OEB 140 Speciation

Selection vs. drift in speciation

Today:

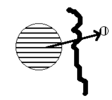
Is speciation driven by random processes:
allopatry, or genetic drift?

What's the evidence for random versus deterministic processes in speciation?

Founder effects?

1

Allopatric speciation - the founder effect



A speedy allopatric mechanism was suggested, the "founder effect," by Mayr (1954). Also called "peripatric speciation":

Founders take a small fraction of available genetic variation (genetic drift as in shifting balance Phase I).

The founder population undergoes "genetic revolution"; reorganizes the entire 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.

No clear Phase III (export of new adaptive peak to other populations). The argument is instead that, after the genetic revolution within the small founder population, the two allopatric populations are already separate species.

2

Evidence

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

3

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.

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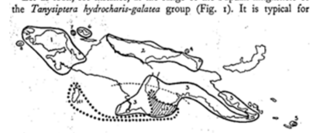

Fig. 1

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

Founder events?
(Mayr 1954)

No genetic data to show genetic drift

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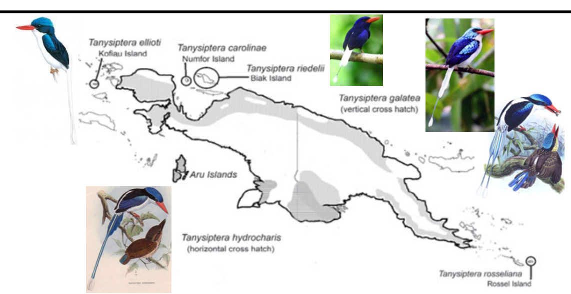

Figure 5. Map of New Guinea and outlying islands depicting the ranges of *Tanysiptera* kingfishers discussed by Mayr (1942). Map drawn by JA.

Ahlquist, J., & Lightner, J. 2018.

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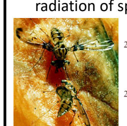
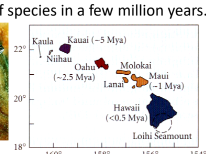
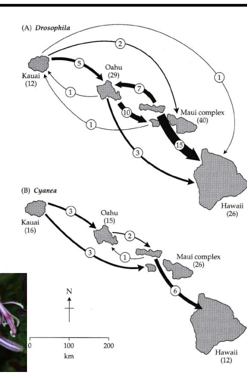
Other examples: Hawaiian *Drosophila*, a huge radiation of species in a few million years.

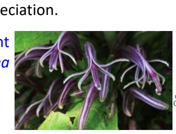






Such speciation events were suggested to have been caused by founder effect speciation.

Hawaiian Haha plant
Cyanea



6

ERNST MAYR

Change of Genetic Environment and Evolution

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.
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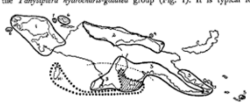

Both Mayr's and Dobzhansky's views of species as "cohesive" wholes, integrated by coadaptation and heterozygous advantage, and protected by homeostatic and isolating mechanisms, went hand in hand with Dobzhansky's (1955) "balance hypothesis" for genetic variation.

This was the proposition that molecular genetic variation (revealed in the 1960s by protein electrophoresis and immunology – blood groups), was due to balancing selection ($W_{Aa} > W_{aa}, W_{AA}$).

Belief in universal heterozygous advantage. The "new population genetics" of Lerner & Bruce, and of Wallace, versus the old "beanbag genetics" of Haldane, Fisher, and Wright.

Mayr, E. 1954. in J. Huxley, A.C. Hardy, and E.B. Ford, eds. Evolution as a Process.

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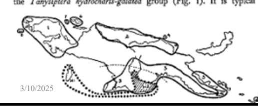

Mayr believed gene flow and natural selection in large populations on continents was largely conservative, and which prevented progressive evolution, and speciation.

"A well integrated genetic system may come into perfect balance with its environment and become so well stabilized that evolutionary change will no longer occur" (Mayr 1963, p. 555).

