

Species and Speciation¹

Conservation Biology

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Historically, we have thought of species as collections of individuals that share a common phenotype including morphology, behavior and ecological relationships with their environment. This view is based on what is known as the **typological species concept** wherein species represent a static type defined by the possession of an essential, non-varying set of characters. Variable characters within a species were considered to be accidental (nonessential) and of no importance.

In the early to mid 1900s this view was replaced by the **biological species concept (BSC)**. The BSC represented a radical departure in thinking about species necessitated by the concept of evolution. According to the BSC, developed by Ernst Mayr of Harvard, species are dynamic entities that interact both with their environment and with other species and are defined as a population or group of populations that reproduce among themselves, but not with other species. The BSC is the product of a shift in the late 1950s from **typological thinking to populational thinking** wherein individuals belonging to a particular species are viewed **not as possessing a fixed set of characters, but rather they fit into a range of variation** described in terms of a statistical mean with variance (standard deviation). Rather than being nonessential, accidental and unimportant, **individual variation is the key to the dynamic nature of species and enables them to vary over both time and space**. Thinking of species in terms of variable populations rather than fixed types was the **major conceptual advance that gave rise to our understanding of cladogenesis** (the multiplication of species) as opposed to **phyletic evolution or anagenesis** (change in a single species over time).

If species aren't types that can be described in terms of phenotypic characters, what are they? Mayr views species in relational terms rather than in absolute terms. **Individuals belong to a particular species because they are bonded to their conspecifics by a relationship (reproduction) and not because of the possession of a set of unique characteristics²**. Hence, the term "species" represents a relationship, not a type, and so is similar to the terms "sister" and "brother" which also describe a relationship between individuals rather than the possession of a set of absolute properties. You cannot know whether or not someone is a brother or sister simply by looking at them. So it is with species

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² Although similar genes, phenotype and common reproduction certainly go together! The point is the reproduction is the central bond, not the shared characters that also usually exist within a species.

which are real, dynamic entities that can change over time and space, yet still maintain their integrity as a unit of discontinuity in nature.

The importance of reproduction among conspecifics (individuals belonging to the same species) as the basis for understanding the nature of species cannot be emphasized enough. Possession of a fixed set of characters (the basis of the typological species concept) implies no relationship among the individuals classified together and so only individuals are real; the collective category (species) is an abstraction which can apply equally well to non-biological species, e.g., mineral and chemical species. **By emphasizing reproduction, the BSC provides a basis for including individuals in the same species and separating them from other species. Accordingly, it is not an artifact of human ability to conceptualize and generalize.** The individuals in the species itself determine the category species by their reproductive behavior. What links individuals together in a species is the continuity between generations afforded by reproduction, or over longer time periods by phylogeny. Parents and offspring and ancestors and descendants are so recognized not due to any essential similarity, but because they are related by a dynamic biological process. This cannot be said for mineral and chemical species. As a consequence of interbreeding, species constitute a genetic system that can vary over space and time. The term "genetic system" admittedly is vague, but it is consistent with the concept of a "gene pool" which forms the basis of microevolutionary analysis and allows individual variation in morphological, ecological and reproductive dimensions. A change in the genetic system over time can produce **anagenesis or phyletic evolution**, and a splitting of the system to form two separate, closed systems (**cladogenesis**).

Reproductive Isolating Mechanisms (RIMs)

Species exist as populations spread out in time and space and so individuals are classified as belonging to the same species if they are judged capable of interbreeding even though separation in time and space prevents them from actually interbreeding.

The key element in the definition of species is reproductive isolation which is effected by attributes called reproductive isolating mechanisms (RIMs). **A reproductive isolating mechanism is a biological attribute of the individuals belonging to the same species that is under genetic control and that prevents members of different species from producing successful offspring.** Since reproductive isolation is achieved by a genetically based characteristic shared by members of the same species, **geographic isolation**, i.e., an **extrinsic barrier** between two populations, unless it has to do with habitat preferences of different populations, is not a reproductive isolating mechanism. RIMs are **intrinsic barriers** to reproduction.

Most species are reproductively isolated from others by possessing several different RIMs because each species represents a different genetic system. There are eight commonly recognized isolating mechanisms that will be presented below in order of their disruption of successful reproduction. The first three mechanisms are **pre mating** mechanisms which prevent successful mating from taking place, while the last five are **post mating** mechanisms that prevent the production of successful offspring once mating has taken place.

