Update on Heterozygote Advantage

According to the Hardy-Weinburg equilibrium, most of the rare alleles in a population are in heterozygotes, where they are not expressed if recessive. If the fitness of the heterozygotes is higher than homozygotes, (i.e. there is an advantage to being a homozygote), this retains variation, even if there is genetic drift.

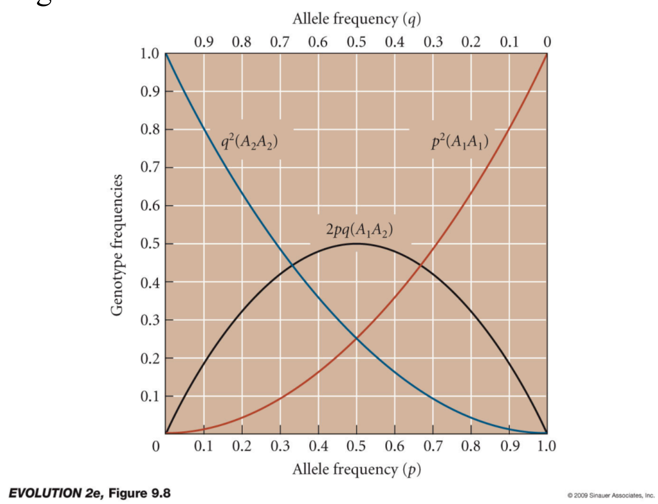

Figure 1: Allele frequency under Hardy-Weinburg Equilibrium.
Evolution 2 edition, figure 9.8. *Copyright 2009 Sinauer Associates, Inc.*

Species Concepts – applied to Ring Species

What happens when two independently evolving lineages meet? When two lineages that evolved from a single ancestral population encounter each other once again, it is called secondary contact. There are several possible outcomes on secondary contact:

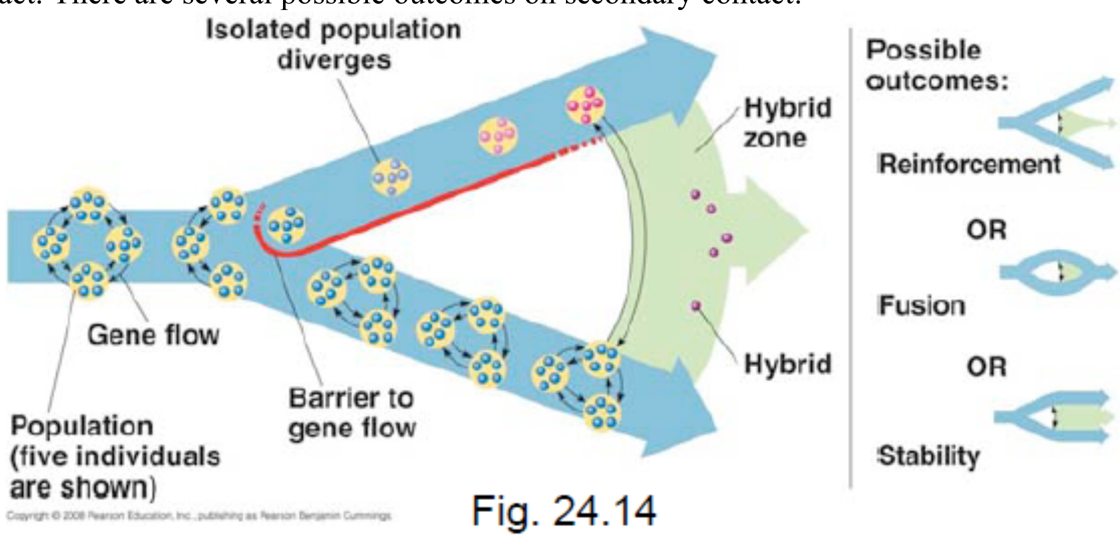

Figure 2: Possibilities of secondary contact: reinforcement, fusion, stable hybrid zone
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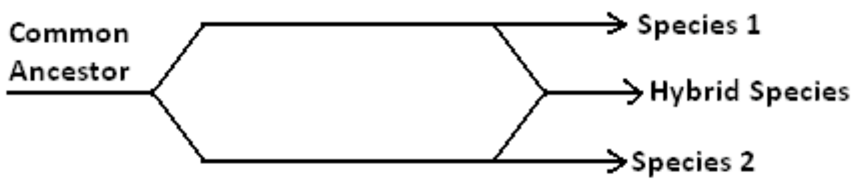

Figure 3: possibilities of secondary contact: Hybrid Speciation
Christopher Pavia, 2009.

1. No **hybridization** occurs; if these two lineages occupy different ecological niches and can exist sympatrically (in the same environment) they are "good species" by any criterion.
2. **Fusion:** members of the two lineages mate together, forming hybrids with normal fitness, and eventually collapse into one species. Note that since independent evolution has been occurring while the two populations were separate, resulting in a linage that will not be identical to the ancestral lineage. Typically this new lineage will be regarded as the same species, however.
3. Stable **hybrid zone:** each lineage maintains its own range separate of each other save for some areas of overlap. In those regions, the hybrids have reduced fitness and the hubrid zone is maintained by immigration from adjacent parent populations.
4. **Reinforcement:** selective pressure to avoid mating (hybrids are either inviable or infertile) will eventually lead to choice #1.
5. **Hybrid speciation:** if the hybrids are diploid (or rather, have the same chromosome number as their parent species) but ecologically different, that can lead to prezygotic isolation. Also, consider plant hybrids and polyploidy, also known as "allopolyplody:" in this case, the new hybrid taxon has another set of chromosomes (e.g. 3x) and will be sterile.