Genes on continents exposed to abundant gene flow are selected for compatibility to this variation. They "do well on a great variety of genetic backgrounds . . . A 'good mixer' rather than a good 'soloist', has a tremendous advantage in such a system".

Mayr, E. 1954. in J. Huxley, A.C. Hardy, and E.B. Ford, eds. Evolution as a Process.

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But couldn't ordinary natural selection while populations are in contact effect evolutionary change and speciation, perhaps in parapatry?

Mayr believed that ecotypic variation, clinal adaptation (produced by standard natural selection) in the face of gene flow, could not lead to speciation.

"Clines indicate continuities, but since species formation requires discontinuities, we might formulate a rule: *The more clines are found within a region, the less active is species formation*" (Mayr 1942, p. 97, Mayr's own italics).

Citing Goldschmidt's (1940) argument for the impotence of natural selection along a cline to effect speciation, Mayr agreed, and wrote:

"Owing to the never-ceasing gene-flow through such a system these [clinal] populations are merely variations on a single theme" (Mayr 1954, p. 159).

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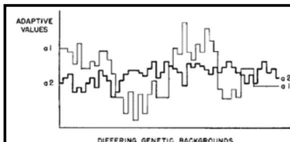

FIG. 2

Supppose we have "... two alleles, ... (a1) is of broad, general efficiency on many genetic backgrounds, while ... (a2) is very superior on some genetic backgrounds but inferior or even lethal on others."

(diagram is I think the other way round!)

A small sample of backgrounds could lead to loss of one or other allele

When a few individuals found a new, isolated colony, the sudden reduction in population size and loss of alleles causes the frequency of homozygotes to rise.

"Isolating a few individuals (the 'founders') from a variable population ... Situated in the midst of a stream of genes which flows ceaselessly through every widespread species will produce a sudden change of the genetic environment of most loci."

"As a consequence, homozygotes will be much more exposed to selection. . . Thus, the 'soloist' is now the favorite rather than the good mixer'". (Mayr 1954).

Mayr, E. 1954. in J. Huxley, A.C. Hardy, and E.B. Ford, eds. Evolution as a Process.

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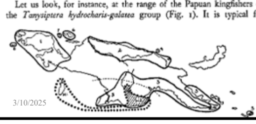

"This change, ... is the most drastic genetic change ... in a natural population, since it may affect all loci at once. Indeed, it may have the character of a veritable 'genetic revolution.' ... This genetic revolution ... may well have the character of a chain reaction, ... until finally the system has reached a new state of equilibrium"

This idea fitted with "typostrophic" or punctuated patterns in evolution, as advocated by the Russian Schmalhausen, and with Goldschmidt's ideas about "bridgeless gaps" between species.

Mayr was pleased with his argument, and was rather upset that the book he wrote this chapter for took two years to be published. He felt that someone else might think of his idea!

Mayr, E. 1954. in J. Huxley, A.C. Hardy, and E.B. Ford, eds. Evolution as a Process.

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It has been questioned whether any natural population can pass through a genetic bottleneck of reduced variability (Fig. 3, B or C).

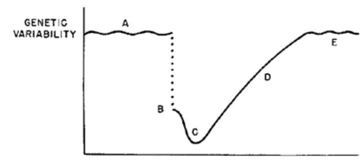

FIG. 3

However, there is abundant evidence that this *is* possible. Less than twenty pairs of the European Starling were introduced to the United States in 1890; and only a fraction of them bred successfully. It took more than fifteen years before they began to increase materially, but now (only forty years after they really started to spread) they are one of the most common birds of North America having increased to an estimated number of over fifty million individuals. The story of the House Sparrow

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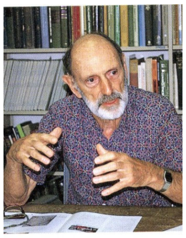
Hampton Carson extended Mayr's founder effect speciation idea based on his field knowledge of Hawaiian *Drosophila.*



Two kinds of genetic variation: "open" and "closed" systems.

Open: freely available to natural selection or drift by recombination.

Closed: cannot be separated from one another so a viable fertile organism of high fitness is produced.

