Mechanisms of Speciation

So...

How can microevolutionary processes of Genetic Drift, Natural Selection, Mutations, etc. lead to more macroevolutionary processes such as the formation of new species?

This gap in understanding was addressed somewhat during the Evolutionary Synthesis.
Some Key Tenets of the Modern Synthesis

- Populations are the units of Evolution
- **Mendel vs Darwin**: Continuous traits are also coded by particulate genes, but many genes
- **Mutation vs Selection**: Mutations are sources of genetic variation upon which Selection acts
- Natural Selection and Mutation are not the only evolutionary forces. Example: Genetic Drift, Recombination
- **Microevolutionary processes**, such as Drift, Selection, Mutation, lead to Macroevolutionary changes (such as speciation)

However, at the time of the Evolutionary Synthesis, the genetic mechanisms of speciation were not well understood

Common Mechanisms of “Speciation” in different taxa

- **Animals**: Outbreeding depression, breakdown of co-adapted gene complexes (Dobzhansky-Müller incompatibilities) → Reproductive Isolation
- **Plants**: Polyploidization
- **Prokaryotes**: Horizontal Gene Transfer but, it’s hard to define what “speciation” is for a prokaryote

Mechanisms of Speciation

(1) **Genetic Models**: (Book doesn’t discuss sufficiently, but important)
- The roles of: Mutations, Natural Selection, Genetic Drift
- The interaction between these three evolutionary mechanisms could cause two populations to become two different species

(1) **Mechanisms of Speciation**

(1.1) **Genetic Models**:
- How do Genetic Drift, Natural Selection, Mutations, etc. create new species?
- Are there “speciation” genes?

(1.2) **Species Concepts**:
- What exactly is a species???

Today’s OUTLINE:

- Focusing on Genetic Mechanisms of Speciation:
  - Dobzhansky-Müller incompatibilities
  - Common mechanisms in plants: Polyploidization
Genetic Model of Speciation: Dobzhansky-Müller Incompatibilities

Covered in 16.3 in your book (Freeman & Herron) but with the details glossed over

- How population genetic processes lead to speciation
- The link between microevolution and macroevolution
- This particular model of speciation applies only to sexual species

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- Speciation: the process by which populations become different species
- Microevolution: results from evolutionary mechanisms (mutation, drift, selection, etc) acting within a population
- Macroevolution: refers to evolutionary change above the species level

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- Reproductive isolation occurs as a byproduct of genetic divergence between two populations
- Mutations accumulate in each population at different loci
- These mutations become fixed by natural selection or genetic drift in each population
- While the mutations are functional on their normal genetic backgrounds, they don't work well together when they are brought together in hybrids (negative epistasis)
- Causing failure to mate or hybrid sterility or inviability (“hybrid breakdown”)

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- As ancestral populations diverge, each lineage evolves independent substitutions that are not detrimental in their native genomic contexts.
- However, because the derived alleles have never been tested together, they can cause genetic incompatibilities when combined in a hybrid.

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- As ancestral populations diverge, each lineage gains different mutations (shown as lower case letter alleles in the figure) that are not detrimental in their native genomic contexts. However, because the new derived alleles have never been tested together (not yet taken out by selection), they can cause genetic incompatibilities when combined in a hybrid.

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- For instance, an enzyme might have 4 subunits. A new mutation in one subunit might make that subunit no longer functionally compatible with a new mutation in another subunit of the enzyme (encoded by a different gene). If these incompatible mutations arise in different populations, they might be fine without the other mutation....
- But, if the two populations come together, and the two incompatible mutations are now brought together in the same individual, the hybrid might now be inviable (die) or sterile (infertile).

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A population with two loci

The population becomes divided and geographically separated (allopatric)

Natural Selection and Speciation
Selection favors different alleles in each population

Natural Selection and Speciation
The different alleles become fixed in each population
In some cases, these new fixed alleles will not function with loci in the other genetic background.

Some Hybrids will be inviable.

Across multiple loci across the genome, such incompatibilities will lead to inviability of hybrids.

Across the genome, the impact of hybrid incompatibilities will differ at different loci, depending on the magnitude of incompatibility between alleles, dominance at each locus (which alleles are expressed), etc.

Case 1: The new alleles are A and B and they are dominant at their own respective loci.
And if A and B are alleles that are incompatible between the two loci.

