Speciation by polyploidy and interspecific hybridization

I. Instantaneous sympatric speciation via ploidy changes

**Autopolyploidization**: a doubling of the diploid chromosome number in a single species.

- Can be considered a type of bifurcating (not reticulating) speciation
- Much rarer than allopolyploidization?
- Examples?? (“stealth speciation”)

As a result, polyploidy generates immediate reproductive isolation and sympatric speciation

II. Rapid sympatric speciation via hybridization+ploidy changes

**Allopolyploidization**: each parent of the hybrid contributes its entire nuclear genome (usually with uniparental inheritance of the organelles)

- Parents needn’t have the same number of chromosomes
- Simplest case is when gametes of both parents are unreduced

Weedy mustard *Brassica napus*, from *B. rapa* x *B. oleracea*. This is found in nature, but can also be produced in the lab (over and over again).
more allopolyplody...

**Spartina**, England:
- S. maritima (native)  
- S. alternifolia (1870 - USA)
- S. townshendii
- S. anglica (vigorous?)

**Cordgrass**

**Gilia,** California:
- G. aliquanta  
- G. minor  
- G. major

Many other California Gilia's have originated similarly.

Repeated sympatric speciation by **allopolyplody** in *Clarkia*, generates **reticulate** evolutionary patterns (after Lewis & Lewis 1955)
Polyphyletic origin of an animal species via autopolyploidy:
Tetraploid treefrogs (Ptacek et al. 1994, Holloway et al. 2006)

- Physical constraints (larger cell size) of tetraploids automatically lower & slow down the male song.
- Apparently, these changes are matched by female preferences (Tucker & Gerhardt 2012)
- This makes for very strong premating reproductive isolation between diploids and tetraploids, based on songs.
- (Triploids are similarly affected, but show intermediate values.)

More sympatric speciation via hybridization

**Diploid (homoploid) hybridization:** each parent contributes half of its diploid chromosome set, as it would with normal sex.
- Parents usually have the same chromosome #, but partially incompatible genomes.
- Relatively rare, because hybrids are often reproductively compatible with parents.
- Occurs if there’s a good niche available.

“Homoploid hybrid speciation” [also called recombinational speciation (Rieseberg), quantum speciation (Grant 1966), etc.]
Homoploid hybrid speciation (HHS): Formation of a new hybrid species without change in chromosome number.

1. **Recombinational speciation** (Rieseberg, many papers)

   "Mosaic Genome" Hybrid Speciation (Jiggins et al. 2008)

   Establishment and stabilization of a recombinant lineage combining compatible regions of the genome in similar proportions from A and B – SLOW; as reflected in a large signal from neutral markers.

Recombinational speciation may be sympatric, but not instantaneous (after Rieseberg and Wendel 1993)

The problem of the initial rarity of hybrids – and concomitant lack of potential mates – is partially solved if other modes of reproduction are available (asexual reproduction or self-fertilization) (Stebbins 1950)
Recombinational sympatric speciation in *Helianthus* sunflowers: Origin of new diploid species through hybridization (after Rieseberg and Wendel 1993)

Another variant of homoploid hybrid speciation:  
2. **Hybrid trait speciation** (Jiggins et al. 2008)

Backcrossing of alleles, i.e. introgression, but limited and unidirectional.  

<table>
<thead>
<tr>
<th>A</th>
<th>C</th>
<th>B</th>
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Alleles control a trait with adaptive potential that also causes reproductive isolation (a "magic trait") –

**FAST;** little sign from neutral markers.

Recent work suggests that homoploid hybrid speciation (either type) is **more common in animals than previously thought**, with evidence from **fishes** (Selz et al. 2014), **birds** (Elgvin et al. 2011; Brelsford 2011), **mammals** (Larsen et al. 2010), & **flies** (Segura 2011; Price et al. 2008).

And **butterflies**: 

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HHS in iconic tiger swallowtails (Papilio): Distribution of conserved genomic clusters among four species (Zhang et al. 2013).

This is type 1, “Recombinational.”

HHS in Müllerian mimics? Examples of hybrid patterns in Heliconius & their progenitors (Jiggins et al. 2008).