"These genes are locked into obligatory epistasis," (may later be in chromosomal inversions)

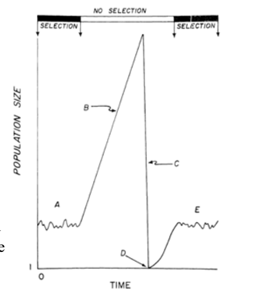


FIG. 2.—The flush-crash-founder cycle. A population under natural selection (*A*) undergoes a population flush (*B*) and crash (*C*). Surviving the crash is a founder individual (*D*) from which is built a new population under natural selection (*E*).

Carson 1975

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Hampton Carson's 'founder-flush' or 'flush-crash' model: 'open' and 'closed' genomic regions

"Speciational events may be set in motion and important genetic saltations toward species formation accomplished by a series of catastrophic, stochastic genetic events."

"The disorganization of the closed system of variability ... accomplished through a permissive populational condition wherein natural selection is temporarily relaxed. Release from natural selection results in a population flush during which the population increases quickly in size. ... Individuals survive ... not able to do so under the usual stringent effects of natural selection."

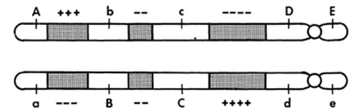

FIG. 1.—A proposed model for the "open" and "closed" genetic systems. A pair of homologues heterozygous at 12 out of 14 loci are shown. Products of crossing over anywhere within the open system (unshaded) produce zygotes with relatively high fitness. Crossovers within the closed system (shaded blocks) result in zygotes having low fitness in most circumstances. Letters represent ordinary genes or polygenes; pluses and minuses represent internally balanced complexes from which any plus-minus combination (within any one block) is relatively unfit. Relational balance keeps most of the blocks from becoming fixed in the homozygous state.

Carson 1975

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Alan Templeton: "Genetic transilience"

Genetic basis of isolating barriers
Type I: many segregating units, sometimes associated with chromosomal rearrangements
Type II: one or a few segregating ('major effect') units, commonly associated with many epistatic modifiers
Type III: with complementary or duplicate pairs of loci (i.e. redundant changes? Dobzhansky-Muller incompatibilities?)

"Genetic transilience"
Founder events lead to rapid evolution of Type II or Type III barriers
Barriers may be pre-mating or post-mating
"Conditions for this mode are very restrictive, so that the vast majority of founder events do not lead to a genetic transilience"
Not whole genome revolution, as proposed Mayr (which would involve Type I barriers). Only a few loci involved
Could involve chromosomal rearrangement, but not necessarily.

Templeton 1981

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Table 1 A comparison of three models of founder-induced speciation

Feature	Genetic revolution	Founder-flush	Genetic transilience
Ancestral population	Peripheral	Outcrossed and polymorphic	Outcrossed and polymorphic
Primary impact of the founding event	Great increase in level of homozygosity	Disruption of co-adapted complex through drift	Disruption of co-adapted complex through drift on major genes
Genetic events following the founding event	Continued loss of genetic variation due to small population size	Flush, recombination, and altered pleiotropic balance. Carry-over and release of genetic variation	Flush, recombination, and altered pleiotropic balance. Carry-over and release of genetic variation
Major source of selection	Genetic environment: homozygosity	External and environmental	Genetic environment: altered frequencies of major genes
Period of strongest selection	When homozygosity is maximal	After flush (relaxed during flush)	During flush, shortly after founding event
Genetic response	Most loci (later revised downward)	Polygenic, but most loci unaffected	A few major genes and their modifiers

Carson & Templeton 1984

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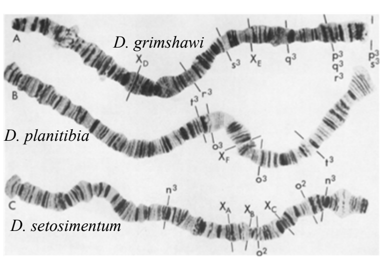

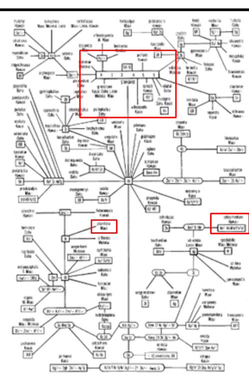

Breakpoints in X chromosomes of Hawaiian "picture wing" *Drosophila* from polytene salivary gland chromosomes: used to draw phylogeny

Carson 1983

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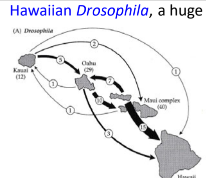
Hawaiian *Drosophila*, a huge radiation of species in a few million years.



