BIOL2007 - THE ORIGINS OF SPECIES

How does speciation happen?

Regardless of species concept, two species form a *bimodal distribution of phenotypes or genotypes*

Even if they hybridise, the 2 species can be distinguished by:
morphology, ecology, behaviour, and/or genetics
A *single* species: *unimodal* distribution.
How are these bimodal distributions of genotypes and phenotypes caused?

Causes of speciation:
random forces (like mutation and drift), or deterministic forces, i.e. natural selection?
Geographical milieu of speciation:
sympatric, parapatric, or allopatric?
Today, we explore both evolutionary causes and geography of speciation.

General rules of speciation

Evidence so far:
1) Speciation is *gradual* (usually), and involves *many loci*. Evidence:
Hybrid zones: hybridising forms differ at many loci, even though not separate species.
Species can overlap without losing identity in parapatry or sympatry; hybridizing races do not.
⇒ species should differ at even more loci. (See Ayala's work in the 1970s on *Drosophila*).
(A major exception to "gradual speciation" rule is speciation via polyploidy).

2) Speciation involves *epistasis*.
To maintain bimodal distribution of genotypes, intermediates must be unfit.
For example, *AABB* and *aabb* have high fitness, whereas *AaBb* and *AAbb* genotypes are less fit.
A and *B* collaborate, or are *epistatic*.

3) *No clear geographic* rule for divergence
Species differ at genes under *intrinsic* or *extrinsic* selection against hybrids.
Extrinsic selection caused by variable *environment*.
Intrinsic selection caused by *heterozygous disadvantage*, *frequency dependent selection* against rare forms, and, very importantly, *epistatic selection*.
Species also differ at loci affecting *mate choice*.
Collectively, these loci cause *reproductive isolation*.

Geography of speciation

Intrinsic selection, extrinsic selection, mate choice.
…just what we have been learning about.
Cline theory: $w = 1.73\sigma/\sqrt{s}$.
So, divergence & speciation possible in *parapatry*.
No requirement for complete geographic isolation.

4) *Species, geographic races, local morphs are part of a continuum*.
No fundamental difference between species and races and morphs genetically. A continuum.
Species just a little bit more divergence
And bimodal when in contact.

Special additional causes of speciation

In addition to the ordinary forces already studied:

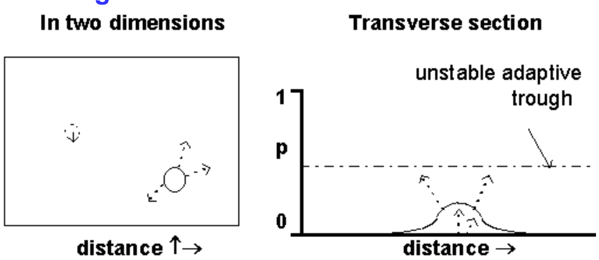
1) Speciation via polyploidy.
Sympatric, sudden. specially plants and more amorphous animals. However, some animals, such as Salmonidae (trout and salmon family) are also polyploids.

Three additional potential causes of speciation:
2) Disruptive selection. A pre-requisite for gradual sympatric speciation.

3) The "shifting balance".
Genetic drift and selection interact (in a *shifting balance* of evolutionary forces).

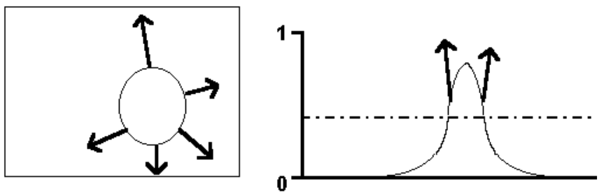
4) "Reinforcement", where direct selection for pre-mating isolation occurs to prevent wastage of gametes on hybridization.
Here we deal with (3) and (4).

The shifting balance

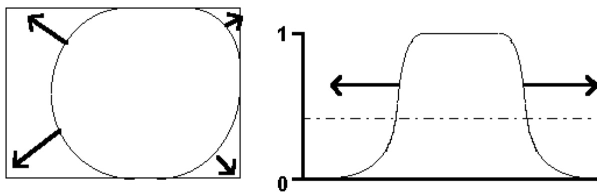


Phase I: local drift (or fluctuation in selection)

Populations move through adaptive trough, and transfer to higher peak in adaptive landscape.



