Evolution is a genetic process - a change in the genetic structure of a single population, or the formation of new genetic lineages.
Since evolution is a property of populations and it is a genetic phenomenon, understanding evolution requires an understanding of how genes behave in populations.

The fundamental principle of population genetics is the Hardy-Weinberg Principle:
If the individuals in a large population mate randomly, and there is no mutational change in the frequency of alleles in the population, and there is no influx of genes from other populations, and there is no difference in the survival and reproductive potential of different genotypes, then the frequency of genotypes in the population will be a binomial distribution derived from the frequency of the two alleles.
Random mating produces a binomial distribution of genotypes

Consider a gene in this population with two alleles, A and a. We will designate the frequency of the AA genotype D (for dominant homozygote), the frequency of the Aa genotype H (for heterozygote), and the frequency of the aa genotype R (for recessive homozygote). Since these are the only genotypes possible, the sum of the three frequencies must equal 1. In summary:

- frequency of AA = D,
- frequency of Aa = H,
- frequency of aa = R

\[ D + H + R = 1 \]

Given any set of genotypic frequencies, the frequencies of the alleles can be calculated as:

\[ f(A) = (2D + H)/2 = D + (H/2) = p \]
\[ f(a) = (2R + H)/2 = R + (H/2) = q \]

\[ p + q = 1 \]
Expected frequencies of different mating combinations between genotypes if genotypes mate randomly.

<table>
<thead>
<tr>
<th>Male</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td>D (AA)</td>
<td>D^2</td>
</tr>
<tr>
<td>H (Aa)</td>
<td>DH</td>
</tr>
<tr>
<td>R (aa)</td>
<td>DR</td>
</tr>
</tbody>
</table>
Expected mating frequencies and offspring genotypic frequencies for a randomly mating population.

<table>
<thead>
<tr>
<th>Mating Combination</th>
<th>Mating Frequency</th>
<th>F2 Genotypic Frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>AA</td>
</tr>
<tr>
<td>AA x AA</td>
<td>D²</td>
<td>D²</td>
</tr>
<tr>
<td>AA x Aa</td>
<td>2DH</td>
<td>DH</td>
</tr>
<tr>
<td>AA x aa</td>
<td>2DR</td>
<td></td>
</tr>
<tr>
<td>Aa x Aa</td>
<td>H²</td>
<td>H²/4</td>
</tr>
<tr>
<td>Aa x aa</td>
<td>2HR</td>
<td>HR</td>
</tr>
<tr>
<td>aa x aa</td>
<td>R²</td>
<td></td>
</tr>
</tbody>
</table>
If we total the columns for each offspring genotype and call the new genotypic frequencies $D'$, $H'$, and $R'$ we get:

$D' = D^2 + DH + H^2/4$

$H' = DH + 2DR + H^2/2 + HR$

$R' = H^2/4 + HR + R^2$

If these expressions are rewritten, factored and simplified we get:

$D' = D^2 + DH + H^2/4 = (D + H/2)^2 = p^2$

$H' = DH + 2DR + H^2/2 + HR = 2(D + H/2)(R + H/2) = 2pq$

$R' = H^2/4 + HR + R^2 = (R + H/2)^2 = q^2$
Genotypic combinations and frequencies with random pairing of gametes

<table>
<thead>
<tr>
<th>Male gamete</th>
<th>Female gamete</th>
</tr>
</thead>
<tbody>
<tr>
<td>A (p)</td>
<td>a (q)</td>
</tr>
<tr>
<td>A (p)</td>
<td>AA (p^2)</td>
</tr>
<tr>
<td>a (q)</td>
<td>Aa (pq)</td>
</tr>
</tbody>
</table>

We imagine that parents combine gametes into one large gamete pool

Then pairs of gametes are drawn at random to form new offspring
If the individuals in a **large population** mate **randomly**, and there is **no mutational change** in the frequency of alleles in the population, and there is **no influx of genes from other populations**, and there is **no difference in the survival and reproductive potential of different genotypes**, then the frequency of genotypes in the population will be a binomial distribution derived from the frequency of the two alleles.