Drift is normally deleterious; unlikely to produce healthy populations
Genetic studies: no evidence of reduction in genetic diversity.
Some closely related species from same island, even more true for snails, crickets.

Drosophila melanogaster mutant inbred lines have been kept for nearly 100 years with no obvious evidence of speciation.

Today most don't think it was a single "event" – slow divergence

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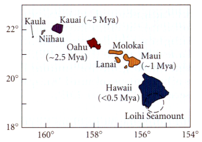

A discussion in 1996:
Mark Williamson: "If you map Professor Carson's inversion phylogeny onto the islands (Williamson 1981, figure 8.3) you will find 90 intraisland speciation events against about 40 interisland events. This ratio of about 2:1 is normal for Hawaiian jumps (Wagner 1995)."
Hope Hollocher: "I do not think that Carson's emphasis on interisland colonization is misleading at all. ... To be able to account for about half the picture-winged species via colonization is remarkable and indicates that colonization was a major contributing factor to speciation in this group."

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Carson & Templeton: *kipukas* as geographic barriers

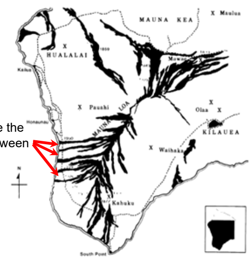

Figure 2 The southern two thirds of the island of Hawaii showing division of *Drosophila silvestris* habitat (stippled rain forest between 1000 and 1700 m altitude) by 100 years of historic lava flows. Sites of collected samples are given by X.

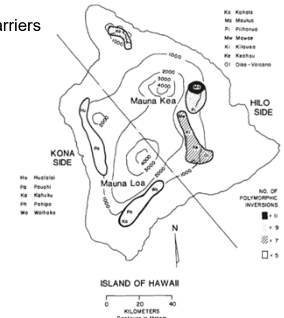

FIG. 2.—Island of Hawaii. The diagonal line separates Kona-side and Hilo-side populations of *D. silvestris*. Collecting localities and inversion frequencies of this species are given.

3/10/2025 Carson & Templeton 1984 20

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Punctuated equilibrium

(I needed to mention this idea but forgot, today – sorry!)
Very much dependent on Mayr's founder effect speciation idea
Based on the fossil record
Noted that sharp changes in fossil morphologies occur in strata
... And that there are long periods of stasis in morphology
Proposed that most morphological evolution occurred during speciation
- in particular, "genetic revolutions" in peripheral populations
Evolution was largely a process of stasis (equilibrium), followed by rapid changes, "punctuations," that disturbed the equilibrium.
Eldredge, N., & Gould, S.J. 1972. Punctuated equilibria: an alternative to phyletic gradualism, Pages 82-115 in T.J.M. Schopf, ed. Models in Paleobiology. San Francisco, Freeman, Cooper, & Co.
https://www.blackwellpublishing.com/ridley/classictexts/eldredge.pdf
Roundly criticized by population geneticists – but what do you think?

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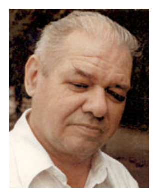

Critiques of founder effect and similar ideas

Interpretation of Mayr (1954) founder effect biogeography might be the wrong way round!

Maybe today's peripheral populations are relictual!

