Lecture Note – Section 1

I. History of evolutionary ideas

1. Evolutionary ideas predate Darwin & Wallace.

2. There were theologically based explanations for biodiversity/complexity as well
    (e.g. William Paley: natural theology)

3. Influence from other disciplines: Adam Smith's economics; Thomas Malthus'
    population biology

4. Industrialized British Empire provided a unique opportunity for naturalists to do
    a global survey

5. Please check Andrew's slides for the saga between Darwin and Wallace.

II. General patterns of evolution

1. Evidences for the hypothesis of "Descent with modification"

    -   Homology. Both physiological/anatomical and genetic/developmental.

    -   Increase of complexity through time (Tianzhu's personal note: I personally
        favor the term "order" over "complexity", because it's more subjective to talk about
        complexity, as it depends heavily on our knowledge of a particular organism.
        However, "order" has some objective measurements, e.g., ice is more ordered than
        water, and to keep a huge eukaryotic cell in good health requires more fine-tuning
        than keeping a virus alive, and so the biochemical systems in a eukaryote may be
        more ordered than a less "complex" organism.)

    -   Molecular phylogenies are in good congruence with phylogenies
        constructed from fossil records. Intermediate forms in fossil records imply
        possible common ancestors or an extinct relative of a current branch of
        life.

    -   Vestiges, atavism.

- Biogeography (Wallace's Sarawak Law). Why is biogeography a piece of evidence for evolution? Think about what is the most parsimonious way to explain the fact that related species tend to be found in contiguous regions, apart from the alternative hypothesis that god enjoys creating related things next to each other?

III. The Hardy-Weinberg equilibrium (HWE)

1. HWE is the zero-force law in evolution, which assumes Mendel's genetics. (Compare with Newton's first law in physics)

2. Assumptions: infinite population size; no selection; no migration; no mutation; random mating within the population

3. Basic statements:

   - Single locus: if two alleles P and Q are segregating at frequencies p and q in one generation, then the genotypic frequencies at HWE in the *next generation* is
     PP : PQ : QQ = p^2 : $2pq$: q^2

     This is the consequence of Mendel's first law

   - Multiple *independent* loci: you just have to multiply the expected frequencies of genotype at each locus to get the frequencies of the overall genotype.

     This is the consequence of Mendel's second law

   - Reaching HWE takes just one generation!

   - Note that anything which breaks Mendel's first law will also break HWE. For example, gene drive systems typically do not transmit via Mendelian genetics. In some cases, sperms with a certain allele can kill other sperms (segregation distortion), then HWE will also break down. You can view these special cases as selection operating *below* the individual level

4. Fun facts about the origin of HWE: After the rediscovery of Mendel's work in early 20th century, it remained controversial for several years. The main critique was from a British mathematician Udny Yule, who claimed that under the Mendelian inheritance, the dominant allele is going to spread through the population. Reginald Punnett (the "Punnett square") knew Yule was incorrect, but was too bad at math and wrote to his friend Godfrey Hardy (one of the most famous mathematicians in Britain) to ask for help. Hardy thought about it and the problem was indeed simple, Hardy even thought it was a joke to let him write a paper about it! He published the result in 1908 and another German physician Wilhelm Weinberg happened to discover the same principle in 1908 as well. Now we call it the Hardy-Weinberg Equilibrium. Under HWE, the frequencies of alleles do not depend on their dominance at all.

IV. Natural selection

1. A great historical debate about the nature of inheritance: Mendelians v.s. Biometricians (early 20th century). Mendel discovered the particular transmission of genetic materials at the end of 19th century, which directly led to Hardy-Weinberg Equilibrium, and the maintenance of genetic variation (as none of the alleles are lost in HWE). However, biometricians, led by Galton et. al., are in favor of the "blending" model of inheritance (e.g. human height). Both have plenty of evidence. However, if one assumes naively the blending model, genetic variation will eventually disappear, and as evolution operates on genetic variation, the blending model is very problematic for evolutionary biologists at the time!

2. The solution to this debate is by R. A. Fisher, who assumed *many loci with alleles of small effects contribute together to a trait.* Such inheritance is called polygenic inheritance, and the trait is called a polygenic trait (also called a quantitative trait) It can be shown that the blending model of inheritance is the statistical outcome of each loci transmitting via Mendelian genetics. In this way, the blending model also maintains genetic variation under HWE.

3. For this reason, natural selection can be understood both at the *allelic* level and at the *trait* level. If we are only interested in the evolution of a polygenic trait such as human height, bird beak length, we introduce the concept of heritability. The narrow sense heritability quantifies the efficacy of selection in face of environmental effects:

$$h^2 = R/S$$

S is the difference of the mean between selected individuals and the entire parental population. These selected individuals mate to generate the next generation. The difference of the mean between the next generation and the previous generation is R.

If environmental effect is zero, then $R = S$, and the trait is totally heritable.

Note that polygenic traits are often assumed to have *many* alleles of *small* effects to make it like a bell-shaped Gaussian distribution. If major alleles of big effects are present, the continuous distribution of trait often breaks down and you can recover classical Mendelian genetics, where trait values are concentrated at several discrete points.