

LEVELS OF SELECTION

We usually think of natural selection as acting on genes or on individuals, but there is long history of consideration of selection acting on populations within species.

Selection actually occurs at many levels, notably:

- Species
- Groups/ populations within a species
- Individuals within a population or species
- Cells within an individual
- Mitochondrial and chloroplast genomes within a cell

1. Intracellular selection

Meiotic drive

Genes that disobey Mendel's law that alleles segregate in meiosis so each allele has probability 1/2 of being in a gamete.

Selfish genes or genomes

Duplicative transposable elements

Increase in number in genome because replicate when chromosome replicates *and* when they transpose.

Suppressive petite mutants in yeast

ρ^+ (wild type) Grows on nonfermentable (ethanol) or fermentable (glucose) substrates.

ρ^- Mutation in mtDNA, blocks mito protein synthesis of components of electron transport chain. Grows on glucose but makes small (petite) colonies.

Yeast contains Intracellular population of mt genomes. Normally homoplasmic.

Mate haploid $\rho^+ \times \rho^- \rightarrow$ diploid zygotes heteroplasmic ρ^+ / ρ^- .

Vegetative segregation: mitotic division of diploids \rightarrow homoplasmic daughter cells.

Suppressive petites: some daughter cells ρ^+ , some ρ^- .

Hypersuppressive petites: $\approx 100\%$ of daughters are ρ^- because ρ^- mtDNA molecules replicate faster than ρ^+ .

These mutants have unconditional advantage so not included in further discussion.

Selection on organelle genomes: Intracellular selection for antibiotic resistant mtDNA or cpDNA genomes

Yeast: erythromycin binds to mito ribosomes and blocks protein synthesis and hence ox phos. Wild type *ery^S* cells don't grow on nonfermentable substrate in presence of antibiotic. Mutant *ery^R* cells do grow.

Mate R X S → heteroplasmic R/S zygote → grow on glycerol + erythromycin → all progeny homoplasmic R.

Intracellular selection. R genomes replicate more often than the S genomes in the presence of antibiotic; mechanism unknown.

Origin of resistant cells: in presence of erythromycin, wild type cells sit around until a mutation occurs in a cell and mutant allele increases in number until there are enough copies to make cell resistant and it starts to grow.

Consequences for evolution of organelle genes:

- Looks like directed mutation, mutation induced by selective agent!
- Affects mutation rate at cell level → increased rate of advantageous mutations and decreased detrimental mutation rate at cell level.

Intracellular populations of organelle genomes also show random drift:

Relaxed genomes:

- Organelles selected at random for replication until number of copies is doubled.
- Organelles partitioned between daughter cells randomly.

2. Intercellular selection: Selection on cells within multicellular organisms

Multicellular organism is a population of cells with some degree of independence.

Plastid genomes in plants: mutations in cp or nuclear genes causing loss of chlorophyll synthesis and photosynthesis. In plants with mixture of green and white cells, some white mutants cause cells to grow and divide more slowly.

2. Group selection

If population is subdivided into groups = populations, demes, etc., then if one group has a trait that allows it to survive and replace other groups that do not have the trait, this can be viewed as selection at the level of groups.

George C. Williams argued that this was extremely unlikely because:

1. It only takes a small amount of migration between groups (≥ 1 migrant per generation) to make them behave almost like a single random-mating population.

Valid argument, but doesn't exclude group selection when groups have lower migration rate.

2. There are many more individual generations than episodes of extinction and recolonization per unit time, so individual selection should be faster/stronger. Therefore selection at level of groups cannot fix a trait that is detrimental at the level of individuals.

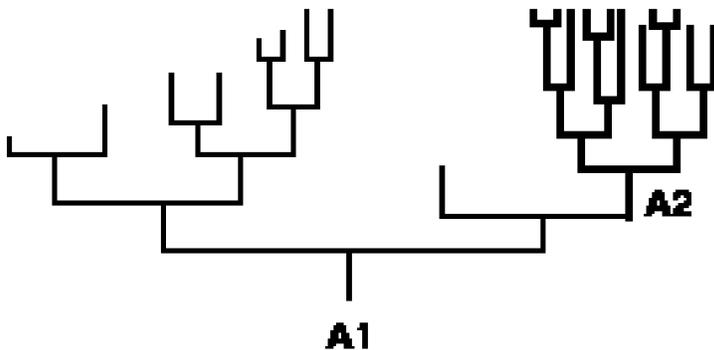
Problem: Speed of gene fixation under selection depends not only on number of generations per unit time but also on selection coefficient and effective size of group. Also ignores cases where selection at both levels is in same direction.