W. L. Brown's "**Centrifugal speciation**" idea:
- rapid evolution of new taxa in the centre of the range
- peripatric (peripheral) isolates instead retained ancestral traits, while modern traits evolved in the centre of the range

Brown 1957

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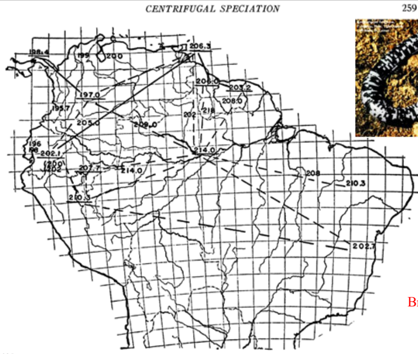
CENTRIFUGAL SPECIATION 259



Brown 1957

3/10/2025 FIG. 5. GEOGRAPHICAL VARIATION IN THE NUMBER OF BODY ANNULI OF THE LEGLESS LIZARD *AMPHISBAENA FULIGINOSA* 23

23

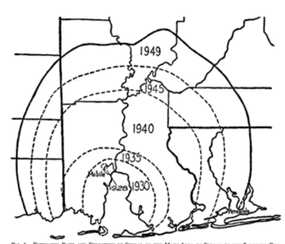
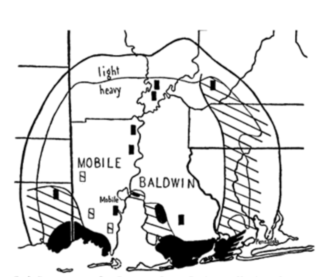


FIG. 6. ESTIMATED RATE AND DIRECTION OF SPREAD OF THE MAIN AREA OF SPREAD OF THE IMPORTED FIRE ANT, *SOLENOPSIS SAEVISSIMA*, IN THE CENTRAL GULF COAST REGION OF THE UNITED STATES, AS OF 1949



Brown 1957

FIG. 7. DISTRIBUTION OF THE COLOR PHASES OF THE IMPORTED FIRE ANT IN THE MAIN AREA OF INFESTATION, AS OF 1949

Solid black represents areas with incidence of dark and intermediate phases of greater than 20 per cent; hatching represents areas with incidence of these phases of 5–20 per cent. Small black rectangles represent minor isolated dark-phase populations. In the centers of infestation outside the area shown in 1949, some populations were dark, others light; the present status of these is unknown. (After Wilson, 1951.)

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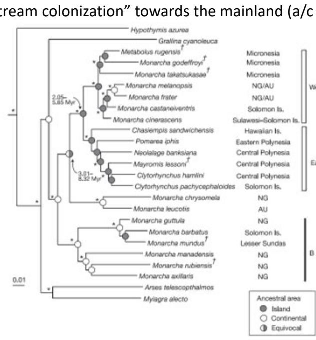
Origins of monarch flycatcher group in Polynesia/
- followed by "upstream colonization" towards the mainland (a/c to Filardi & Moyle)

● = island ancestor inferred
○ = continental ancestor inferred

"These results strongly support a recent, rapid sequence of colonization and diversification across all major archipelagos in the Pacific, followed by subsequent recolonization of Australia and New Guinea"



Filardi & Moyle 2005

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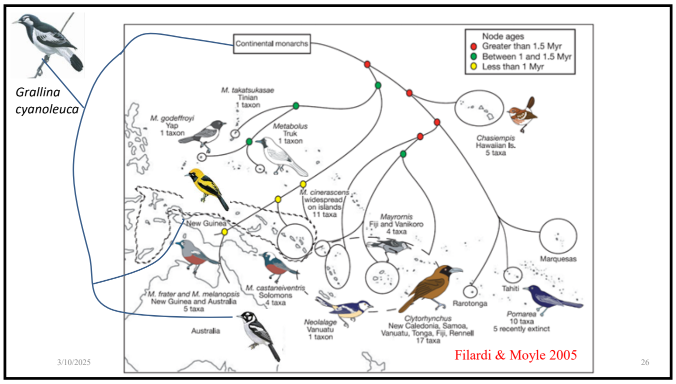

Filardi & Moyle 2005

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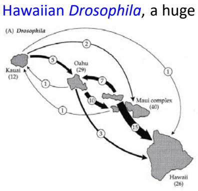

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Today most don't think it was a single "event" – slow divergence