Premating RIMs

Premating isolating mechanisms presumably evolved not to keep species from interbreeding with members of a different species but rather to adapt individuals of the same species to the environment in which they live, or to ensure successful reproduction among conspecific individuals. Since reproduction is the be all and end all of existence according to evolutionary theory, **natural selection will obviously favor mechanisms that ensure the success of reproductive efforts between conspecifics**. The following specific premating mechanisms have been described which emphasize the unique ecological, behavioral and morphological properties of species respectively.

1. **Ecological isolation** - prevents potential mates from even meeting. There are two forms of ecological isolation: **habitat isolation** and **seasonal isolation**. Habitat isolation occurs when different species **choose to breed** in separate areas that are ecologically different, e.g., pond vs. stream or woodland vs. meadow. Due to this physical separation individuals belonging to different species don't meet during the breeding season. Seasonal isolation occurs when members of different species breed at different times of the year even though they occupy the same habitat.
2. **Ethological or behavioral isolation** - involves species - specific courtship patterns or recognition cues so that even if members of two species breed in the same habitat at the same time, they will not mate with one another. Because species comprise separate genetic systems whose genes are often incompatible, any individual who mates with a member of a different species is in effect wasting its gametes and sacrificing its fitness. Natural selection will obviously favor any mechanism that enables individuals to recognize and mate only with conspecifics. **Ethological isolation is a product of selection for species-specific recognition cues**. Such cues could be (a) visual, e.g., the flash sequence in fireflies or the complex series of stimulus and response behaviors that characterize courtship patterns in birds (b), auditory, e.g., the species-specific calls of frogs and birds, or

(c) olfactory as found in insects which release species-specific chemical attractants or pheromones.

3. **Mechanical isolation** - results from incompatibility of sex organs between males and females from different species. This form of isolation was once considered to be the main isolating mechanism that separated species of insects when it was believed that insect genitalia operated in a key-in-lock fashion. Males of one species could not mate with females of another because they possessed the wrong key. Since that time variation in genitalia within insect species has been shown to be so extensive that it minimizes the importance of this form of reproductive isolation. Instead mechanical factors work in conjunction with other RIMs that tend to largely supersede it in importance. Mechanical isolation is still important, however, in some species of plants due to the location and configuration of stigmas and styles.

4. Postmating RIMs

For the purposes of our class, you should generally understand what postmating RIMs are but you don't need to know the names of the different types - please just read them so that you have a general idea

Postmating isolating mechanisms are the by-product of genetic divergence between species and incompatibility between their distinct genetic systems. The following mechanisms prevent successful breeding and gene flow between the two systems after mating has taken place.

1. **Gamete mortality** - occurs when the sperm from a male of one species dies in the reproductive tract of the female of a different species before fertilization can occur. Sperm death is caused by hostile chemical secretions in the female reproductive tract, e.g., the pH of the female's secretions may not be favorable to the survival and mobility of the sperm from a different species.
2. **Zygote mortality** - fertilization occurs but the zygotes die before undergoing development due to the incompatibility of their gene complexes.
3. **Hybrid inviability** - development progresses up to a point but the hybrid dies before reproducing.
4. **Hybrid sterility** - the hybrid survives and may even be robust due to hybrid vigor, but it is sterile, e.g., mules that are hybrids between a horse and a donkey are physically robust but cannot reproduce. Consequently, horse genes cannot enter the donkey population (and vice-versa) to cause reticulate evolution (the fusion of two species due to hybridization) because mules can neither breed among themselves, nor backcross with horses and donkeys.

5. Hybrid (F₂) breakdown - interspecific hybrids are viable and fertile but these F₁ hybrids produce inviable or sterile offspring after mating among themselves, or when they backcross with either of the parental species. Recall that the process of recombination produces mosaic chromosomes - part maternal and part paternal. The F₁ hybrid contains intact chromosomes from both parents, each of which contains harmonious gene combinations tested by natural selection. These adaptive gene complexes are broken up, however, through recombination when these hybrids produce gametes, and subsequent syngamy produces F₂ zygotes with **epigenotypes** (genotypes which interact during the process of development) consisting of various combinations of genes from the two different species. Hence, **the integrity of the two genetic systems collapses in these zygotes.**

Problems with the BSC

Over the years, it became evident that the BSC concept worked well in certain groups but not so well in others. Moreover, it was absolutely of no use at all with regard to asexual species (where reproductive isolation is meaningless) and with describing extinct species (since obviously reproductive behavior could not be observed).

