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THE ORIGINS OF SPECIES

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Biodiversity
1.5 million described species
Maybe as many as 30 million species overall

How does speciation happen?
Speciation – genetic divergence within a population

Need to prevent/reduce gene flow for species to form.

Process is usually slow. Genetic divergence takes time

How do species evolve?

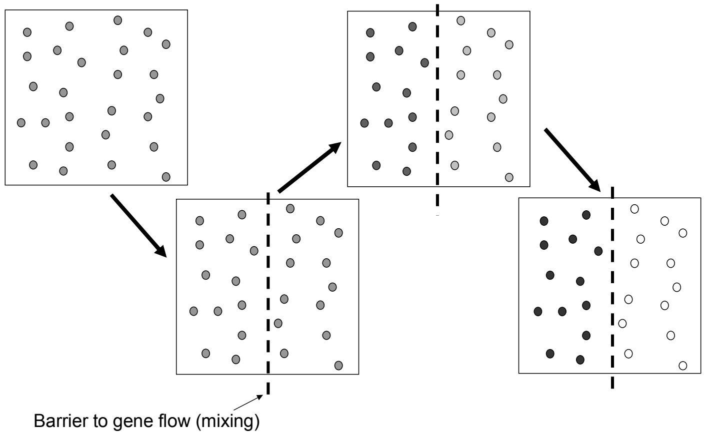
Geographic modes of speciation

- allopatric
- parapatric
- sympatric

Causes of speciation

- random forces (mutation and drift)
- deterministic forces (natural selection)

Allopatric speciation: vicariance



1) Allopatric speciation

a) Vicariance

Range of a species split in two.
No gene flow.
Divergence in separate populations

Eventually, barriers erode and maybe *secondary contact*.
Three outcomes are possible:

1) Little divergence: broad or narrow hybrid zone.

2) Hybrid inviability/sterililty

3) May have already become separate species

Alpheus snapping shrimps

Snapping shrimps

Alpheus snapping shrimps

across Isthmus of Panama

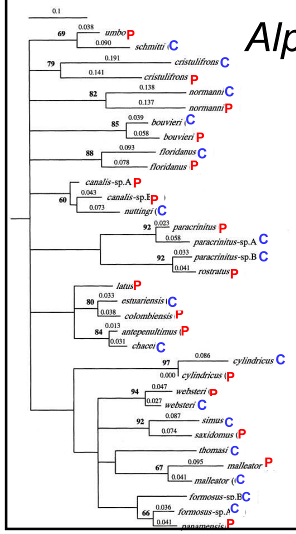
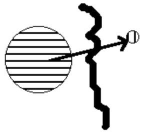


Figure 1. COI-based maximum likelihood approximation (Puzzle 4.0) (Strimmer *et al.* 1997) phylogeny of *Alpheus* taxa with possible transisthmian sister species. Morphological (see Knowlton *et al.* 1993) and molecular assignments of sister species were entirely consistent. Likelihood approximation reliability estimates are shown in bold to the left of the 15 transisthmian pairs. Branch lengths are shown above each Caribbean (C) and Pacific (P) pair member.

b) Allopatric speciation - the founder effect

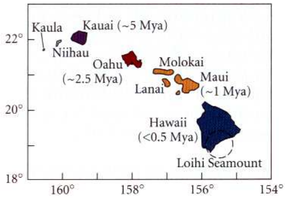
A speedier allopatric mechanism was suggested: "founder effect" Mayr (1954):



1) founders, take small fraction of available genetic variation (genetic drift).

2) Strong selection leading to adaptation to different ecological in new home.