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Critique of founder event speciation by Barton & Charlesworth (1984)

Table 1 Some speciation models classified according to the features described in the text

Features	Peripatric[a]	Founder-flush[b]	Genetic transilience[c]	Classic allopatric[d]	Parapatric[e]	Stasipatric[f]	Shifting-balance[g]	Sympatric[h]
Mechanism driving divergence	Background homozygosity; drift	Relaxation of selection; drift	Deviation from Hardy-Weinberg; drift	Changing selection; accumulation of different mutations	Spatial variation in selection	Drift; meiotic drive	Drift; fluctuations in the adaptive landscape	Disruptive selectio
Genetic basis of isolation:								
Incompatibility per step	Substantial	Moderate	Moderate	Weak to moderate	*[i]	Moderate	Weak to moderate	Strong
Number of genes per step	Many	Many	A few	One or a few	One or a few	One	A few	One or a few
Type of variation	Epistatic polymorphisms	Epistatic polymorphisms	Major gene + modifiers	New mutations; polygenic	*	New mutations	Polygenic	Frequency-depende polymorphism
Geographic relations:								
During divergence	Allopatric	Allopatric	Allopatric	Allopatric	Parapatric	Parapatric	Allopatric	Sympatric
During spread	*	*	*	*	Parapatric	Parapatric	Parapatric	Sympatric
Mechanism of spread	*	*	*	*	Spread into sympatry	Moving hybrid zone	Extinction-recolonization	*
Types of genetic system	*	Mating behavior	*	*	*	Chromosomal	*	Habitat choice

[a] See 120, 124.
[b] See 27, 29.
[c] See 176.
[d] See, for example, 133.
[e] See 45, 58, 64, 102.
[f] See 188, 189.
[g] See 193.
[h] See 116.
[i] An asterisk indicates that the feature is irrelevant, ambiguous, or unspecified

Barton & Charlesworth 1984

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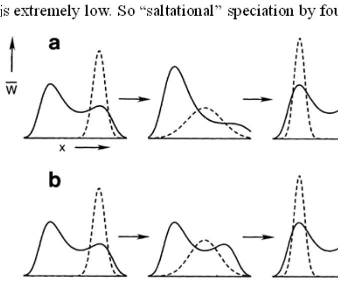
Critique of founder event speciation by Barton & Charlesworth (1984)

1) Drift may occur, but it won't cause major change in allele frequency unless effective population size is extremely low. So "saltational" speciation by founder effect unlikely.



Peak shift by selection:
Environment changes

Peak shift by drift:
Requires small effective population sizes and shallow fitness trough (so change small)

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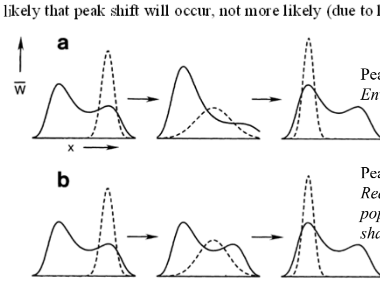
Critique of founder event speciation by Barton & Charlesworth (1984)

2) Reduction in variability due to founder event leading to very low population variability makes it less likely that peak shift will occur, not more likely (due to lack of variability to explore).



Peak shift by selection:
Environment changes

Peak shift by drift:
Requires small effective population sizes and shallow fitness trough (so change small)

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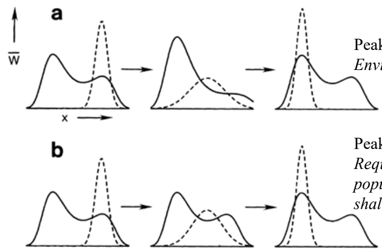
Critique of founder event speciation by Barton & Charlesworth (1984)

3) Loss of heterozygosity at allozyme loci is anyway not observed in e.g. Hawaiian *Drosophila*. In Carson's data, chromosomal polymorphisms are often preserved through inter-island colonizations



Peak shift by selection: *Environment changes*

Peak shift by drift: *Requires small effective population sizes and shallow fitness trough (so change small)*