The proponents of the BSC expected that there would be problems with the concept, especially in cases where species had large ranges where individuals at the extreme ends of the range had had considerable time to diverge. Thus, they were not surprised when numerous examples of *rassenkreis* or "race circles" were discovered. The interesting feature of these circles is that adjacent populations have no reproductive isolation but if members from populations at the extreme ends (individuals who would normally never encounter each other) were brought together, they cannot successfully interbreed or they have low breeding success. This sort of thing is not a problem for the BSC because it is exactly what you would expect to see -- the process of divergence towards producing a new species (cladogenesis) is viewed before it is complete.

That said, there are more serious problems, especially in flowering plants. Here, it is often no problem to cross what appear to be perfectly good species and produce viable fertile hybrid offspring. Sometimes successful crosses can even be made across families. Failures of the BSC "species hypothesis" at minimum requires that we realize that it is not a universal definition of a species. But it worth emphasizing that it tends to work well with animals (although once again, failures of the concept are observed on occasion).

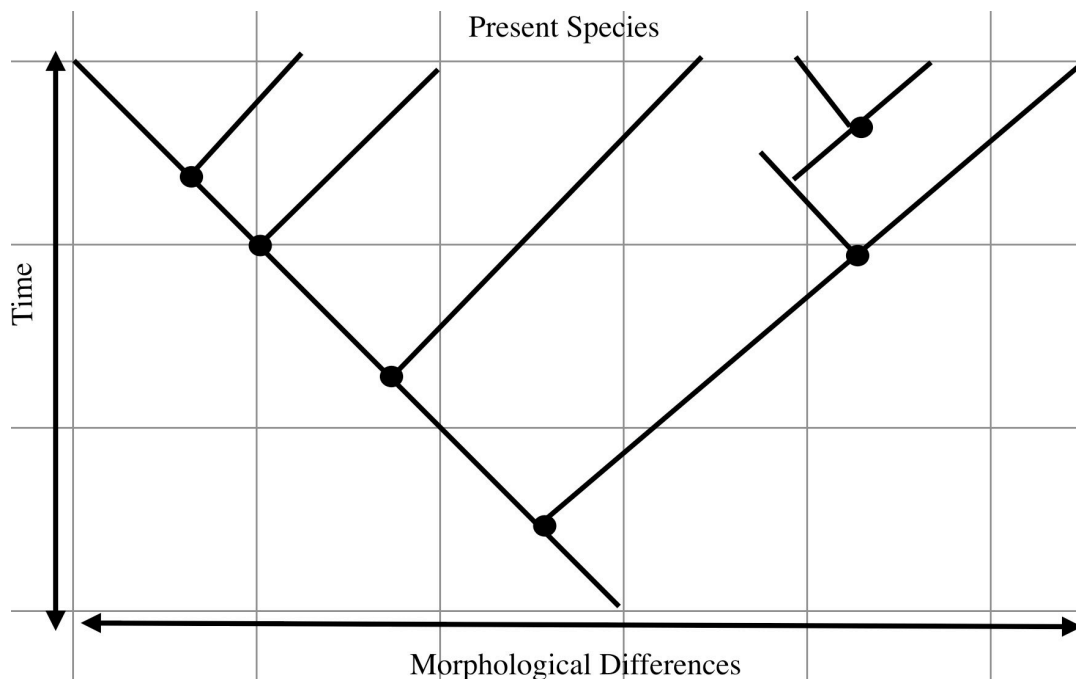
Evolutionarily Significant Units: Phylogenetic Species Concept

Although the BSC was prominent, typological species work continued. The reason was that the fact was that morphology very often does correlate with "biological species" and often it was not feasible to

test for reproductive isolation. Identification of biological species can be, if nothing else, very time-consuming. So, classification based on morphology continued. Beginning in the late 1960s, typologists (morphology based taxonomists) began looking for ways to rely less on species descriptions that were based at least in part on intuition that came from years of experience with a group of animals. Thus, an experienced expert would examine specimens and look at characteristics that had been useful in separating species in the past. He or she would then describe a new species if, based on their experience, the differences looked great enough to justify such a description. This is essentially what most taxonomists from Linnaeus on had been doing. Its biggest problem was that the methods were not readily testable and were hardly transparent--both major goals of science.

To get around these problems, systematists adopted two new approaches. First, W. Hennig, a German entomologist developed a method of classification called **cladistics**. Cladistics is a complicated topic that we will not explore in detail. Essentially, it is a scientifically rigorous methodology that features well defined techniques to use the morphological characteristics of living organisms to work out a **phylogeny**.

A phylogeny is a lineage -- kind of like a genealogy except that instead of following near relatives it looks at the descent of populations. Phylogenies are typically displayed as trees.