3. Species selection

Consider two species, species A with trait α , species B with trait β . If trait α causes species to either speciate more often or go extinct less often than trait β , then eventually descendants of species A will replace those of species B. This is species-level selection.

Net rate of speciation = speciation rate – extinction rate.

Common features of selection at all levels



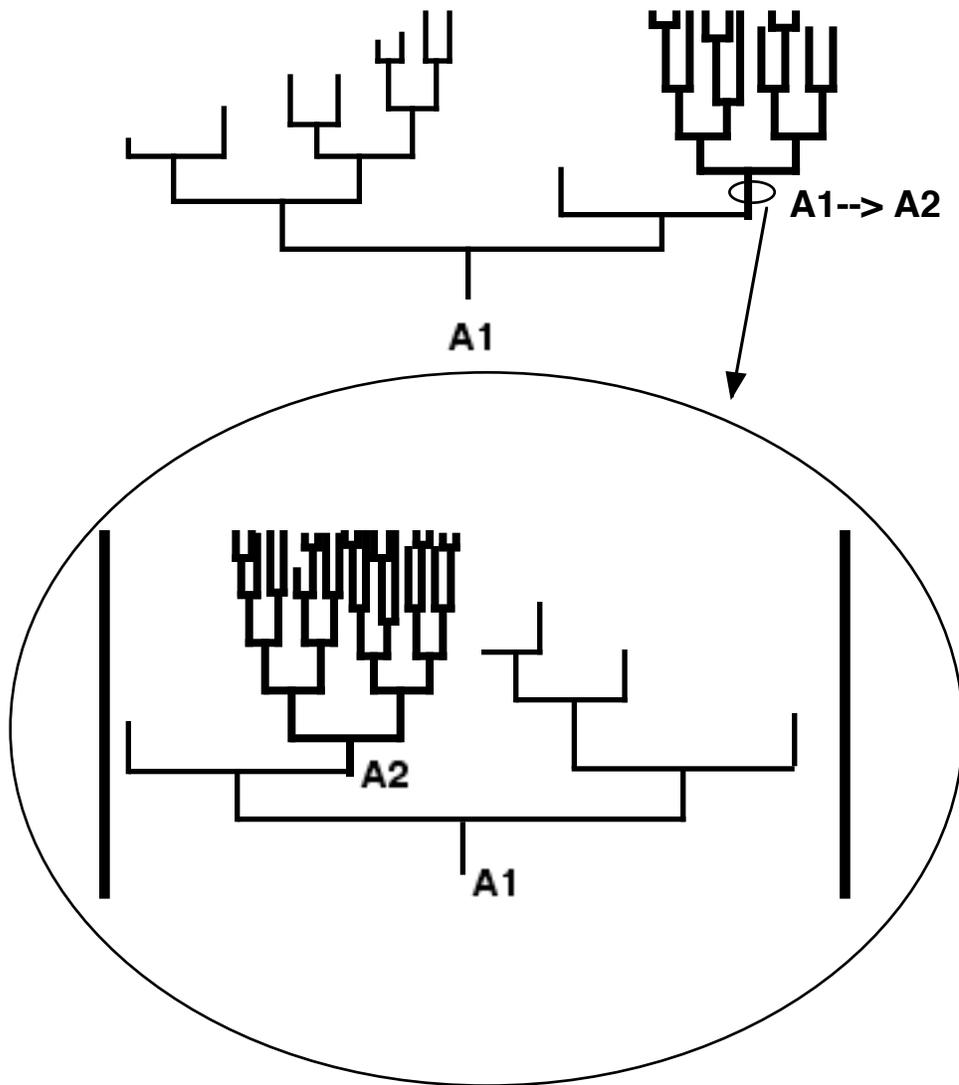
Here coalescent has allele/genotype/trait A1. Changes to A2 in one lineage, which consequently has higher net speciation rate.

Important point: Could use same diagram for any level:

- Pedigree of antibiotic-resistant and sensitive organelle genes within a cell.
- Pedigree of green and white cells in a leaf.

- Pedigree of more and less fit alleles of a gene, or of individuals with more and less fit genotypes in asexual population.
- Groups in a species with traits causing differential extinction and recolonization.
- Species with traits causing different net rates of speciation.

Levels of selection as nested trees:



Williams 1992 *Natural Selection. Domains, Levels, and Challenges*. Recognized the above point. Talked about natural selection acting at many levels on codeds = units of information. Called this clade selection. Unfortunate terminology. Also unfortunately included section titled Species Fallacies which seems to deny that species are significant units of evolution.