This is type 2, “Hybrid trait.”
Evidence of hybrid trait speciation in *Heliconius heurippa*
(Melo et al. 2009; Salazar et al. 2010; but see Brower 2011, 2013)

Gene genealogies for 39 kinesin and its flanking regions (nexin & 59 kinesin)

Rates of Speciation: The ubiquitous “Hennigian comb.”
Clearly, accumulating extinctions have erased the signal of rapid diversification.
Rapid, recent, and repeated speciation of 1000 Cichlidae in Lake Malawi: ecological, sexually-selected and possibly sympatric? (Kocher 2004)

A. Habitat adaptation
B. Diversification of feeding apparatus
C. Diversification of colour pattern

ecological adaptation — sexual selection

Age of lake is estimated at 40,000 yrs to 1-2 million yrs → **FAST speciation!**

How does one measure the rate of speciation? Two metrics: **TFS** (time for speciation) and **BSI** (biological speciation interval) (Futuyma 2005)

- **TFS**: the time between the beginning and end of the evolution of reproductive isolation.
- **BSI**: the average time that has elapsed between two sequential bifurcations.
- \(1/\text{BSI}\): the speciation rate (number of species per unit time – usually, *per million years*), (either linear or log scale)
How much time does it take for speciation? (1)

Measuring this involves overcoming several obstacles:

1. How can we tell when speciation began and ended, when we can’t see it happening?
   - “Time for speciation” (TFS) is best measure, but it is also the hardest to determine (and therefore rarely used).
   - “Biological speciation interval” (BSI) is often the best we can do, but it’s realistic only for clades that have speciated recently (unmodified by extinction).

2. Even if we had evidence of this, how do we put a date or time span on the events?
   - Geological and radiometric dating? – very inaccurate at these small time scales.
   - Genetic distances (Nei, Rogers, or Cavalli-Sforza), based on allozyme or sequence data? – but big assumption is that of a molecular clock.
   - Sequence divergence, based on nucleotide data? – but again, must assume clock-like evolution.

How much time does it take for speciation? (2)

Various bits of indirect evidence:

Genetic distance, $D_*^*$ has been shown to measure 0.10-2.00 for different species, and above 1.00 for different genera (note that in theory $D$ can vary from zero to infinity).

1. Nei estimated that it takes on average 5 million years for $D$ to go from 0 to 1.00 (based on many studies)

2. In Coyne & Orr's survey of Drosophila, average $D$'s for reproductively isolated species pairs were:
   - 0.54 for pairs that remain allopatric.
   - 0.04 for pairs that were always, or become, sympatric.

3. Implication: “sympatric speciation will take less than 1/10 the time of allopatric speciation.” Converted to time, this means:
   - 2.7 million years for pairs that remain allopatric.
   - 200,000 years for pairs that were always or become sympatric.

* a measure of the dissimilarity of genetic material between different species or individuals of the same species
Some data: *mtDNA sequence divergence of pairs of North American songbirds* (after Klicka & Zink 1997)

Most pairs of species seem to be more than 2 my old, so BSI should be at least this long.

Sequence divergence of 2% (not Nei’s D) represents about 1 my since separation.

Note: For insects: mtDNA COI barcode value (685 bp) of 2.3% sequence divergence per MY (Brower 1994). Or 3.54%/MY (Papadopoulou et al. 2010).

**Hawaiian silversword diversity**

Asteraceae, Heliantheae: 30 spp. in 3 genera; monophyletic (hybrid of 2 Calif. tarweeds?)
Rates of speciation for some plant lineages, measured as $1/\text{BSI}$ (from Kadereit & von Hagen 2003)

