Processes of Evolution

Evolution is the process by which modern organisms have descended from ancient ancestors. Evolution is responsible for both the remarkable similarities we see across all life and the amazing diversity of that life. Evolution even in its vastness occurs through multiple processes. These processes may act on small scale via changing allele frequencies in populations of a species or may occur on much larger scale via differential proliferation or extinction of species or mass extinction.

Fundamental to the process of evolution is the genetic variation upon which selective forces can act in order for evolution to occur. Multiple mechanisms of evolution are there, some of which are listed below:

- Descent and the genetic differences that are heritable and passed on to the next generation;
- Mutation, migration (gene flow), genetic drift, and natural selection as mechanisms of change;
- The importance of genetic variation;
- The random nature of genetic drift and the effects of a reduction in genetic variation;
- How variation, differential reproduction, and heredity result in evolution by natural selection; and
- How different species can affect each other's evolution through coevolution.
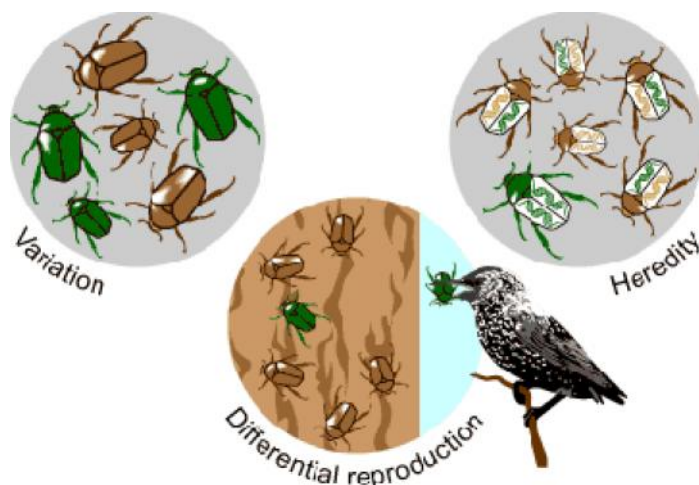
Microevolution

- Microevolution is evolution on a small scale — within a single population. By population here we mean a group of organisms that interbreeds with each other, or as we call it biologically a species.
- Microevolution more scientifically can be defined as a change in allele frequency within a population, i.e. at or below the level of species

- Numerous examples abound of this kind of evolution, which is small scale and so rapid that can occur even within a generation. This is the kind of evolutionary process that makes evolution seem tangible and real to us.
- Insecticide and antibiotic resistance are very good examples of microevolution
- It is easy to observe microevolution in any rapidly growing organism, i.e. one with short life cycle. For e.g. bacteria grown in a Petri dish can be given an antibiotic, such as penicillin, that is just strong enough to destroy most, but not all, of the population. If repeated applications are used after each population returns to normal size, eventually a strain of bacteria with antibiotic resistance may be developed. This more recent population has a different allele frequency than the original population, as a result of selection for those bacteria that have a genetic makeup consistent with antibiotic resistance.
- Suppose we take another example of beetles living on a mountaintop. It is essential for us to take a population that interbreeds within itself and shares a common gene pool.
- Suppose you went to the mountaintop last year, sampled these beetles, and determine that 80% of the genes in the population are for green coloration and 20% of them are for brown coloration. This year on your return visit to the same population you found that there were 60% green genes to 40% brown genes. The frequency of genes has changed! What you are witnessing is microevolutionary change. And should this change persist, and the prevailing abiotic and biotic factors causing this change continue in the same direction as last year, it is likely that over a span of time, this particular beetle population may result in subspecies variants followed eventually the formation of a new species.
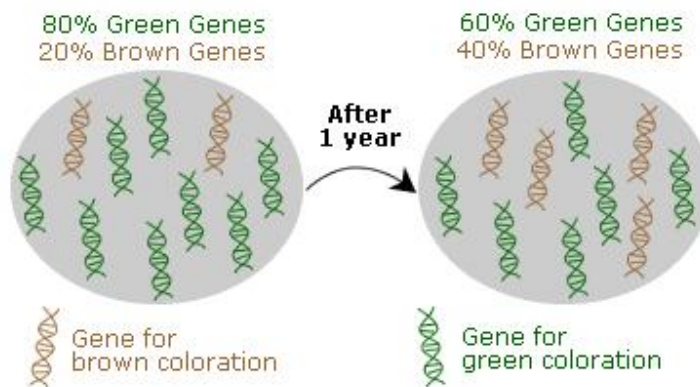
- This ability to witness microevolution in fast evolving species has led to distinct branch of experimental science called as "**Experimental evolution**". This allows to test our various hypotheses of how speciation might have occurred by subjecting isolated micropopulations to various stressors such as high temperature, crowding, food deprivation, etc.