For examples, consider the *Ensatina* lizards from the previous lecture. Each subspecies (i.e. lineage) has its own distinct range. Some of these lineages overlap, especially in southern California. Some of these overlaps form stable hybrid zones, where the hybrids are viable. In other overlaps of the same two lineages there is strong reproductive isolation, and thus no hybrids.

Fossil Record

(speciation)
Microevolution ——————▶ Macroevolution

The **fossil record** is our primary source of information on the past, including the timing of various extinction and evolutionary events and the phenotypes of ancestral forms. Sedimentary rocks created by erosion (often in a marine environment) form strata, with different layers corresponding to different time periods. Consider the Grand Canyon, formed by the Colorado River over 20 million years: the exposed strata, from the top of nearby Bryce Canyon to the bottom of the Grand Canyon itself, cover the last billion years. These layers can be dated by analyzing proportions of different isotopes present in the strata.

Fossils provided both key evidence and frustration to Darwin when writing *the Origin of the Species*. Fossils showed there were many creatures which no longer existed; but these animals existed at some point, and must have been adapted to the environment in which they lived. This further reinforced the idea that the present and past are ruled by the same physical processes. However, it was frustrating in that many complex creatures seemed to suddenly appear in the fossil record, without preceeding transitional forms. Darwin predicted that these gaps would be filled, and many of the gaps he predicted have now been filled.

Some major transitions in earth history	**Billions of Years Ago**
Earth and Solar System formation	4.5
Earliest prokaryote fossils	3.5
Increase in oxygen – implies photosynthesis	2.7
Single-celled fossil eukaryotes	2.1-1.2
Complex metazoan (multi-celled animals)	0.5
Hominids (apes and humans)	0.005

The Cambrian Explosion is a time period from 550 million years ago (appearance of complex metazoans) when many species and new body forms appear in the fossil record. The fossils preceding that 550 million years ago mark are very scarce, then suddenly there is a large diversity of fossils and body forms.

What caused this diversity? There are several possibilities. Firstly, perhaps before the Cambrian period, all organisms were soft-bodied, and thus did mineralize and leave behind fossils. Supporting this hypothesis is that scientists have discovered fossil impressions of organisms older than the Cambrian period. Another possibility is that the rapid appearance of new species was due to an evolutionary innovation allowing the rapid diversification of body forms that did not exist before. Consider hox genes, and how they allow for entirely different body plans. The evolution of this innovation could allow for rapid diversification of body plans.

The **Burgess Shale** is a site in Canada excavated by Charles Walcott that has given us many excellent Cambrian fossils.

Now, consider fossils in tandem with extinction. Extinction is normal enough: 97% of all species ever extant on Earth are now extinct. We can determine extinction rates by following species that fossilize well through the various rock strata. Eventually, having gone extinct, they stop appearing in the fossil record. The background rate of extinction for marine invertebrates is around 1-5 species per million years; therefore, the typical species exists for 5-10 million years. However, there are some large peaks in the extinction rates which we call **mass extinctions**. Two major extinctions we will explore further are the **Permian-Triassic** extinction (250mya) and the **Createous/Paleogene (k/t)** extinction (65mya), which pushed the dinosaurs into extinction and lead to adaptive radiation of mammals.

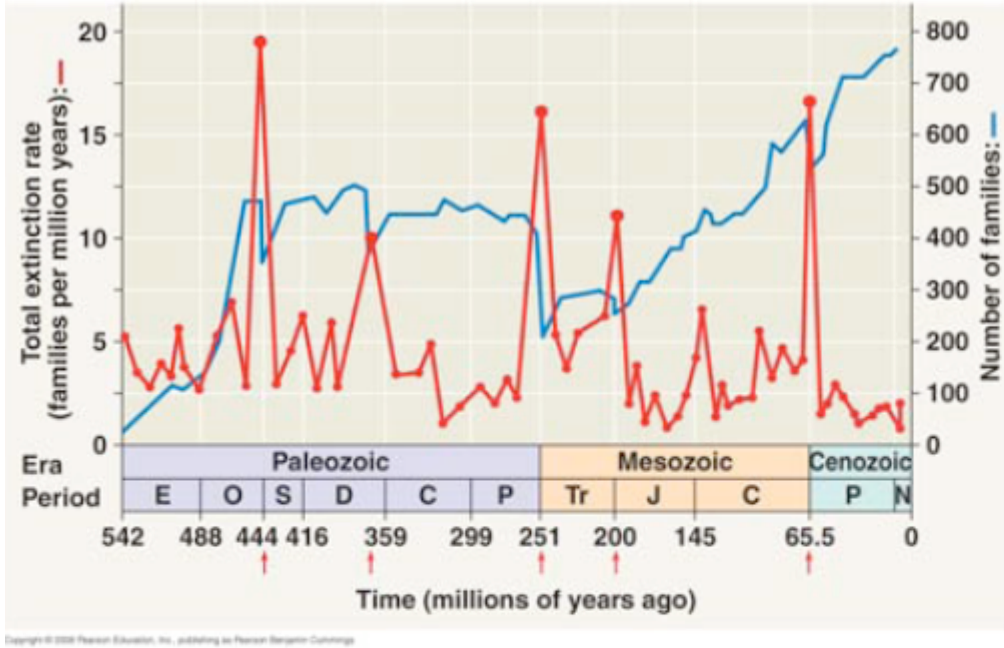

Figure 4: Graph of extinction rates over time, showing mass extinction events.