The **top of the phylogeny tree** -- the tips of the branches— represent present-day **populations**. These could actual populations of a species to species or even higher taxa such as genera, families, etc. As

we work our way down from the tips, **each branch represents a line of descent**. Branches reinforce **the notion of independence -- genes move from the past to the present but only the within branches -- not between them**. Thus, when branches separate, we have created separate lineages. Each division point is referred to as a "**node**." Branches that do not make it to the top of the page represent lineages that have become **extinct**. Finally, the bottom of the tree (the start of the main trunk, usually referred to as the "**root**") represents a **common ancestral population to all members of the tree**. Notice that a crucial element of the tree is **monophyly** -- all of the lineages on the phylogeny are descendents of a single ancestral population.

We need not understand exactly how cladistic systematists come up with their phylogenies. This said, it is important to realize that when using cladistics, it is often possible to generate multiple phylogenies from the same data set. How is one to decide which to adopt as a tentatively correct phylogeny? The answer is to rely on the **principle of parsimony** -- nature general prefers the simplest possible explanation. Systematists use mathematical programs to estimate which phylogenies are overall the simplest and they use these until other data suggest they are incorrect.

At about the same time that cladistics was being developed, another group of taxonomists were seeking to improve their classifications by using many more phenotypic characteristics than had been used in the past and then by identifying groups such as species by mathematical techniques that looked for overall similarity and gaps between groups. Although this approach, termed, **numerical taxonomy**, did not gain many adherents, it is important because some of its main ideas influenced the present generation of taxonomists.

So what do present day taxonomists do that is different from the past? Essentially, they have merged ideas from cladistics and molecular genetics to produce a new approach to taxonomy that relies heavily on **differences in genetic sequences** combined with sophisticated mathematical techniques to generate phylogenies. The modern approach is to extract DNA from members of a population. Next, specific genes or genetic regions are sequenced and their nucleotides are sequenced. Often genes that come from mitochondrial DNA are used. These genes are particularly useful because they only inherited along the female line and because many of them do not code for functional proteins. The result is that since selection does not work on them, differences accumulate at random over time and at a steady rate. Thus, if a population diverges from one ancestral population, then we must assume that over time their respective mitochondrial DNA sequences will begin to diverge and become more and more different. This forms the basis of a molecular clock whereby we can estimate how long it has been since they diverged. The result, when combined with sophisticated

mathematical analyses (and especially when a number of genetic sequences from different genes are employed) will produce very useful phylogenies.

Notice that these phylogenies essentially define species as groups that have diverged genetically enough to be seen as independent evolutionary lines – separate lineages. Thus, species are now defined as phylogenetically or evolutionarily independent lineages. Notice that this approach is largely consistent with both the typological biological species concepts and in fact has several advantages over each. For instance, it does not require the extensive and time consuming field work of the biological species concept and it is more likely to reveal morphologically very similar species than is typology. On the other hand, it has the disadvantage that it is relatively expensive and it is often difficult to use on extinct species (DNA samples from long dead organisms are not quite as easy to obtain as was suggested in Jurassic Park).

Speciation

Now that we have defined species as reproductively isolated units and have examined the mechanisms that result in reproductive isolation, we can address the problem of the origin of new species. A new species can arise in either of two ways:

- Transformation of an existing species over time (**anagenesis** or **phyletic evolution**), or through the
- **Speciation**, which results in the multiplication of species.

Note that in phyletic evolution the number of species is not changed, but that speciation increases the number of species. The process of **anagenesis results from** the action of **natural selection and random factors** operating over long time periods and species transformation occurs as the environment changes and the species goes through various genetic bottlenecks. The end result is that species A has become so modified that taxonomists recognize it as a different species (species B). At any time during this transformation only one species existed.

Cladogenesis, on the other hand, results in the production of a new species, e.g., species A perhaps continues (or itself changes) but it also gives rise to species B. Before the process of speciation takes place there is only one species (species A) but afterwards there are two species living at the same time (species A and species B).

The process of cladogenesis ultimately entails the creation of separate lineages, each of which may be reproductively isolated from the other and will to some degree differ in morphology and will certainly have genetic differences.

The Theory of Allopatric Speciation

Several hypotheses to explain how speciation occurs have been proposed and these are called **modes of speciation**. The process of

allopatric speciation is believed to be the most common mode of speciation among animals and plants and is supported by the near universal existence of geographic variation among widely separated populations of a single species and the occurrence of examples of incipient species (populations on the way to becoming new species but not quite there yet) which give taxonomists fits. If geographic variation is extreme enough, a taxonomist will have a difficult time deciding whether individuals from allopatric populations belong to the same or different species.

Two models have been proposed to explain the process of allopatric speciation: the **range splitting model** and the **peripheral bud or peripatric model**.