Mechanisms of Microevolution

- Now what are the possible mechanisms that lead to microevolutionary changes. There are four major mechanisms that are identified as facilitators of microevolution
  - Mutation
  - Migration (or gene flow)

- o Genetic drift
- o Natural Selection
- But before we begin to understand these mechanisms that bring about microevolution, i.e. change in the gene frequency within a population, we need to understand the concept of gene frequency distribution in a population.
- This can be explained through the Hardy Weinberg Law

Hardy Weinberg Law
- The field of biology that studies allele frequencies in populations and how they change over time is called population genetics. Before we begin to understand population genetics in general and Hardy Weinberg law in particular we need to clarigy some key definitions
  - o **Population:** is a group of organisms of the same species that are found in the same area and can interbreed. A population is the smallest unit that can evolve—in other words, an individual can't evolve.
  - o **Allele**: a version of a **gene**, a heritable unit that controls a particular feature of an organism.
  - o **Allele frequency** refers to how frequently a particular allele appears in a population. It's also possible to calculate **genotype frequencies**—the fraction of individuals with a given genotype—and **phenotype frequencies**—the fraction of individuals with a given phenotype.
  - o **Gene pool:** The total set of gene copies for all genes in a population. The gene pool gets its name from the idea that we are essentially taking all the gene copies—for all genes—in the individuals of a population and dumping them into one large, common pool. So suppose there are five individuals in a population, with each individual having 10 genes. Now Gene A will have 5*2. i.e. 10 individual gene types, then if we did study for all 10 genes and put all the information together, then that is what a gene pool would look like.

- Now that the clarifications of the terms are out of the way we now need to get down to the basics of understanding the Hardy Weinberg Law

- For understanding this law, we need to make certain assumptions
  - o When a population is in **Hardy-Weinberg equilibrium** for a gene, it is not evolving, and allele frequencies will stay the same across generations.
  - o That is the population in Hardy Weinberg Equilibrium will show
    - ▪ **No mutation**: No new alleles are generated by mutation, nor are genes duplicated or deleted.
    - ▪ **Random Mating**: Organisms mate randomly with each other, with no preference for particular genotypes.
    - ▪ **No gene flow**: Neither individuals nor their gametes (e.g., windborne pollen) enter or exit the population.
    - ▪ **Infinite population size**
    - ▪ **No natural selection**: All alleles confer equal fitness (make organisms equally likely to survive and reproduce).

- The above assumptions or exceptions mean that the population which is in Hardy-Weinberg equilibrium is not evolving.
- Then you might wonder, why study Hardy Weinberg Law.
- Population geneticists often check to see if a population is in Hardy-Weinberg equilibrium *because* they suspect other forces may be at work. If the population's allele and genotype frequencies are changing over generations (or if the allele and genotype frequencies don't match the predictions of the Hardy-Weinberg equation), the race is on to find out why.
- Other than these assumptions, there are some other minor ones that Hardy Weinberg Law makes:
  - Organisms are **diploid**. Thereby excluding haploid and polyploid organisms.
  - Reproduction is **sexual**. Thereby excluding asexually reproducing organisms
  - Populations have **non-overlapping generations**. However, this is not always true. Most populations have overlapping generations.
  - **Allele and genotype frequencies don't differ between males and females**. Thereby excluding sex alleles.

- There are modified forms of the Hardy-Weinberg equation to deal with overlapping generations, polyploid organisms, and sex linkage. However, those are complex and for higher classes.
- Hardy-Weinberg equilibrium *per se* doesn't apply to haploid or asexually reproducing organisms, but we can predict that the allele and genotype frequencies in the populations of these organisms would tend to remain stable in the absence of outside forces.
- Now after understanding these assumptions, let us understand what exactly is the Hardy-Weinberg Law.
- Let us consider a population which has at a locus two alleles A and a which have frequencies p and q, respectively. We are talking about a single locus here to make things easier.
- In such a scenario, there will be individuals in a population that will have genotype AA, Aa and aa.
- Which in turn means that the frequency of genotype AA is p^2, of Aa is 2pq and of aa is q^2.

|	A (p)	a (q)
A(p)	AA (pp=p^2)	Aa (pq)
a (q)	Aa (pq)	aa (qq=q^2)

AA= p^2; Aa=2pq; aa=q^2

- Which means that the total genotype frequencies in a population are p^2 +2pq+q^2, which mathematically is an expansion of $(p+q)^2$.
- And also equal to 1. Which means that in a population $(p+q)^2$ or p^2+2pq+q^2=1
- For animation of Hardy Weinberg see the following link
  https://youtu.be/oc9fJCAIRJs

- It is possible to apply the Hardy-Weinberg to loci with more than two alleles, in which case the expected genotype frequencies are given by the multinomial expansion for all k alleles segregating in the population: $(p1 + p2 + p3 + \ldots + pk)^2$.
- If the genotype frequencies in a population deviate from Hardy-Weinberg expectations, it takes only one generation of random mating to bring them into the equilibrium proportions, provided that the above assumptions hold, that allele frequencies are equal in males and females (or else that individuals are hermaphrodites), and that the locus is autosomal.
- If allele frequencies differ between the sexes, it takes two generations of random mating to attain Hardy-Weinberg equilibrium. Sex-linked loci require multiple generations to attain equilibrium because one sex has two copies of the gene and the other sex has only one.
- It is important to recognize that the Hardy-Weinberg equilibrium is a neutral equilibrium, which means that a population disturbed from its Hardy-Weinberg genotype frequencies will indeed reach equilibrium after a single generation of random mating (if it conforms to the other assumptions of the theorem), but it will be a new equilibrium if allele frequencies have changed.
- This property distinguishes a neutral equilibrium from a stable equilibrium, in which a perturbed system returns to the same equilibrium state.
- Hardy-Weinberg equilibrium is not stable, since a change from the equilibrium genotype frequencies will generally be associated with a change in allele frequencies (p and q), which will in turn lead to new values of p2, 2pq and q2. Thereafter, a population that meets Hardy-Weinberg assumptions will remain at the new equilibrium until disturbed again.