If the frequency of A = p, and the frequency of a = q, then the frequency of the genotypes will be:

\[
\begin{align*}
    f(AA) &= p^2 \\
    f(Aa) &= 2pq \\
    f(aa) &= q^2
\end{align*}
\]

And, so long as the conditions stated above hold, the frequencies will not change from generation to generation.

The binomial distribution of genotypes is preserved from generation to generation if there are no factors operating that can change allele or genotypic frequencies.
Darwin did not have an understanding of the mechanisms of inheritance and thus did not understand how natural selection would alter the patterns of inheritance in a population. It took an understanding of genetics and an understanding of evolution to merge the two fields into the cornerstone of modern evolutionary theory – The Genetical Theory of Natural Selection – Sir Ronald Fisher was the first to begin to develop this theory.

Natural Selection ≠ Evolution

For natural selection to produce evolution selected traits must be heritable

Natural selection can not increase or decrease the frequency of a trait in a population unless the trait influences reproductive success.
Modes of selection:

Quantitative trait

Parental population

Offspring 
($F_1$)

Phenotype frequency

Directional

Stabilizing

Diversifying

Character value
Polymorphism

Parental population

Genotype frequency

Offspring ($F_1$)

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Parental advantage</th>
<th>Heterozygote advantage</th>
<th>Heterozygote disadvantage</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A_1A_1$</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>$A_1A_2$</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>$A_2A_2$</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
</tr>
</tbody>
</table>

Directional selection increases the proportion of genotypes with a more extreme value of the trait.

Stabilizing selection does not alter the mean, but may reduce the variance.

Diversifying selection is unlikely to be exactly symmetrical, and thus usually shifts the mean.
Selection can go on at different stages in the life cycle.

1. Viability selection
2. Sexual selection
3. Fecundity selection
4. Gametic selection
5. Compatibility selection
# TABLE 12.1 Components of selection in sexually reproducing organisms

## I. Zygotic selection

A. **Viability.** The probability of survival of the genotype through each of the ages at which reproduction can occur. After the age of last reproduction, the length or probability of survival does not usually affect the genotype’s contribution to subsequent generations, and so does not usually affect fitness.

B. **Mating success.** The number of mates obtained by an individual. Mating success is a component of fitness if the number of mates affects the individual’s number of progeny, as is often the case for males, but less often for females, all of whose eggs may be fertilized by a single male. Variation in mating success is the basis of sexual selection.

C. **Fecundity.** The average number of viable offspring per female. In species with repeated reproduction, the contribution of each offspring to fitness depends on the age at which it is produced (see Chapter 17). The fertility of a mating may depend only on the maternal genotype (e.g., number of eggs or ovules), or it may depend on the genotypes of both mates (e.g., if they display some reproductive incompatibility).

## II. Gametic selection

D. **Segregation advantage** (meiotic drive or segregation distortion). An allele has an advantage if it segregates into more than half the gametes of a heterozygote.

E. **Gamete viability.** Dependence of a gamete’s viability on the allele it carries.

F. **Fertilization success.** An allele may affect the gamete’s ability to fertilize an ovum (e.g., if there is variation in the rate at which a pollen tube grows down a style).
Fitness can be defined for a single genotype as the average contribution of individuals of that genotype to the population after one or more generations.

**Relative fitness** - $W$ – the average contribution of individuals of a given genotype to the population relative to the fitness of the genotype with the highest fitness.

**Coefficient of selection** – $s$ – the amount fitness of a genotype is reduced relative to the genotype with the highest fitness.

The rate of genetic change in a population depends on the relative fitness of genotypes.
The mathematics of a selection model

For simplicity assume that selection acts through differences in viability and otherwise the population satisfies all of the Hardy-Weinberg conditions (large population size, random mating, etc.)