Hawaiian *Drosophila*

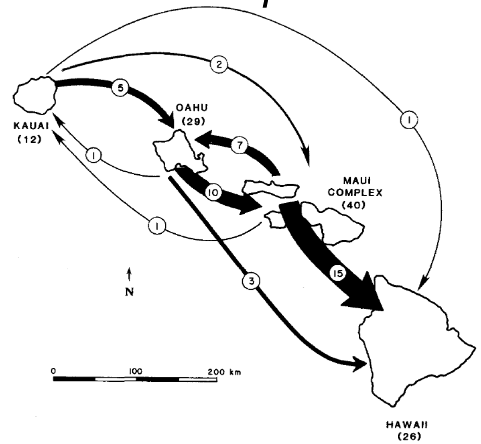


500 named species + 350 other known but undescribed species

Start of Hawaiian *Drosophila* radiation dated to 20 Mya

Similar speciation patterns for Hawaiian snails and crickets

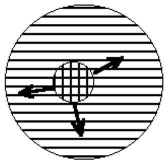
Hawaiian *Drosophila*



Carson 1983 *Genetics*

FIGURE 5.—Geographical summary of the proposed founder events invoked to explain the origin of the fauna of each island. The width of the arrows is proportional to the number of proposed founders. The number of species found on each island is given in parentheses.

2) Sympatric speciation



Genetic divergence of populations inhabiting the same geographical area

Speciation must occur under very high levels of gene flow. Selection causing speciation must be very strong.

Host races in the apple maggot, *Rhagoletis pomonella*

Native host: *hawthorn*

Became *apple* pest in 1860s, due to a host switch

Apple-eating form quickly spread all over E. USA

Reduced gene flow of 6% between races

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

Cichlid fish in African Great Lakes

Lake	Area / km²	No. endemic species
Victoria	68,600	~500
Malawi	29,600	660-1000
Tanganayika	32,900	170-250

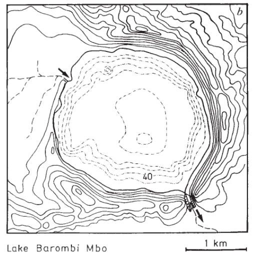
One or two colonisations in Lake Victoria and Malawi

Specialised feeders

Sexual dimorphism: males often brightly coloured

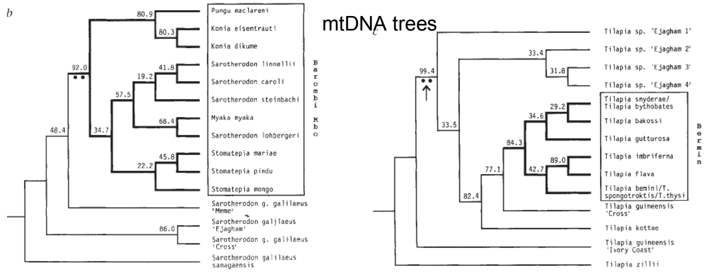
Cichlid fish in crater lakes

Schliewen et al (1994) *Nature*



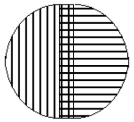
Lake	Area / km²	Endemic species
Barombi Mbo	4	11
Bermin	0.6	9

mtDNA trees



3) Parapatric speciation

Speciation due to non-random mating of a population within a continuous geographic area.



Difficult to prove parapatric speciation.

In any case allopatry only superficially different from parapatry; gene flow is always somewhat restricted

Causes of speciation

random forces (mutation and drift)

deterministic forces (natural selection)

Speciation by polyploidy

Chromosome doubling by **autopolyploidy** or **allopolyploidy**

This type of speciation is rapid

Whether new polyploid species survives is stochastic.

Needs to establish local population not swamped
by parental gametes

Polyploidy very common: 40-70% of plant species

Reproductive isolation by selection or drift?

Drosophila pseudoobscura

4 populations raised on starch-rich diet: Ist, IIst , IIIst, IVst

4 populations raised on maltose-rich diet: Ima, IIma, IIIma, IVma

One year of adaptation to diet

like mates with like

Mate choice experiments: there is assortative mating?

Selection and NOT drift causes assortative mating

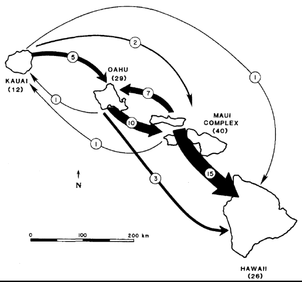
Dodd (1988) *Evolution*

Speciation by drift + selection

Hawaiian *Drosophila* radiation

New species clearly due to founders from older islands

But NO evidence for low genetic diversity in these species



Speciation on new islands due to
selection in new environment
NOT due to drift in founders