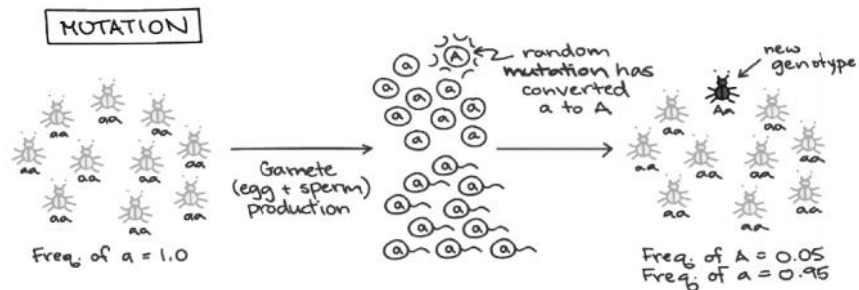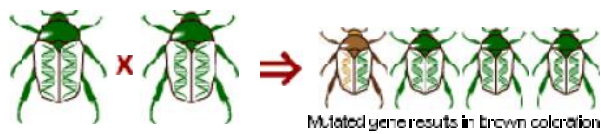**Evolutionary Implications of the Hardy-Weinberg Theorem**
- Hardy-Weinberg demonstrates that Mendelian loci segregating for multiple alleles in diploid populations will retain predictable levels of genetic variation in the absence of forces that change allele frequencies.
- A common way of visualizing these expectations is to plot p2, 2pq and q2 as a function of allele frequencies. This graphical presentation emphasizes two important consequences of the Hardy-Weinberg principle:
  - Population heterozygosity (the frequency of heterozygotes) is highest when $p = q = 0.5$.
  - Rare alleles are found primarily in heterozygotes, as they must be, given that q^2 is much smaller than 2pq when q is near zero, and p^2 is much smaller than 2pq when p is near zero
  -
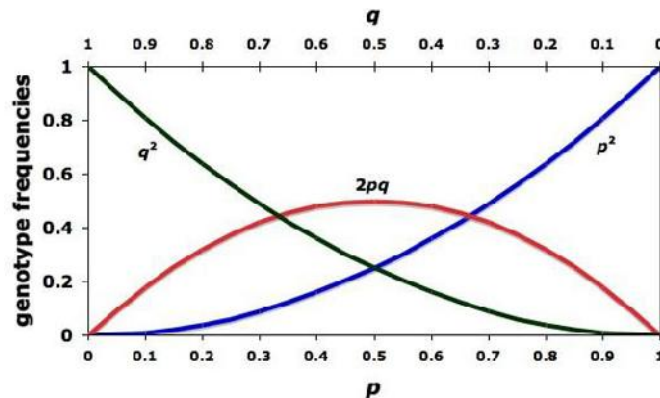
- The second point is especially important if we see it in the light of the potential for natural selection to influence the frequencies of new mutations.
- If a population conforms to all other Hardy-Weinberg assumptions, selection will eventually fix an advantageous allele in the population such that all individuals are homozygous for that allele.
- The initial increase in frequency of a rare, advantageous, dominant allele is more rapid than that of a rare, advantageous, recessive allele.
- This is because, as we have seen, rare alleles are found mostly in heterozygotes, such that a new recessive mutation can't be "seen" by natural selection until it reaches a high enough frequency (perhaps by drift in a real, finite population) to start appearing in homozygotes.
- A new dominant mutation, however, is immediately visible to natural selection because its effect on fitness is seen in heterozygotes.
- Thus, although Hardy (1908) demonstrated that dominance alone does not change allele frequencies at a locus, the dominance relationships among alleles can have substantial influence on evolutionary trajectories.
- Selection, mutation, migration, and genetic drift are the mechanisms that effect changes in allele frequencies, and when one or more of these forces are acting, the population violates Hardy-Weinberg assumptions, and evolution occurs.
- The Hardy-Weinberg thus constitutes a null model for the discipline of population genetics, and is fundamental to the study of evolution.
- Now we will discuss the factors which cause change in allele frequencies, thereby causing the disruption of the Hardy Weinberg equilibrium of a population leading to evolution
  - Mutation
  - Migration (or gene flow)
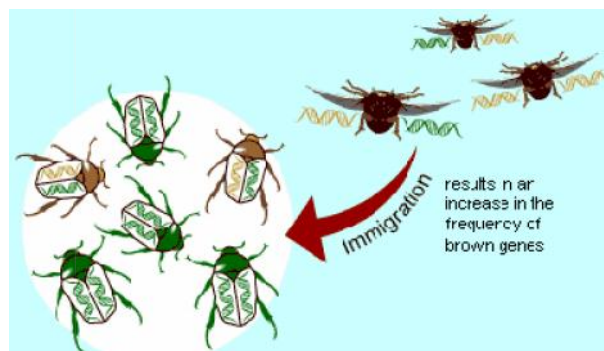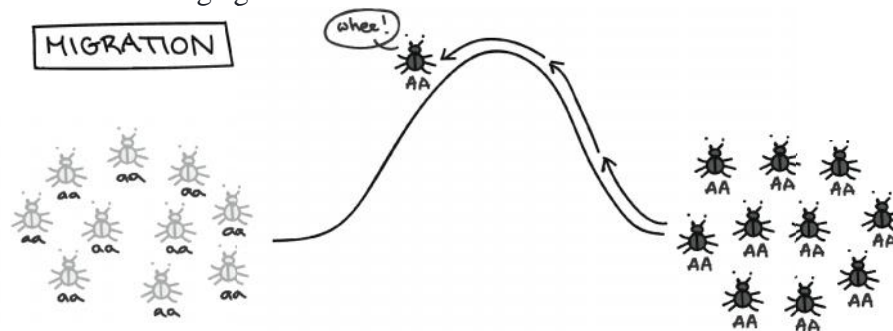 - Genetic drift
  - Natural Selection

Mutation
- Although mutation is the original source of all genetic variation, mutation rate for most organisms is pretty low.