Phase II: local selection to a new adaptive peak



Phase III: Interdemic selection, or spread of new adaptive peak

Proposed by Sewall Wright in 1931-1932
Fisher thought his rival's idea was daft.
Coyne, Barton and Turelli 1997 long paper: argued that no evidence for shifting balance.

Evidence:Unfortunately, the weak part of the theory!

Chromosomal evolution seems, on the surface, well-explained by a variant of the shifting balance.
Patchwork distribution suggests het. disadvantage.
But Coyne et al. argue this is wrong. Chromosomal heterozygous disadvantage could be due to divergence on each chromosome *after* separation.
But maybe perverse to explain away ALL chromosomal negative heterosis in this way.
So: shifting balance is a nice idea, but little direct evidence, and lots of critics.

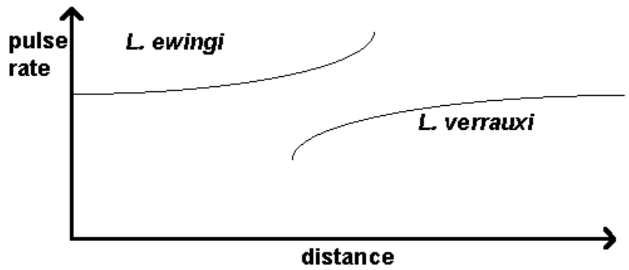
Importance for speciation. Shifting balance one idea how evolution between adaptive peaks could occur in parapatry → intrinsic selection (epistasis).
However, most species differ at many loci (Rule 1).
Drift means each shift creates very little reproductive isolation. (Selection towards must be overcome to reach adaptive trough).
Unlikely that a single shifting balance could generate a new species.
Even if shifting balance happens frequently, must occur many times to generate separate species.

Reinforcement

Divergent forms meet in *secondary contact*.
Random mating may now create unfit hybrids.
Hybridization opposed by natural selection. Direct selection for *assortative mating* (Dobzhansky 1940)
Adaptive mate choice, now termed *reinforcement*.
A kind of disruptive selection on mate choice, or a *good genes* mechanism of sexual selection.

Evidence for reinforcement

Australian tree-frogs *Litoria ewingi* and *L. verrauxi.*
Pulse rate of the males used in mate recognition.



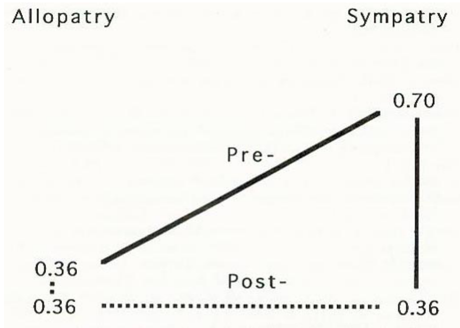
However, since hybrids completely inviable, this example now seen as an example of *reproductive character displacement*, not reinforcement.
And, when hybrids NOT completely inviable, maybe recombination PREVENTS reinforcement.

Evidence from *Drosophila*

171 pairs of closely related divergent forms.
Post-mating isolation = fraction of crosses in which hybrids sterile or inviable.
Pre-mating isolation = fraction of trials of males and females of two species resulting in mating.
Investigated the rate of increase of pre- and post-mating isolation with genetic distance (≈time).

Results from *Drosophila*

Allopatric pairs (I=0.36) ≈ sympatric pairs (0.36), and similar average *genetic distances*.
But average pre-mating isolation higher quicker in sympatric prs (av 0.70) than allopatric prs (0.36).



Differences expected under reinforcement.

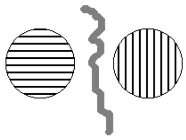
Recent evidence

D. pseudoobscura and *D. persimilis* hybridize (about 1/30,000) in the wild
Some hybrids known to be fertile.
Mating between strains taken from areas of overlap more assortative than when taken from in areas where one species was absent.
We don't know how common reinforcement is; but it almost certainly can occur under certain circumstances.

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 (see your essay references!).

Allopatric speciation
a) Vicariance



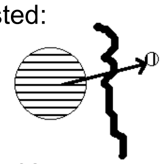
Range of a species split in two.
Divergent drift or selection in different environments. Could even be due to *similar* selection.
Eventually, barriers erode and maybe *secondary contact*. Three outcomes possible:
1) Little divergence: broad or narrow hybrid zone.
2) Hybrid inviability/sterililty, then reinforcement? (But if overlap narrow, not so likely).
3) May have already become separate species.