For a single gene with two alleles (A,a) there are three genotypes AA, Aa, and aa. Each genotype has a fitness \( W (W_{AA}, W_{Aa}, \text{and } W_{aa}) \). Fitness is the relative probability of successful survival and reproduction. Fitness will have a value between 0 and 1. If a genotype has a fitness of 1 this means that genotype has the highest relative fitness. A fitness of 0 means that genotype has no chance of survival to reproduction. A fitness of 0.5 means that genotype has a chance of survival and reproduction that is half that of the genotype with the highest fitness.
Example 1: **Selection against a recessive phenotype.**
In this model $W_{AA} = W_{Aa} > W_{aa}$. For example $W_{AA} = 1.0$, $W_{Aa} = 1.0$ and $W_{aa} = 0.5$. We can start with any initial genotypic frequencies. Here we’ll start with the frequency of $AA = 0.36$, the frequency of $Aa = 0.48$, and the frequency of $aa = 0.16$ among the newborn, newly hatched, newly sprouted, or newly established generation.

We’ll allow survival to reproductive age using the fitness values of each genotype. This is shown in the table on the next slide. To calculate the frequency of each genotype at reproductive age, we first multiply the initial frequency of each genotype and its fitness. The sum of the three products gives the average fitness ($\bar{w}$). Dividing each product by $\bar{w}$ gives the frequency of each genotype at reproduction. Allele frequencies after selection ($p’$ and $q’$) can be calculated from the genotypic frequencies. If there is random mating the frequency of offspring in the next generation as a binomial distribution of the allele frequencies:
<table>
<thead>
<tr>
<th>Genotypes:</th>
<th>AA</th>
<th>Aa</th>
<th>aa</th>
<th>Alleles:</th>
<th>A</th>
<th>a</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial Frequencies</td>
<td>0.36</td>
<td>0.48</td>
<td>0.16</td>
<td>p = 0.36 + 0.48/2 = 0.6</td>
<td>q = 0.16 + 0.48/2 = 0.4</td>
<td></td>
</tr>
<tr>
<td>Fitness (W)</td>
<td>1.0</td>
<td>1.0</td>
<td>0.5</td>
<td>$\bar{W}$ = 0.36 + 0.48 + 0.08 = 0.92</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Product</td>
<td>0.36</td>
<td>0.48</td>
<td>0.08</td>
<td>$p' = 0.39 + 0.52/2 = 0.65$</td>
<td>$q' = 0.09 + 0.52/2 = 0.35$</td>
<td></td>
</tr>
<tr>
<td>Frequencies after selection, or at reproduction (with rounding)</td>
<td>0.36/0.92 = 0.39</td>
<td>0.48/0.92 = 0.52</td>
<td>0.08/0.92 = 0.09</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Frequencies among offspring of the next generation</td>
<td>$(p')^2 = 0.42$</td>
<td>$2p'q' = 0.46$</td>
<td>$(q')^2 = 0.12$</td>
<td>0.65</td>
<td>0.35</td>
<td></td>
</tr>
</tbody>
</table>

The process can be repeated in each generation indefinitely to follow changes in genotypic and allele frequency change through time.
If we say that selection against the recessive is equal to 1 minus its fitness \((s = 1 - W)\) we can use algebra to determine how much the frequency of the A will change in each generation. The algebraic treatment in your text (Box 12.A) shows that the change in the frequency of the A allele for this case is

\[
\Delta p = \frac{spq^2}{1 - sq^2}
\]

A check of this formula for the example:

\[
\Delta p = p' - p = 0.65 - 0.6 = 0.05
\]

\[
spq^2/1-sq^2 = 0.5*0.6*0.4*0.4/(1-0.5*0.4*0.4) = 0.048/0.92 = 0.05.
\]

The algebraic formula can be applied to all cases of fitness difference (survival difference, reproductive difference, or a combination). The change will continue until the a allele is no longer in the population.
Example 2: **Selection against a dominant phenotype.**
In this model $W_{AA} = W_{Aa} < W_{aa}$. For example $W_{AA} = 0.5$, $W_{Aa} = 0.5$ and $W_{aa} = 1.0$. Here we’ll start with the frequency of $AA = 0.36$, the frequency of $Aa = 0.48$, and the frequency of $aa = 0.16$ among the newborn, newly hatched, newly sprouted, or newly established generation.