Mutated gene results in brown coloration

MUTATION

random mutation has converted a to A

new genotype

Gamete (egg + sperm) production

Freq. of a = 1.0

Freq. of A = 0.05
Freq. of a = 0.95

- So, the impact of brand-new mutations on allele frequencies from one generation to the next is usually not large. (However, natural selection *acting* on the results of a mutation can be a powerful mechanism of evolution!)
- Already discussed above in relation to the genotype frequency distribution
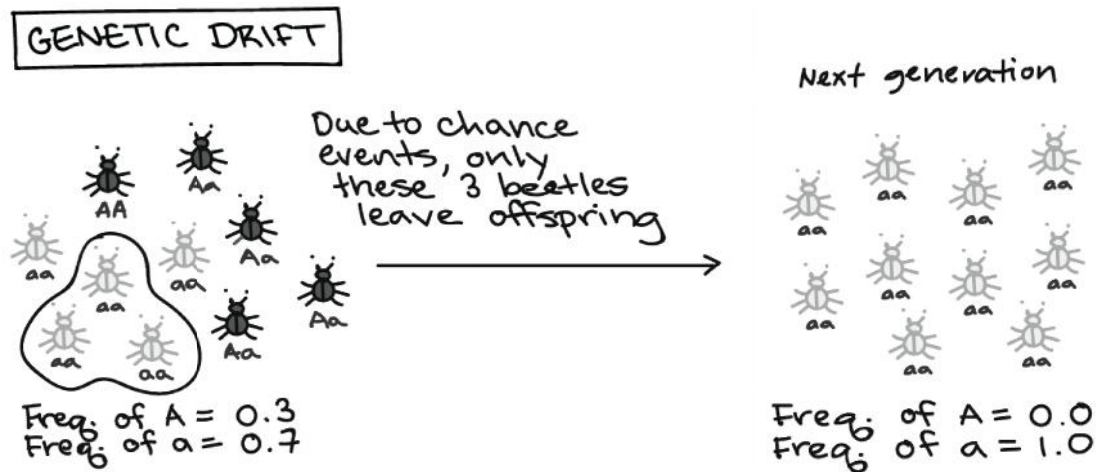
Migration (or Gene Flow)

- Gene flow involves the movement of genes into or out of a population, due to either the movement of individual organisms or their gametes (eggs and sperm, e.g., through pollen dispersal by a plant).
- Organisms and gametes that enter a population may have new alleles, or may bring in existing alleles but in different proportions than those already in the population. Gene flow can be a strong agent of evolution.
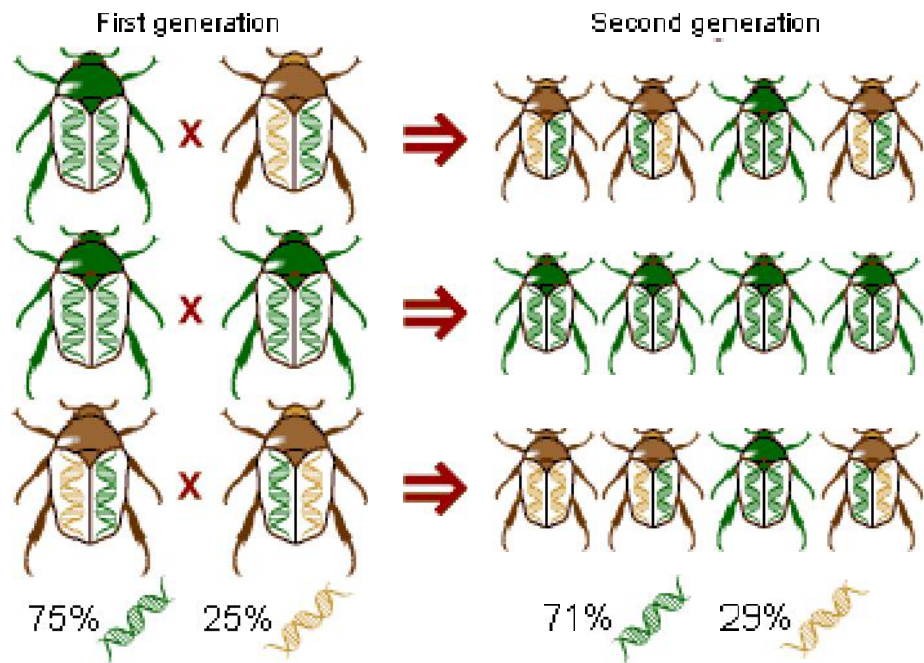

MIGRATION

whee!

