Events Leading to Speciation

Slide 2 As we have seen, populations of organisms tend to change genetically over time due to various agents of evolution, such as natural selection, genetic drift, or non-random mating. In the previous lesson, we focused mainly on the genetic change within individual populations. What would happen, however, if two populations of a particular species of organism were isolated from one another in some way. Over time, the genetic makeup of each population would change independently of the other population, due to the various agents of evolutionary change. If enough change occurred in the members of each population, it is possible that the two populations would not be able to interbreed if brought back together. The process just described, that of genetic isolation and the resulting genetic incompatibility of populations, is called speciation.

There are numerous ways by which speciation can occur. A common theme to all of them is the cessation of gene flow, or reproductive isolation, between populations, and the resulting independent genetic change of each population over time. In addition, you should note in this lesson that reproductive isolation, and the resulting speciation events, are often a result of some significant change in the environment.

Slide 3 Changes in the environment leading to speciation may be very marked, or may be quite subtle. For example, consider a population of plants that occupies facing mountain ranges and the intervening valley. At some point in time, this continuous population could be divided into two separate, isolated populations by some physical barrier, such as a change in water levels that results in the flooding of the valley. Since the two new populations are now separated from each other, changes may occur independently within each population, due to differing selective pressures, genetic drift, or other agents of evolution. If water levels remained high for long enough, perhaps several hundreds or thousands of years, enough differences might accumulate between the two isolated populations that they might not be able to interbreed if and when water levels recede and each population re-colonizes the valley. If this were the case, the two populations might then be considered different species.

The rising and falling water levels in our hypothetical valley are only one example of a geographic barrier. It should not be difficult to imagine other possible geographic barriers that could effectively block gene flow between populations. Examples could be the rising of a mountain range, or the formation of a canyon, or even, on a smaller level, the construction of a highway. Speciation resulting from such geographic barriers is called allopatric speciation.

In our previous lessons on the evolution of populations, we discussed the evolution of both fruit flies on the Hawaiian Islands and finches on the Galapagos Islands. Both of these groups of organisms represent good examples of allopatric speciation. In both cases, the geographical barrier separating populations of these organisms is water. This is true whether one is considering populations on different islands or comparing island populations to mainland populations. The isolation of the island populations, coupled with time, genetic drift, and selective pressures, has ultimately resulted in the complete reproductive isolation of different populations, and the development of new species.

Slide 4 In many cases, the environmental changes that separate two populations may be less obvious than in the previous example. For instance, consider environments where a sharp temperature gradient exists, such as the thermocline of an underwater spring in a warm lake. Alternatively, imagine a soil substrate that varies from shallow and rocky to deep and loamy due to the underlying bedrock. In such cases, the environments of organisms may vary over short distances, to the point that very different environmental conditions exist directly adjacent to one another. If individuals in a population of one species were spread out over such an area, they would be subject to very different environmental conditions, depending on the habitat in which they are found. The differing conditions may lead to different selective pressures, which in turn could result in genetic divergence between the individuals in each habitat. If enough divergence occurs, speciation may be the result. Speciation that occurs due to differences in directly adjacent environments is termed parapatric speciation.

A possible instance of parapatric speciation is currently occurring in a European grass, *Anthoxanthum odoratum*. Some populations of this species live in soil contaminated with the heavy metals from nearby mining activity. Directly adjacent to this contaminated soil, however, can be uncontaminated soil that also supports populations of *A. odoratum*. Populations of *A. odoratum* living in contaminated soil have been selected for a genotype that allows them to be tolerant of heavy metals. In addition, the flowering period of populations in contaminated soil has changed since mining activity began so that these plants now flower at a different time than populations of *A. odoratum* living in non-contaminated soils. Researchers have discovered that the different populations of this grass are still able to cross-fertilize to produce viable offspring, but only by manually cross-pollinating since they flower at different times of the year. It is likely that the change in flowering period, and different selective pressures in the adjacent soil types, are both leading to divergence of what was once one continuous population into two distinct populations and, perhaps, two distinct species.

Slide 5 While speciation often occurs as a result of differences or changes in the environment, there are instances where speciation is essentially independent of environmental conditions. In such cases, speciation may occur within the same environment, and so is called sympatric speciation. Often, sympatric speciation involves a change in the ploidy level of certain members of a population, so that some members carry extra chromosomes or entire extra sets of chromosomes. Individuals with extra sets of chromosomes are known as polyploids. Polyploid individuals in many cases are not able to mate with individuals carrying the original genotype.