- Parents: AAbb x aaBB
- F1: AAbb x AAbb
- If any of the incompatible alleles are dominant, selection will act very quickly on the F1 generation.

Case 2: At loci where the alleles are codominant at their own loci (both alleles expressed).
And if a and b are alleles that are incompatible across the two loci.

- Parents: aaBB x AAbb
- F1: aaBB x AAbb
- Hybrid breakdown could proceed at the first generation (though selection might not act as strongly as in Case 1)... as the incompatible alleles will both be expressed.
Crossing between two divergent populations

Case 3: At loci where there is dominance, the new mutations are more commonly recessive at their own loci
- And if a and b are alleles that are incompatible between the two loci
- Parents: \(aaBB \times AAbb\)
- F1: \(AaBb \times AaBb\)
- F2 (different combos, numbers not indicated): \(AABB, AaBB, aaBB, AAbb, AaBb, AAbb, AaBb, aaBb\)
- Hybrid breakdown most commonly appears at the F2 generation because dominance typically masks deleterious alleles at the F1 generation

Crossing between two divergent populations

Case 3: At loci where there is dominance, and the new alleles are typically recessive, and if the new mutations are incompatible with each other
- Parents: \(aaBB \times AAbb\)
- F1: \(AaBb \times AaBb\)
- F2 (different combos, numbers not indicated): \(AABB, AaBB, aaBB, AAbb, AaBb, AAbb, AaBb, aaBb\)
- At any one locus, only a fraction of the hybrids are likely to show deleterious effects

Crossing between two divergent populations

Case 3: At loci where the new mutations are recessive and incompatible with each other
- Parents: \(aaBB \times AAbb\)
- F1: \(AaBb \times AaBb\)
- F2 (different combos, numbers not indicated): \(AABB, AaBB, aaBB, AAbb, AaBb, AAbb, AaBb, aaBb\)
- If you sum across the entire genome, many many individuals will show F2 hybrid breakdown across some of their loci.
- So, you will see many inviable F2 offspring in divergent populations

So, eventually the two populations can no longer come together (due to hybrid breakdown) and they become different species
- Speciation could happen gradually in that some genes might become more diverged and unable to function in the genetic background of the other population more quickly than others
- So, during the process of speciation, some hybrid individuals might by chance be more viable than others, depending on the combination of alleles that the individual happens to have

Genetic Models

Genetic Drift and Speciation
- Genetic drift can work the same way, but often takes longer (even weak selection can speed rate of speciation; Gavrilets 2000)
- Random drift of genes in each population can lead to incompatibilities
- So far, evidence suggests that speciation occurs more readily through selection on different populations than through genetic drift.
- Speciation could arise with the breakdown in coadapted gene complexes for any functional gene that affects survival.
- However, mutations in any genes that affect reproductive compatibility (sperm, eggs) could lead to rapid speciation (“Speciation Genes”)
“Speciation genes”:
- Evolutionary changes (mutations) at genes that affect reproduction (e.g. sperm motility, egg coat protein) could make speciation happen rapidly.
- Sometimes divergence in single genes could cause speciation (often those involved in mating or reproduction).
- These genes could have diverged through selection or genetic drift.


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**So, what about the genus *Homo***?

- We have interbred with 3-5 other species of *Homo*.
- Are we the same species, or not?

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**Speciation through Polyploidization**

Herron & Freeman, pp. 634, but with more mechanism presented here.

Example: Dandelion, Eurasian origin.
Diploid, triploid, tetraploid populations.
North American invasive populations are triploid and sterile, reproduce asexually.

*Taraxacum officinale*
**Polyploidy**

- Polyploidy is much more common in plants than in animals, and polyploidization is an important mechanism for speciation in plants.
- Estimates suggest that 30–80% of living plant species are polyploid, and many lineages show evidence of ancient polyploidy (palaeopolyploidy) in their genomes (Rieseberg 2007).
- Polyploidization is estimated to be associated with ~15% (most according to Pam Soltis) of speciation events in angiosperm (flowering plants), and ~31% in ferns (Wood & Rieseberg 2009).

**Polyplody**

- Often, especially in the case of allopolyploidization, the hybrid can no longer cross with parental species, especially when the hybrid has an odd number of chromosomes → chromosomes cannot line up during meiosis → cannot make viable gametes, must reproduce asexually.
- Such hybrids can no longer intercross with parental species, and become reproductively isolated → on a separate evolutionary trajectory.
- → Instant new species in one generation!
Failure of cell division after chromosome duplication gives rise to tetraploid tissue (a mutation).