AA

Immigration results in an increase in the frequency of brown genes

Genetic drift

- Genetic drift involves changes in allele frequency due to chance events – literally, "sampling error" in selecting alleles for the next generation.
- Drift can occur in any population of non-infinite size, but it has a stronger effect on small populations.
- Genetic drift may result in the loss of some alleles (including beneficial ones) and the fixation, or rise to 100%, percent frequency, of other alleles.
- Genetic drift can have major effects when a population is sharply reduced in size by a natural disaster (bottleneck effect) or when a small group splits off from the main population to found a colony (founder effect)
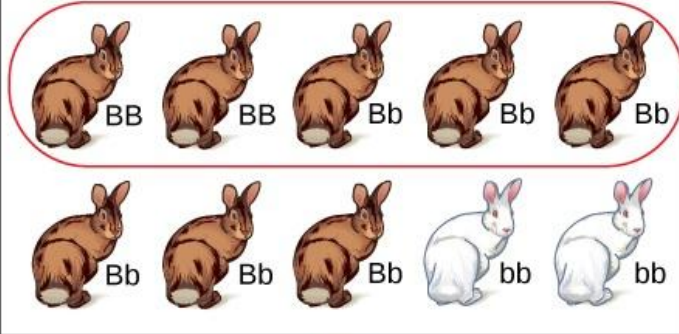

GENETIC DRIFT

Next generation

Due to chance events, only these 3 beetles leave offspring

AA
Aa
aa
Aa
aa
aa
Aa
aa
aa
Aa

Freq. of A = 0.3
Freq. of a = 0.7

aa aa aa
aa
aa aa
aa aa
aa aa

Freq. of A = 0.0
Freq. of a = 1.0

First generation   Second generation

75%   25%   71%   29%

Genetic Drift

First generation
p (B gene frequency) = .5
q (b gene frequency) = .5

BB BB Bb Bb Bb

Bb Bb Bb bb bb

5 rabbits reproduce

Second generation
p = .7
q = .3

BB BB BB BB bb

BB Bb Bb Bb Bb
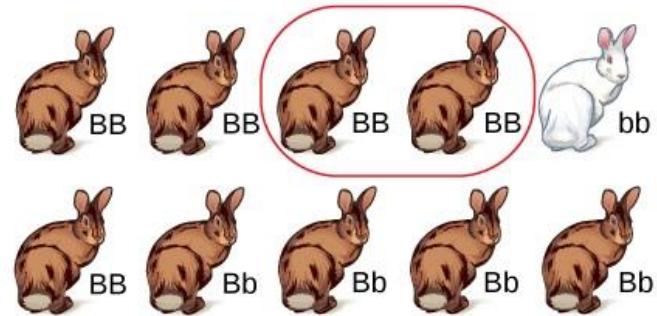
2 rabbits reproduce

**Third generation**
p = 1
q = 0

BB BB BB BB BB

BB BB BB BB BB
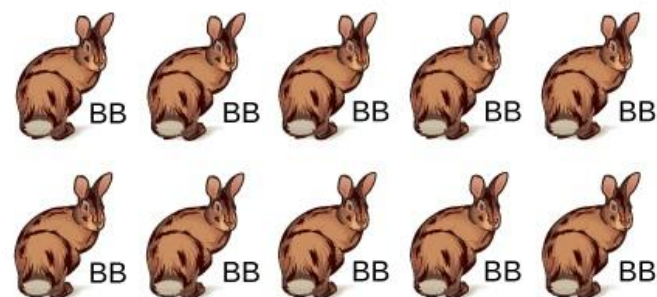
- Larger populations are unlikely to change this quickly as a result of genetic drift. For instance, if we followed a population of 1000 rabbits (instead of 10), it's much less likely that the b allele would be lost (and that the B allele would reach 100%) percent frequency, or **fixation**) after such a short period of time.
- If only half of the 1000-rabbit population survived to reproduce, as in the first generation of the example above, the surviving rabbits (500 of them) would tend to be a much more accurate representation of the allele frequencies of the original population – simply because the sample would be so much larger.
- Genetic drift, unlike natural selection, does not take into account an allele's benefit (or harm) to the individual that carries it. That is, a beneficial allele may be lost, or a slightly harmful allele may become fixed, purely by chance.

The bottleneck effect
- The **bottleneck effect** is an extreme example of genetic drift that happens when the size of a population is severely reduced. Events like natural disasters (earthquakes, floods, fires) can decimate a population, killing most individuals and leaving behind a small, random assortment of survivors.
- The allele frequencies in this group may be very different from those of the population prior to the event, and some alleles may be missing entirely.
- The smaller population will also be more susceptible to the effects of genetic drift for generations (until its numbers return to normal), potentially causing even more alleles to be lost.