<table>
<thead>
<tr>
<th>Genotypes:</th>
<th>AA</th>
<th>Aa</th>
<th>aa</th>
<th>Alleles:</th>
<th>A</th>
<th>a</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial Frequencies</td>
<td>0.36</td>
<td>0.48</td>
<td>0.16</td>
<td>p = 0.36 + 0.48/2 = 0.6</td>
<td>q = 0.16 + 0.48/2 = 0.4</td>
<td></td>
</tr>
<tr>
<td>Fitness</td>
<td>0.5</td>
<td>0.5</td>
<td>1.0</td>
<td>$W$</td>
<td>$W$ = 0.18 + 0.24 + 0.16 = 0.58</td>
<td></td>
</tr>
<tr>
<td>Product</td>
<td>0.18</td>
<td>0.24</td>
<td>0.16</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Frequencies after selection, or at reproduction (with rounding)</td>
<td>0.18/0.58 = 0.31</td>
<td>0.24/0.58 = 0.41</td>
<td>0.16/0.58 = 0.28</td>
<td>$p’ = 0.31 + 0.41/2 = 0.515$</td>
<td>$q’ = 0.28 + 0.41/2 = 0.485$</td>
<td></td>
</tr>
<tr>
<td>Frequencies among offspring of the next generation</td>
<td>$(p’)^2 = 0.27$</td>
<td>$2p’q’ = 0.5$</td>
<td>$(q’)^2 = 0.24$</td>
<td>0.515</td>
<td>0.485</td>
<td></td>
</tr>
</tbody>
</table>
If we say that selection against the dominant is equal to 1 minus its fitness \((s = 1 - W)\) we can use algebra to determine how much the frequency of the A will change in each generation. An algebraic treatment similar to that in your text (Box 12.A) shows that the change in the frequency of the A allele for this case is:

\[
\Delta p = \frac{-spq^2}{1 - sp(2 - p)}
\]

Checking this formula against our example
\[
\Delta p = p' - p = 0.515 - 0.6 = -0.085
\]
\[
spq2/1-sp(2-p) = -0.5*0.6*0.4*0.4/(1-(0.5*0.6)(2-p)) = -0.048/0.55 = -0.087.
\]
Example 3: **Selection favoring the heterozygote.**
In this model $W_{AA} < W_{Aa} > W_{aa}$. For example $W_{AA} = 0.5$, $W_{Aa} = 1.0$ and $W_{aa} = 0.4$. We can start with any initial genotypic frequencies. Here we’ll start with the frequency of AA = 0.36, the frequency of Aa = 0.48, and the frequency of aa = 0.16 among the newborn, newly hatched, newly sprouted, or newly established generation.

<table>
<thead>
<tr>
<th>Genotypes:</th>
<th>AA</th>
<th>Aa</th>
<th>aa</th>
<th>Alleles:</th>
<th>A</th>
<th>a</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Initial Frequencies</strong></td>
<td>0.36</td>
<td>0.48</td>
<td>0.16</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Fitness</strong></td>
<td>0.5</td>
<td>1.0</td>
<td>0.4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Product</strong></td>
<td>0.18</td>
<td>0.48</td>
<td>0.064</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Frequencies after selection, or at reproduction (with rounding)</strong></td>
<td>$0.18/0.724 = 0.25$</td>
<td>$0.48/0.724 = 0.66$</td>
<td>$0.064/0.724 = 0.09$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Frequencies among offspring of the next generation</strong></td>
<td>$(p')^2 = 0.34$</td>
<td>$2p'q' = 0.49$</td>
<td>$(q')^2 = 0.18$</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$$W = \frac{0.18 + 0.48 + 0.064}{0.724} = 0.724$$