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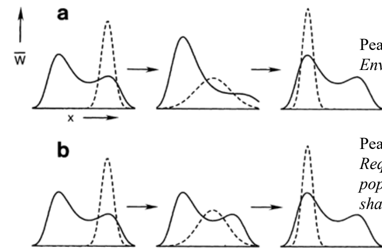
Critique of founder event speciation by Barton & Charlesworth (1984)

4) As a result of all this, "Speciation is therefore more likely to involve many shallow peak shifts than a few strong ones." (p. 148)



Peak shift by selection: *Environment changes*

Peak shift by drift: *Requires small effective population sizes and shallow fitness trough (so change small)*

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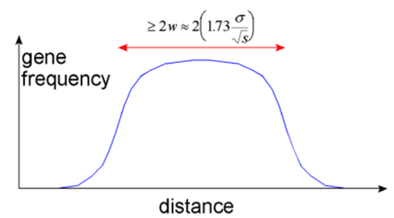
Critique of founder event speciation by Barton & Charlesworth (1984)

5) Mayr's argument for cohesion of the mainland species due to gene flow is wrong:
(a) many small changes can cause divergence; each can take place on the supposedly "cohesive" genetic background
(b) gene flow is only effective over a small range, a few multiples of gene flow distance, σ.



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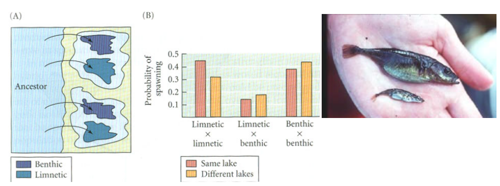
Ecological speciation:
Pleiotropy between ecological adaptation and mating behaviour: maybe common!



Example: Stickleback (*Gasterosteus*) benthic and limnetic forms in Canadian Lakes

An example of parallel evolution in different lakes

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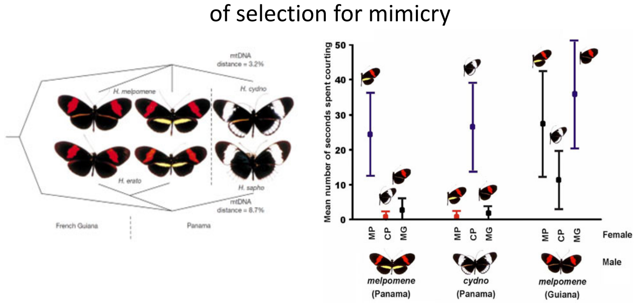
Assortative mating as a by-product of selection for mimicry



CD Jiggins et al. 2001. Nature 411, 302-305

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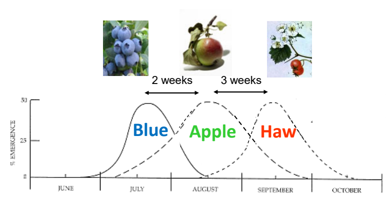
Allochronic (seasonal) ecological isolation



Ripe host fruit for adult mating, female oviposition, and larval feeding are seasonal resource islands. Overwinter diapause timing of flies must match to maximize fitness

Flies have one generation per year, live < 1 month, results in pre- and postzygotic RI

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Selection versus drift in speciation

Could saltational speciation via founder effects, founder flush models, or genetic transilience be justified on the basis of population genetics and new genetic data?

Today's prevailing opinion: No!

Drift may be involved, but if so, it would most likely involve many small changes, rather than a few massive reproductive isolation-causing events.

Selection is likely more important, in allopatry as well, potentially, as in parapatry or sympatry.

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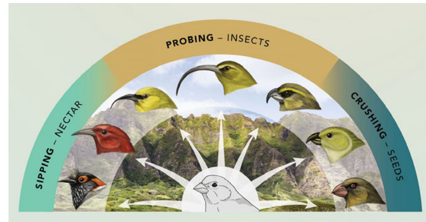
ADAPTIVE RADIATION

microevolution process → macroevolutionary pattern



Pattern biodiversity in which monophyletic group of rapidly diverging species covaries phenotypically with resources they use and environments they inhabit (Schluter 2000)

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