Original population

Bottlenecking event

Surviving population
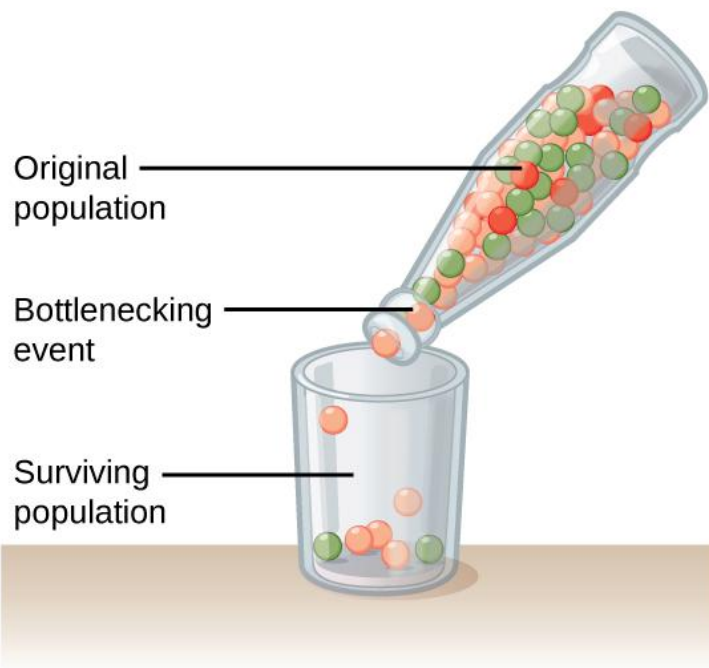
The founder effect
- The **founder effect** is another extreme example of drift, one that occurs when a small group of individuals breaks off from a larger population to establish a colony.

- The new colony is isolated from the original population, and the founding individuals may not represent the full genetic diversity of the original population.
- That is, alleles in the founding population may be present at different frequencies than in the original population, and some alleles may be missing altogether.
- The founder effect is similar in concept to the bottleneck effect, but it occurs via a different mechanism (colonization rather than catastrophe).
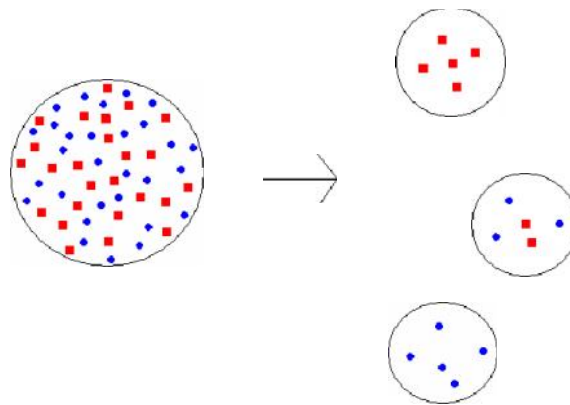
Natural selection
- Natural selection occurs when one allele (or combination of alleles of different genes) makes an organism more or less fit, that is, able to survive and reproduce in a given environment.
- If an allele reduces fitness, its frequency will tend to drop from one generation to the next. We will look in detail at different forms of natural selection that occur in populations.
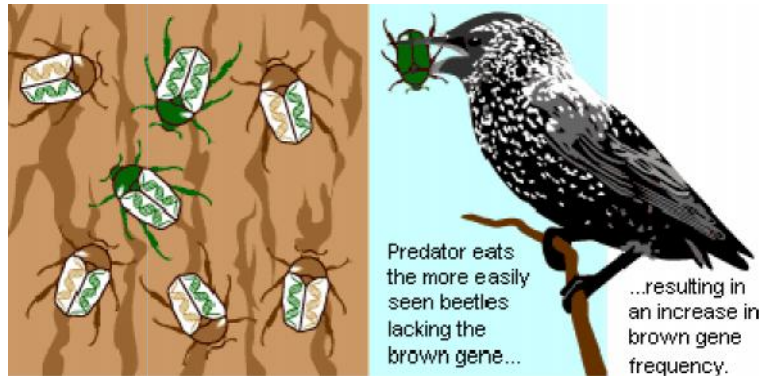
- All five of the above mechanisms of evolution may act to some extent in any natural population.
- In fact, the evolutionary trajectory of a given gene (that is, how its alleles change in frequency in the population across generations) may result from several evolutionary mechanisms acting at once.
- For instance, one gene's allele frequencies might be modified by both gene flow and genetic drift. For another gene, mutation may produce a new allele, which is then favored (or disfavored) by natural selection.

The mechanism of non-random mating is not however not known to cause much effect on displacement of Hardy Weinberg.

Non-random mating
- In non-random mating, organisms may prefer to mate with others of the same genotype or of different genotypes.
- Non-random mating will not make allele frequencies in the population change by itself, though it can alter genotype frequencies.
- This keeps the population from being in Hardy-Weinberg equilibrium, but it's debatable whether it counts as evolution, since the allele frequencies are staying the same.
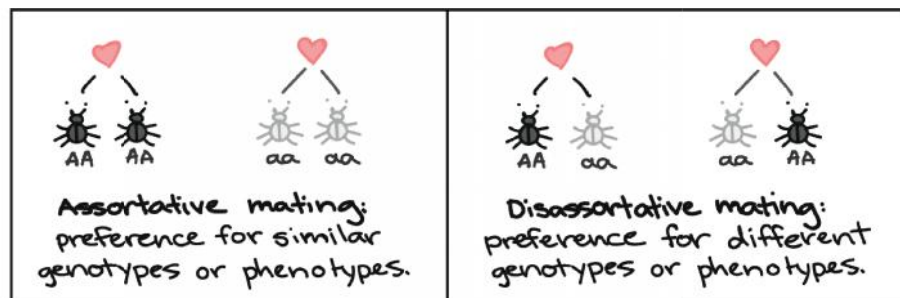
Speciation

- This topic will involve discussion on what is a species and how does one evolve
- According to the biological species concept, organisms belong to the same species if they can interbreed to produce viable, fertile offspring.
- Species are separated from one another by prezygotic and postzygotic barriers, which prevent mating or the production of viable, fertile offspring.
- Speciation is the process by which new species form. It occurs when groups in a species become reproductively isolated and diverge.
- Because members of a species can interbreed, the species as a whole has a common **gene pool**, a collection of gene variants.
- On the other hand, genes are *not* exchanged between different species. Even if organisms of different species combine their DNA to make offspring, the offspring will be sterile, unable to pass on their genes. Example of such a sterile offspring is a mule.
- Because of this restricted gene flow, each species evolves as a group distinct from other species.
- Now different species cannot interbreed because of the presence of isolating mechanisms also known as pre- and post-zygotic reproductive barriers.