$$p' = 0.25 + \frac{0.66}{0.58} = 0.58$$
$$q' = 0.09 + \frac{0.66}{0.42} = 0.42$$
If we say that selection against the AA phenotype is equal to 1 minus its fitness \( (s = 1 - W_{AA}) \) and selection against the aa phenotype is 1 minus its fitness \( (t = 1 - W_{aa}) \) we can use algebra to determine how much the frequency of the A will change in each generation. An algebraic treatment similar to that in your text (Box 12.A) shows that the change in the frequency of the A allele for this case is:

\[
\Delta p = \frac{pq(tq - sp)}{1 - sp^2 - tq^2}
\]

Checking this formula against our example:
\[
\Delta p = p' - p = 0.58 - 0.6 = -0.02
\]
\[
pq(tq - sp)/(1 - sp^2 - tq^2) = 0.6*0.4(0.4*0.6-0.6*0.5)/(1-(0.5*0.6*.06)-(0.6*0.4*0.4)) = -0.0144/0.724 = -0.02.
\]
In this case the allele frequencies will change until an equilibrium is reached.

At equilibrium the frequency of the A allele will be:

\[ p = \frac{t}{s + t} \]

and the frequency of the a allele will be:

\[ q = \frac{s}{s + t} \]

In this case both allele will remain in the population indefinitely. This is a balanced polymorphism.
Selection against a dominant phenotype or selection against a recessive phenotype will remove deleterious alleles from a population or at least reduce their frequencies to very low levels.

Mutation can reintroduce alleles into a population. At equilibrium the rate of introduction of alleles into a population by mutation should equal the rate of loss of alleles from the population due to selection. For a deleterious recessive allele:

\[
\mu_p = \frac{spq^2}{1-sq^2}
\]

If the recessive allele is rare, the denominator is \(\sim 1\). And the equation simplifies to:

\[
\mu = sq^2
\]

So, at equilibrium the recessive allele should have the frequency:

\[
\hat{q} = \sqrt{\frac{\mu}{s}}
\]
Nonrandom mating causes a deviation from the binomial distribution

Read: Disassortative mating in white-throated sparrows.

Assortative mating – like mating with like – does not change allele frequencies but produces a deficiency of heterozygotes relative to that expected with random mating.

Inbreeding is the most common type of assortative mating.
Selfing is the most extreme type of inbreeding

Continued inbreeding produces increasing deficiencies of heterozygotes
The difference between the observed frequency of heterozygotes (H) and the expected frequency of heterozygotes (H₀ - if mating was random) relative to the expected frequency (H₀) is a measure of inbreeding - the inbreeding coefficient (F).

\[ F = \frac{H₀ - H}{H₀} \]

If inbreeding is the cause of the heterozygote deficiency, then F should be nearly the same for all genes.
Inbred populations often exhibit “inbreeding depression” – a reduction in the average fitness of individuals in the population. This can be due to increased expression of deleterious recessive alleles.
Studies of inbred lines of *Drosophila* revealed that heterozygotes often have higher viability than homozygotes. There is a large amount of deleterious genetic variation in natural populations that is not expressed in heterozygotes.

Other studies have confirmed the high degree of deleterious recessive genetic variation in wild populations of other organisms.
Inbreeding results in greater expression of deleterious recessive alleles than would be seen in randomly mating populations. The overall reduction of the average fitness of individuals in the population is called “inbreeding depression.”

From a study of humans in Italy 1903-1907.

Viability was increased in a small population of adders in Sweden when individuals from outside were introduced in 1992.
Migration homogenizes genetic variation among populations. If one population donates migrants to another population, the allele frequencies in the receiving population will change to be more like those in the donating population.