Polyploidy can arise in different ways. In some instances, errors in DNA replication or cell division result in cells with twice the amount of DNA than they would normally have. An example of this would be a diploid organism producing diploid, rather than haploid, gametes. Alternatively, errors in DNA replication could result in a chromosome doubling event, where the entire genome of a cell is doubled. Imagine if a chromosome doubling event occurred in a diploid zygote. A tetraploid zygote would result. The subsequent mitotic cell divisions that occur would lead to a multicellular, tetraploid individual.

Polyploidy may also occur when closely related species interbreed, resulting in hybrid offspring that carry a set of chromosomes from each of the parent species. Because these chromosomes are from different species, they are not homologous chromosomes, and so cells of the hybrid offspring cannot undergo meiosis. The result? Hybrid offspring are often infertile, at least initially, and cannot mate with each other or with either of the parent species. Once again, there is a barrier to gene flow. Several species of *Tragopogon*, a sunflower relative introduced to eastern Washington and northern Idaho, appear to have evolved due to hybridization.

Sympatric speciation seems to be most important in organisms that are able to reproduce asexually, such as plants, although the polyploid condition is fairly common in some other types of organisms, most notably amphibians. Asexual reproduction in plants and parthenogenetic animals allows the polyploid condition, such as that resulting from hybrid offspring, to persist for many generations. This in turn increases the chance that at some point a duplication of chromosomes will occur, allowing the polyploid cells to once again go through meiosis and produce gametes.

Slide 6 Sympatric speciation does not always involve changes in the ploidy level of members of a population. In some cases, relatively small changes in morphology or behavior can also apparently lead to sympatric speciation, or speciation within the same geographic area. In one well-studied case, a species of fruit fly of the genus *Rhagoletus*, historically reproduced by depositing eggs in the fruits of hawthorn trees. However, in the early 1800s, many domesticated apples were introduced into the native ranges of *Rhagoletus*. In some areas, populations of *Rhagoletus* diverged to include individuals who deposited eggs on hawthorn fruits, and individuals who deposited eggs on domesticated apples. Over the last two centuries, these populations have diverged sufficiently so that in a given area containing both types of flies, only about 6% of matings involve crosses between the different types of flies. In addition, other differences, including the metabolic rate of pupa, breeding time, and response to the different smells of apples and hawthorns, appear to have evolved along with egg-laying habits.

Slide 7 As you can probably guess, the genetic isolation that develops between separated populations varies in its degree, depending on a number of factors. In turn, the degree of divergence between isolated populations determines the likelihood of successful interbreeding if and when the populations are brought back together. What are the factors that influence the divergence between populations? First, because genetic differences between populations accumulate over time, it would seem reasonable to conclude that the longer two populations of one species are separated, the more likely it is that they will accumulate enough differences to prevent successful interbreeding if they are brought back together.

But what if two populations were isolated from each other over time, yet their environments remained essentially identical? It is probable that the populations would diverge more slowly than if they were subject to very different environments, hence very different selective pressures. In addition to time, then, the environments that different populations inhabit also play an important role in determining speciation rates.

You might also consider how speciation rates can be affected by other factors, such as the size or range size of a population, or mating behavior, or generation times. For example, species that reproduce very quickly may be able to adapt to changing environments at a more rapid rate than species that reproduce more slowly (compare bacteria to elephants). A population with a large range, or one that is very mobile, may be subject to very different environmental conditions over its range, as opposed to a population that inhabits only a very small area.

In essence, the more that isolated populations evolve independently, regardless of whether their evolution is due to genetic drift, natural selection, or other influences, the less likely they will be able to interbreed when brought back together.

Slide 8 In the end, it may be helpful to view divergence between populations as a 'sliding scale'. The amount and types of differences, such as genetic differences, that accumulate between isolated populations determine the eventual genetic isolation between the members of each population. If the differences are substantial enough, so that gene flow is blocked between members of the two populations, the populations may continue to diverge over time as two separate species. On the other hand, populations that have not accumulated substantial differences are more likely to be able to interbreed when brought together.

In the cases where populations are brought back together before substantial differences have accumulated, reproductive isolation is often incomplete. Because of this, hybrid zones, consisting of fertile hybrid individuals that may mate with members of either population or with each other, may be present where the ranges of the two populations overlap.