Prezygotic barriers
- Prezygotic barriers prevent members of different species from mating to produce a zygote, a single-celled embryo.
    - **Habitat isolation**: Two species might not be able to encounter each other dues to different habitats.
    - **Temporal isolation**: might reproduce at different times of the day or year and thus unlikely to meet during mate search
    - **Behavioural Isolation**: Might have different courtship behaviors or mate preferences and thus find each other "unattractive".
    - **Gametic Isolation**: Incompatible gametes incapable of fertilization
    - **Reproductive Isolation**: Two species might have bodies or reproductive structures that simply don't fit together.

Post-zygotic barriers
- These barriers prevent hybrid zygotes—one-celled embryos with parents of two different species—from developing into healthy, fertile adults.
- Postzygotic barriers are often related to the hybrid embryo's mixed set of chromosomes, which may not match up correctly or carry a complete set of information.
- This chromosome mismatch may be lethal
- In a milder form it a hybrid can survive to adulthood in good health but is infertile because it can't split its mismatched chromosomes evenly into eggs and sperm.

- These barrier keep species neatly partitioned and also play a role in formation of a new species.
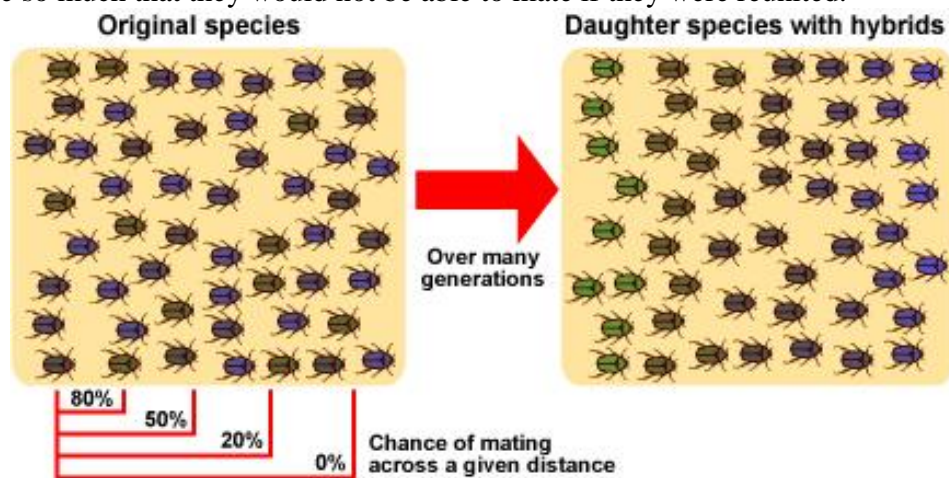
Speciation
- Speciation is a lineage-splitting event that produces two or more separate species.
- Or in other words, an ancestral species splits into two or more descendant species that are genetically different from one another and can no longer interbreed.
- Imagine that you are looking at a tip of the tree of life that constitutes a species of fruit fly.
- Move down the phylogeny to where your fruit fly twig is connected to the rest of the tree. That branching point, and every other branching point on the tree, is a speciation event.
- At that point genetic changes resulted in two separate fruit fly lineages, where previously there had just been one lineage.
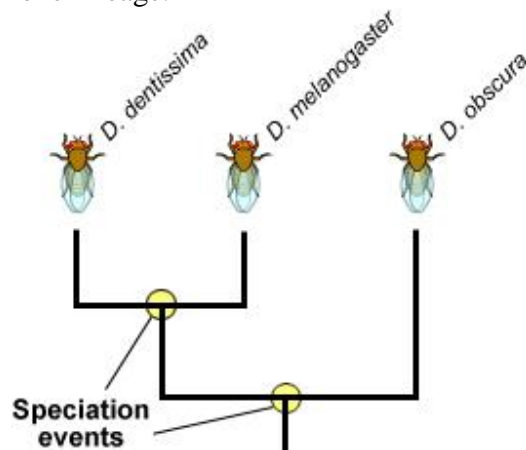
- For speciation to occur, two new populations must be formed from one original population, and they must evolve in such a way that it becomes impossible for individuals from the two new populations to interbreed.
- Speciation can occur into two broad categories:
  - **Allopatric speciation**—allo meaning other and patric meaning homeland—involves geographic separation of populations from a parent species and subsequent evolution.
    - This separation can be a result of any physical barrier, such as a mountain range, rockslide, or river
    - A part of a population might get split by a physical barrier at some point of time leading to reproductive isolation
    - Now that the subpopulations of the original are being exposed to different abiotic and biotic conditions, they will face different selection pressures leading to possible genetic divergence. That is with time they may gradually become more and more different in their genetic make and heritable features over generations.
    - As they diverge, the groups may evolve traits that act as prezygotic and/or postzygotic barriers to reproduction.
    - If the reproductive barriers that have arisen are strong—effectively preventing gene flow—the groups will keep evolving along separate paths. That is, they won't exchange genes with one another even if the geographical barrier is removed. At this point, the groups can be considered separate species.

o **Sympatric speciation**—sym meaning same and patric meaning homeland—involves speciation occurring within a parent species remaining in one location. This speciation is characterized by reduction of gene flow.
o Imagine a situation in which a population extends over a broad geographic range, and mating throughout the population is not random.
o Individuals in the far west would have zero chance of mating with individuals in the far eastern end of the range.
o So we have reduced gene flow, but not total isolation. This may or may not be sufficient to cause speciation.
o Speciation would probably also require different selective pressures at opposite ends of the range, which would alter gene frequencies in groups at different ends of the range so much that they would not be able to mate if they were reunited.