Gametes produced are diploid, instead of haploid.

Offspring with tetraploid karyotypes may be viable and fertile.

Hybrids between different species where chromosome # not reduced (a type of mutation).

Applies to many plants, most weeds

Some are cannot reproduce sexually (often when odd number chromosomes), but can reproduce asexually

Often results in “fixed heterosis” (fixed heterozygous advantage)

Numerous examples of successful invaders in recently-derived allopolyploids (such as Barnyard grass, reed canary grass, Spartina anglica)

Can reproduce sexually

Cannot reproduce sexually (odd # of chromosomes, can’t segregate during meiosis)
Several different pathways of allopolyploid formation have been described.

**One-step model:** Allotetraploids are formed by fusion of unreduced male and female gametes from two diploid species. Direct hybridization between two autopolyploid species is also categorized in a one-step model.

**Two-step model:** An allotetraploid is formed by an inter-specific cross between two diploid species followed by somatic doubling in meristematic tissues.

**Triploid-bridge model:** triploids are formed by fusion of unreduced and reduced gametes from two diploid species and then unreduced gametes from triploids fuse with reduced gametes from diploids, which can generate stable allotetraploids.
**Species A**

- $2n = 6$
- Normal gamete $n = 3$

**Species B**

- $2n = 4$
- Unreduced gamete with 4 chromosomes

**Hybrid**

- With 7 chromosomes
- Unreduced gamete with 7 chromosomes
- Normal gamete $n = 3$

- Sexually fertile hybrid (allopolyploid) $2n = 10$

**Allopolyploidization**

- These hybrids have more than two copies of homologous chromosomes, and are polyploid
- The homologous chromosomes are not identical, as they come from different species, but they do share many genes, and have a lot of redundancy

**Many plants are allopolyploids**

- Polyploidy is much more common in plants than in animals
- Polyploidization is an important mechanism for speciation in plants
- Many important crops (oats, cotton, potatoes, tobacco, and wheat) are polyploids

**Many invasive plants are allopolyploids**

- Many Allopolyploids are asexual and have rapid population growth rate
- Polyploids have the capacity for greater physiological buffering than their diploid progenitors because multiple copies of genes often leads to increased function... Such as increased enzyme activity due to enzyme multiplicity
- Polyploids often become diploidized over time, so that they could have sex and increase genotypic diversity, and respond to natural selection (odd# chromosome polyploids cannot undergo meiosis, and even# chromosome polyploids still have trouble with lining up the chromosomes during meiosis)

**Ecological Implications**

Many species have arisen through allopolyploid hybridization

Many new species are arising today through the hybridization of native and exotic species (or between exotic species)

**Big Concern:** hybridization between weeds and genetically engineered crops!
Diploidization of Polyploids tends to occur over time

- **Diploidization**: the evolutionary process whereby a polyploid species ‘decays’ to become a diploid (paleotetraploid) with twice as many distinct chromosomes
- For example, for a tetraploid, the key event is the switch from having four chromosomes that form a quadrivalent at meiosis, to having two pairs of chromosomes each of which forms a bivalent.
- In population-genetics terms, this is the switch from having four alleles at a single locus to having two alleles at each of two distinct loci
- This process of evolution probably happened in vertebrates (which includes humans)

Diploidization of Polyploids tends to occur over time

- The genome often ends up larger
- While the overall gene content is sometimes reduced to one that is similar to the pre-duplicated ancestry, the overall architecture of the diploidized genome will be vastly different from the original pre-duplicated genome
- Almost all angiosperms are likely to be ancient polyploids that have undergone diploidization

Mechanisms of Diploidization:

- Differentiation or translocation so that homologous loci are no longer homologous → end up with more genes
  - Differential mutation of gene duplicates, leading to neofunctionalization or subfunctionalization
  - Transposition events
  - Chromosomal rearrangements, such as inversions in duplicated chromosomes
- Mutations that lead to loss of function → gene loss, gene silencing
- In some gene families, duplicate copies are retained
- Overall, end up with larger genome size after polyploidization followed by diploidization