<table>
<thead>
<tr>
<th>Lineage</th>
<th>No. of species</th>
<th>Estimated age of range (my)</th>
<th>(expon.) $\text{BSI}_e$ (yrs)</th>
<th>(linear) $\text{BSI}_l$ (yrs)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Island radiation (allopatric speciation)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cyanoa孤独ia + Botryotrocha ampullaceae Islands</td>
<td>74</td>
<td>17.4 (max)</td>
<td>6.23</td>
<td>2.8</td>
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<tr>
<td>Rodriguezia DC + Juan Fernandez Islands</td>
<td>57</td>
<td>8.7 (max)</td>
<td>4.45</td>
<td>3.4</td>
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<tr>
<td>Aboriginal Chile, atoll + Austral Highlands Islands</td>
<td>18</td>
<td>1.2 (max)</td>
<td>0.49</td>
<td>0.6</td>
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<tr>
<td>Monotropa + Biodiversity Pacific Islands</td>
<td>26</td>
<td>6.6 (max)</td>
<td>3.12</td>
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<tr>
<td>Najas in Central America</td>
<td>15</td>
<td>ca. 2.7</td>
<td>1.00</td>
<td>0.5</td>
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<tr>
<td>Gentianella acaulis + species Andes</td>
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<td>ca. 3</td>
<td>1.71</td>
<td>0.97</td>
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<tr>
<td>Gentianella acaulis + species New Zealand</td>
<td>12</td>
<td>ca. 2</td>
<td>1.73</td>
<td>1.00</td>
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<tr>
<td>Najas in South America</td>
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<td>ca. 1.9</td>
<td>1.79</td>
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<tr>
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<tr>
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<td>16</td>
<td>ca. 0.8</td>
<td>0.47</td>
<td>0.4</td>
</tr>
</tbody>
</table>

Attributed to innovative nectar spurs & colonization of Andes mountains (a Gentian)

Attributed to Pleistocene aridity

How fast is speciation? Desert Pupfish from Death Valley, etc. (Cyprinodon spp.)

> 10,000 yrs ago: the Mojave Desert was not a desert

Postglacial climate change in southwestern North America led to allopatric isolation.
Shrinking and disappearing lakes over the past 10,000-30,000 years

then...(>10,000 years ago)  ...and now.

There are about 20 desert pupfish species in all, each restricted to a few springs, streams, or other such refuges (allopatric speciation). Must be only ≈ 10,000 years old (BSI=0.01my).
Rapid speciation: more fishes (and note convergent evolution)

Estimates of clade ages range from 2,000 – 4,000,000 years

Lake Tanganyika (oldest): Lake Malawi (younger):
- {species}
- {species}
- {species}
- {species}
- {species}

Lake Nabugabo (new):
Five cichlids derived from Lake Victoria (youngest), radiocarbon dated at precisely 4,000 years ago (Martens 1997).

Allopatric or sympatric? – not determined.

Lake Victoria: 500 species of Cichlidae in 14,500 years (Genner et al. 2007)

(but note uncertainty: maybe as much as 200,000 yrs., and 3 or more founders)
Neighbor-joining phenogram of 670 species of **African Lake Cichlidae**, based on mtDNA control region sequences (Nagl et al. 2000)

Lake Tanganyika

Lake Malawi

Lake Victoria (some are very young clades!)

Lake Nabugabo

...and is it metabolism-dependent? (Allen et al. 2006 on Foraminifera; Ricklefs 2006 on birds: tropical bias)

Summary of speciation vs. time for some familiar radiations/bifurcations (Seehausen 2006; et al.)

- postglacial salmonids, sticklebacks
- Hawaiian Laupala; S. Afr. Poaceae; S. Amer. Halenia; Eurasian Dianthus
- 3.47-4.18 spp/my
- H. sapiens 4.5 mya
- Howea palms 0.47 mya
- allopatic Drosophila 1.1-2.7 my
- Hawaiian honeycreepers
- Average for Arthropoda 6.25 my
- Approximate age of clades, TFS or BSI

- Carribean anole lizards

Sockeye salmon (56 yrs), Anthoxanthum meadow grass (144), Rhagoletis flies (150-350), Hawaiian banana moths (1000), sympatric Drosophila (800-200,000); Lake Victoria cichlids (75.6 spp/my), Hawaiian cave planthoppers (400 spp/my)
Effect of time and niche heterogeneity on speciation:
Evidence from multiple African cichlid radiations (Seehausen 2006)

Supports ecological speciation via habitat heterogeneity

This explains Hennigian combs: role of extinction

No difference in TFS

Older lineages have disproportionately fewer species

(20 cichlid radiations)
(29 radiations)
(20 radiations; effect of lake size removed)