- In plants, polyploidy is also a sympatric speciation inducing factor

Macroevolution

- Macroevolution is evolution on a grand scale — what we see when we look at the over-arching history of life: stability, change, lineages arising, and extinction.
- Macroevolution generally refers to evolution above the species level.
- Macroevolution encompasses the grandest trends and transformations in evolution, such as the origin of mammals and the radiation of flowering plants. Macroevolutionary patterns are generally what we see when we look at the large-scale history of life.
- It is not necessarily easy to "see" macroevolutionary history; there are no firsthand accounts to be read. Instead, we reconstruct the history of life using all available evidence: geology, fossils, and living organisms.
- Once we've figured out *what* evolutionary events have taken place, we try to figure out *how* they happened. Just as in microevolution, basic evolutionary mechanisms like mutation, migration, genetic drift, and natural selection are at work and can help explain many large-scale patterns in the history of life.
- The basic evolutionary mechanisms — mutation, migration, genetic drift, and natural selection — can produce major evolutionary change if given enough time.

Mutation
Gene Flow
Genetic Drift **+ 3.8 billion years = Macroevolution**
Natural Selection

Patterns in macroevolution

- **Stasis**
  - Many lineages on the tree of life exhibit stasis, which just means that they don't change much for a long time
  - In fact, some lineages have changed so little for such a long time that they are often called living fossils.
- **Character change**
  - Lineages can change quickly or slowly. Character change can happen in a single direction, such as evolving additional segments, or it can reverse itself by gaining and then losing segments.
  - Changes can occur within a single lineage or across several lineages.
- **Lineage-splitting (or speciation)**:
  - Patterns of lineage-splitting can be identified by constructing and examining a phylogeny.
  - The phylogeny might reveal that a particular lineage has undergone unusually frequent lineage-splitting, generating a "bushy" tuft of branches on the tree (Clade A, below).
  - It might reveal that a lineage has an unusually low rate of lineage-splitting, represented by a long branch with very few twigs coming off (Clade B, below).

- o Or it might reveal that several lineages experienced a burst of lineage-splitting at the same time (Clade C, below).
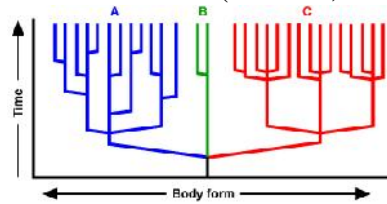

  - o
- **Extinction**
  - o Extinction is extremely important in the history of life.
  - o It can be a frequent or rare event within a lineage, or it can occur simultaneously across many lineages (mass extinction).
  - o Every lineage has some chance of becoming extinct, and overwhelmingly, species have ended up in the losing slots on this roulette wheel: over 99% of the species that have ever lived on Earth have gone extinct.
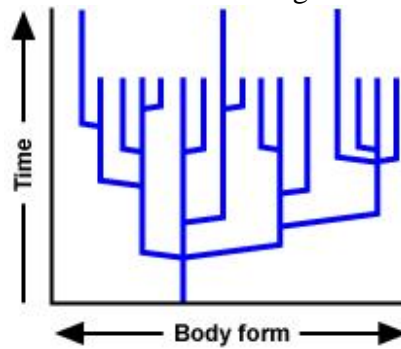
Genetic Death

- Genetic death is defined as the removal of a gene from the gene pool of a population.
- Also known as reproductive death
- It can be a result of infertility, failure to reproduce, or death before sexual maturity of all individuals carrying that gene.
- It is not necessarily associated with poor health or loss of life but refers to the impediment of passage of genes to the next generation,
- This facilitates natural selection

Chose not to reproduce

Infertile, cannot reproduce

Death before sexual maturity
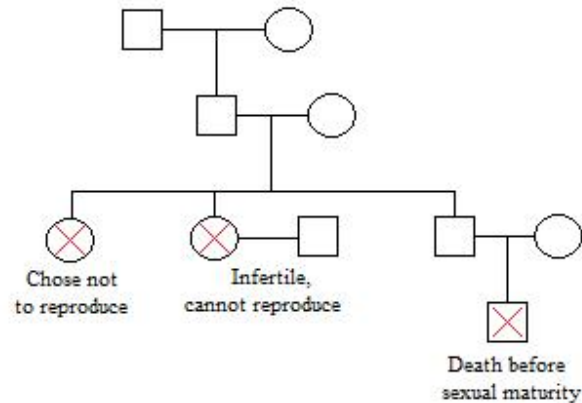
Bioinvasion

- This refers to the introduction of new competing exotic species in ecosystems that were not theirs traditionally.
- This may lead to extinction of native species, due to increased competition for resources as well as lack of natural enemies of the exotic species.