Disruptive selection

Selection against intermediates

Disruptive selection + assortative mating can
produce a bimodal distribution

Probably important for sympatric speciation

Host races *Rhagoletis pomonella*

Native host: *hawthorn*

Became *apple* pest in 1860s, due to a host switch

Apple-eating form quickly spread all over E. USA

1. Parasitoids less successful with apple larvae (selective advantage of host switch)
2. Females have genetic preference for laying on fruits of own host (disruptive selection on host choice)
3. Males use host fruits as mating venue. So host switch has a *pleiotropic effect* on assortative mating
4. Apple race flies earlier than hawthorn race. *Pleiotropy* again
5. Leading to genetic differentiation

Speciation in cichlids

Sympatric speciation due to disruptive selection leading to ecological specialisation?

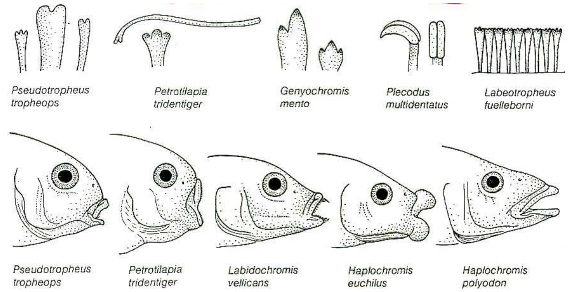


FIGURE 13
A sample of the diverse tooth forms and head shapes among the Cichlidae of the African Great Lakes. The differences in morphology are associated with differences in diet and mode of feeding. (Redrawn from Fryer 1959 and Fryer and Iles 1972, after various sources. Courtesy of the Zoological Society of London)

Speciation in cichlids: sexual selection

Sexual dimorphism: males often brightly coloured

Closely related species often different colours

Assortative mating: female preference based on male colour

Random mating when no colour information (e.g. when water is turbid).

Seehausen et al. (1997) *Science* **277**: 1808-1811

Reinforcement

Reinforcement: the enhancement of prezygotic isolation in sympatry by natural selection

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*.

Prediction: Premating isolation stronger in sympatric compared to allopatric populations.

Reinforcement in *Drosophila*

Coyne & Orr (1997) *Evolution* 51: 295-303

171 pairs of closely related divergent forms.

Pre-mating isolation = fraction of trials of males and females of two species resulting in mating.

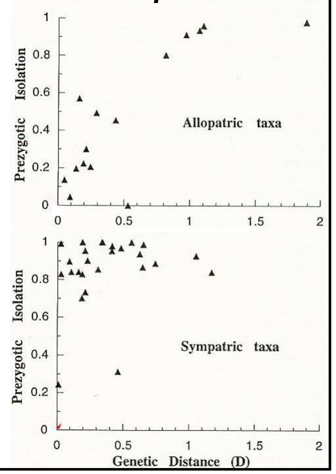
Post-mating isolation = fraction of crosses of males and females of two species in which hybrids sterile or inviable.

Reinforcement in *Drosophila*

Coyne & Orr (1997) *Evolution* 51: 295-303

Pre-mating isolation
in sympatric pairs > allopatric pairs

Post-mating isolation
in sympatric pairs ≈ allopatric pairs



Brief summary

Geographic modes of speciation	Status
Sympatrc	Known, but good examples are rare
Parapatric	Known, likely Little different in theory from allopatric
Allopatric	Known. Slow?

Brief summary

Causes of speciation		Status
Random	Mutation + drift	Deeply suspect! If occurs, probably very slow, needs allopatry
	Chromosomal mutation (polyploidy)	Known
Selection	Environmental, pleiotropic and disruptive	Known
	Reinforcement	Known. Possibly uncommon?
	Sexual selection	Suspected
Random + selection	Founder effect	Dubious, contested
	Shifting balance	Possible, contested

Further Reading

FUTUYMA, DJ 1998. Evolutionary Biology. Chapter 16 (pp. 481-516). Speciation.

BARTON, NH (ed.): Trends in Ecology and Evolution, Speciation special issue, July 2001.

COYNE, JA & ORR, HA 2004. Speciation. Sinauer Associates, Sunderland, Mass. xiii+545 pages.