Tradeoffs between polyploidy and diploidy

**Benefits of Polyploidy**
- Grow faster
- Larger
- Rapid population growth rate in asexuals
- Often results in “fixed heterosis” (fixed heterozygous advantage among the multiple chromosomes) in asexuals
- Gene redundancy, greater genetic robustness (if one gene is bad, have another copy)
- Polyploids have the capacity for greater physiological buffering than their diploid progenitors due to enzyme multiplicity
- Increased enzyme activity, novel enzymes and metabolites, increased metabolic regulation
Tradeoffs between polyploids and diploids

Benefits of Polyploidy

- Majority of agricultural crop species appear to be polyploids (oats, cotton, potatoes, tobacco, and wheat)
  - Polyploidy has conferred distinct advantages for the development of agronomically important traits.
  - For example, polyploidization has been associated with increased size of harvested organs

- Many invasive species are recently-derived allopolyploids (such as Barnyard grass, reed canary grass, Spartina anglica, Dandelion)
  - Rapid somatic growth and rapid population growth would enable invasive species to outcompete native species

Costs of Polyploidy

- In asexual polyploids: No recombination with genomes of other individuals (no sex), no increase in genotypic diversity

- Problems during Mitosis and Meiosis: Polyploidy increases the complexity of the processes that are involved in managing and partitioning chromosomes during cell division.

- Epigenetic Instability: Epigenetic remodeling occurs during polyploidization, which leads to both the activation and suppression of gene expression... sometimes this leads to nonadditive changes in gene expression, some of which could be deleterious

Concepts

Speciation
Genetic Models & Genetic Drift & Natural Selection
Polyploid Speciation

1. How might microevolutionary mechanisms (genetic drift, selection, mutation) lead to the formation of new species? Which of the following is FALSE?

(A) Disruptive selection could act to cause genetic differentiation between two populations

(B) Hybrid breakdown between two populations can be a key factor

(C) Mutations could accumulate in two populations and become fixed through selection or genetic drift, leading to hybrid sterility or inviability

(D) Genetic drift is thought to be more effective at causing two populations to diverge and become separate species than natural selection

(E) Geographic separation between two populations could start the process of speciation

2. You are a geneticist working for an agricultural research firm. Your job is to create new crop species of commercial value. You decide to hybridize two species that differ in chromosome number, and end up with hybrids with a chromosome number that differs from its parents. Which of the following is most FALSE?

(A) You have created a new allopolyploid species.

(B) Such species created through hybridization are always sterile, and can never reproduce without human assistance because the chromosomes cannot line up during meiosis.

(C) Such new species are often more vigorous (greater fitness, growth rate) than either parent species because of fixed heterosis (heterozygous across loci).

(D) Such ability for very different plants species to hybridize poses a challenge to the biological species concept and is a major mechanism for speciation in plants.

3. Which of the following is TRUE regarding speciation (the formation of new species)?

(a) Speciation requires geographic separation

(b) Dobzhansky-Müller incompatibilities can result in more rapid speciation in asexual species

(c) Dobzhansky-Müller incompatibilities require changes in "speciation genes," or genes that affect reproduction (sperm coat protein, sperm motility, etc.)

(d) Speciation requires disruptive selection to act

(e) None of the above
4. Many polyploids become diploids over time. Which of the following is NOT a contributing cause or mechanism of diploidization?
(a) The key event is the switch from having four (or more) chromosomes line up during meiosis to having two chromosomes line up during meiosis
(b) Diploidization occurs so that the organism could revert back to the more compact genome size and similar gene number prior to polyploidization
(c) Some gene copies lose function due to random mutations
(d) Some gene copies become novel genes due to random mutations
(e) Some homologous gene copies become transposed to other parts of the genome and become new genes

5. Which of the following scenarios is likely to lead to the most rapid formation of new species?
(a) Two populations become geographically separated, and there is continued migration between the populations
(b) Two populations become geographically separated, and then new mutations arise in each population that become fixed due to genetic drift
(c) Two populations that are in the same location diverge due to sexual selection for different traits in the two populations
(d) Two populations become geographically separated, and then new mutations arise in each population that become fixed due to selection favoring different egg coat proteins in the different habitats
(e) All of the above would on average lead to equivalent rates of speciation

Answers

- 1D
- 2B
- 3E
- 4B
- 5D

Reproductive isolation could occur at many different levels

- **Prezygotic** (before the egg is fertilized)
  - Genetic drift and divergence in bird song—won’t mate
  - Selection on coat color—don’t recognize each other

- **Postzygotic** (after the egg is fertilized)
  - DM incompatibilities cause embryo to not develop (enzymes don’t work together)