

Founder events?

(Mayr 1954)

But could be *vicariance speciation*,

or even *parapatric speciation* aided by habitat differences on the islands

No genetic data to show genetic drift

We deal with the founder effect model in about a week

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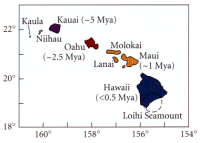
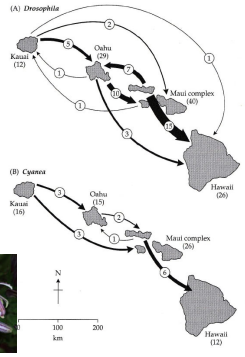
Other examples: Hawaiian *Drosophila*, a huge radiation of species in a few million years.





These speciation events were suggested to have been caused by founder effect speciation.

We'll discuss this in a later lecture

Hawaiian Haha plant
Cyanea

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2) Parapatric speciation
Extrinsic selection plus reinforcement
Ecological selection plus reinforcement might lead to speciation (Endler 1977).

Any type of selection plus pleiotropic evolution of mate choice

Reinforcement not necessary for speciation either. Could have assortative mating via *pleiotropy*.

Could be intrinsic, as well as extrinsic selection. A process like the shifting balance, for example.

Allopatry only superficially different from parapatry; gene flow is always somewhat restricted; e.g. *"ring species"*

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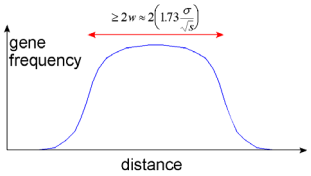
No clear geographic rule for genetic divergence
Intrinsic selection, extrinsic selection, mate choice, all under selection. … from cline theory:



So, divergence (& speciation) possible in *parapatry*.
Speciation, like any other form of genetic divergence, can occur in the presence of gene flow: no requirement for complete geographic isolation.

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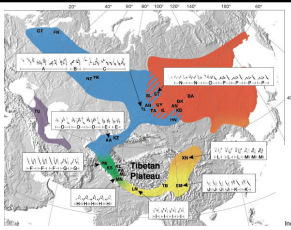

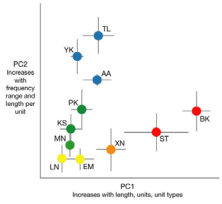

Phylloscopus trochiloides
Greenish warbler ring species

song varies gradually around the Tibetan plateau (due to local sexual selection?)

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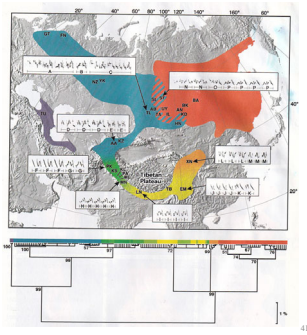
Phylloscopus trochiloides
Greenish warbler

A break in the mtDNA genealogy?
Perhaps allopatry in the past?
(a/c Coyne & Orr)

But not necessary. "mid-domain effect" expected in a neutrally evolving molecule due to spatial isolation.

The first bifurcation has to occur somewhere, and most likely somewhere in the middle!



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3) Sympatric speciation

Like parapatric speciation, sympatric speciation requires (a) disruptive selection or (b) polyploidy to generate post-mating isolation, and … (c) reinforcement and/or pleiotropic changes in mate choice (to generate pre-mating isolation).

Selection must occur under high levels of gene flow within the normal "cruising range" of individuals, so selection must be very strong ⇒ unlikely in each case?

However, sympatric speciation is potentially rapid, so important? (e.g. speciation due to polyploidy ≈ 3%-7% of total speciation in flowering plants and ferns).

We deal with this in the next lecture

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Allopatric speciation

- It clearly will happen eventually
- How much it might contribute to the diversity of life is questionable:
  - It's "more likely" due to lack of gene flow
  - But maybe waiting for allopatry is slower than sympatric and allopatric speciation?
  - Sympatric processes like reinforcement and character displacement allow build-up of local diversity
- Perhaps a more interesting question: how much of speciation requires gene flow?