Evidence

1) Vicariant speciation does eventually occur.
Reductio ad absurdum: marsupials in Australia are distinct species from placentals in rest of world.
2) However, can be very slow:
London plane tree *Platanus*. A hybrid between *P. orientalis* (Asian) and *P. occidentalis* (U.S.: "sycamore").
No contact for > 20 My.
Yet hybrid London plane is fertile seed, and the two have not really "speciated" at all.

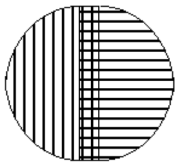
b) Allopatric speciation - the founder effect

A speedier allopatric mechanism was suggested: "founder effect"



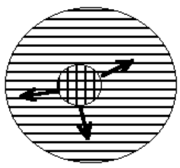
Mayr (1954): founders, take small fraction of available genetic variation (genetic drift as in shifting balance Phase I).
Genes undergo "genetic revolution"; reorganizes genome (selection as in Phase II).
Strong selection, leading to genetic revolution due to (a) genes being unused to low diversity, and (b) different ecological conditions in new home.
→ Secondary contact etc., as for vicariance

Evidence
Spectacular New Guinea birds called the racket-tailed kingfishers, genus *Tanysiptera*. [overhead].
Vicariance speciation, or even parapatric speciation aided by habitat differences on the islands seem as likely. No genetic data to show genetic drift.
Other examples: Hawaiian *Drosophila*, a huge radiation of species in a few million years,
Genetic studies: no evidence of a reduction in genetic diversity. Some closely related species from same island, even more true for snails, crickets.
Lab studies? No evidence for founder effect.

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. 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.

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

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

Example: Host races in the apple maggot.
Native host: hawthorn.
Became apple pest in 1860s.
Quickly spread all over E. USA.

1. Females prefer own host. “Host races”.
2. Host races do not differ in survival; both worse on apple.
3. Parasitoids less successful with apple larvae.
4. Males use host fruits as mating platform. Host switch causes assortative mating via *pleiotropy*.
5. Apple race flies earlier than hawthorn race. More assortative mating via *pleiotropy*.
6. Frequency differences in molecular markers.
7. Host races hybridize, $m \approx 0.06$ per generation.

In this case, little evidence for reinforcement.

But assortative mating via pleiotropy seems likely. With m = 6% gene flow, many deny the apple and haw races have speciated.

But if this kind of sympatric evolution (or almost-speciation) can occur in a few tens of years, could be *extremely important* over geological time.

BRIEF SUMMARY

Causes of speciation	***Status***
Random	
Mutation + drift	Deeply suspect! Would be slow, needs allopatry
Chromosomal mutation (polyploidy)	Known
Selection	
Environmental, pleiotropic, and disruptive	Known, and probably extremely important.
Epistatic incompatibilities	Known, e.g. Haldane's Rule
Reinforcement	Known, but rare?
Sexual selection	Suspected
Random + selection	
Shifting balance	Possible, contested
Founder event	Dubious, contested

Geographic milieu	***Status***
Sympatric	Known, but rare?
Parapatric	Known, likely; little different in theory from allopatric evolution
Allopatric	Known; slow?

CONCLUSION: Some observations...
1) Sympatric speciation: instantaneous (via chromosomal doubling, polyploidy), or gradually (e.g. *Rhagoletis*).
2) Sympatric speciation rapid; important even if rare. Allopatric speciation slow, never observed.
3) Parapatric speciation needs reduced gene flow. So not really different from allopatric speciation.
4) Many intrinsic, extrinsic, mate choice differences are maintained in parapatry.
5) Yet some still argue that sympatric and parapatric speciation must be rare.

FURTHER READING
FUTUYMA, DJ 2005. Evolution. Chapter 16 (pp. 379-404). Speciation.
COYNE, JA, BARTON, N, and TURELLI, M. 1997. A critique of Wright's shifting balance theory of evolution. Evolution 51: 643-671.
BARTON, NH (ed.): Trends in Ecology and Evolution, Speciation special issue, July 2001.

Science Library: View B242 Teaching Collection by going to eUCLid; use Keyword, Basic Search, All Fields: b242