- Range splitting involves the appearance of an extrinsic barrier that separates the distribution of the species into two or more isolated clusters of populations. A river that changes course or a lava flow can affect such a barrier.
- The peripatric model relies on a particular population structure without the sudden intervention of a barrier.

The "classic model of allopatric speciation is the range splitting model. It is easiest of the two to understand. If a population becomes sufficiently isolated from the rest of a species and if it does not become extinct, it will begin to diverge from the other as a result of selection and random effects such as drift and founder/bottleneck effects. If the changes become great enough, we end up with a new species.

Read the section below, not so much to learn about peripatric speciation because as I indicated in class, this will not be on the test. Nevertheless, it will help you better understand populations that make up a species interact genetically and with the environment. Those topics will be very important to us in the rest of the course.

Model of Peripatric Speciation

A species whose populations are contiguous (bordering one another) will not speciate because gene flow and identical selective pressures act as a cohesive force to keep its populations from diverging genetically, and **without evolution (genetic divergence) speciation cannot occur**. For many species, however, all populations are not contiguous. In particular, populations located at the edge of the species range tend to be more isolated. These geographic isolates are formed by emigrants from the central populations but the opportunity for successful colonization diminishes near the edge of the range because suitable habitats are few and far between. Ernst Mayr in proposing the peripatric model noted the following differences between **central** and

peripheral populations in a species whose population structure consisted of geographical isolates.

Central vs. peripheral populations (very useful)

1. **Density** - population size is low in peripheral populations but high in central populations. This difference in density can be attributed to the harsher environmental conditions experienced at the end of the species range. The central populations occupy the habitat most favorable to the species but the further one moves away from this favorable area, the harsher and less hospitable the environment becomes. Consequently, few individual variants will be able to cope with these harsher environmental conditions. Beyond the existing edge of the species' range these conditions are so severe that no individual can survive and reproduce and so a population cannot be maintained.
2. **Intrapopulation variability** - individual variation would be lower *within* peripheral than central populations because the harsher selective pressures would weed out variants that could not survive in the peripheral populations but could flourish in the more benign environment occupied by the central populations. Notice also that genetic drift would contribute to differences as peripheral populations would undoubtedly be smaller than central demes.
3. **Interpopulation variability** - the level of variation *between* geographic isolates should be much greater than between central populations. Since geographic isolates are widely separated from each other (they occupy the periphery of the entire range), they are exposed to quite different environmental conditions and selective pressures that will cause them to diverge in different directions. Central populations, on the other hand, are largely contiguous and so are kept from diverging by gene flow and similarity in selective pressures.

Evolution vs. Speciation

A successful genetic revolution does not automatically make the isolated population a new species. The genetic changes described so far only constitute evolution through the agency of migration (in the founder effect), selection and genetic drift in producing homozygosity, and mutation and selection in the genetic revolution producing a new system of allelic variation **after the bottleneck of homozygosity** has been passed. Should this new population become phenotypically distinct from all others through this process, it might be classified as a subspecies. Even so, if it expanded its range after evolving adaptations to this new environment and came in contact with other populations of its species, it could still exchange genes (BSC) or would not be considered independent enough to constitute a separate lineage (phylogenetic species concept).

One way to understand the difference between evolution and speciation is to assume that we are dealing with a population (probably animal but could be plant) where reproductive isolation is evolving. As mentioned before, this is generally but not always a very useful way to define separate species. A peripheral isolate will become a new species only if the genetic revolution produces a RIM. Thus, **THE PROCESS OF SPECIATION REQUIRES BOTH EVOLUTION AND THE ACQUISITION OF A REPRODUCTIVE ISOLATING MECHANISM**. Evolution without a RIM will only produce interpopulational variation. But, the origin of a RIM requires some degree of evolution. Why? The reason is that RIMs are intrinsic (genetically-based) barriers to reproduction and cannot arise unless the gene pool has changed, at least sufficiently to produce a RIM.

Origin of Reproductive Isolation

Because a peripheral isolate is physically separated from the rest of the species, there is no gene flow and no reason why selection should operate to reduce gene flow. Consequently, **selection will not produce an isolating mechanism directly for the purpose of preventing reproduction with members of the central populations**. But, selection can produce an isolating mechanism **indirectly as a by-product of adaptation to the environment in which the geographical isolate finds itself**.

Selection for gene complexes which adapt individuals to the physical and biotic components of the environment inhabited by the peripheral population may result in postmating mechanisms if the new gene complexes differ sufficiently from those found in the central populations. Premating mechanisms may be developed as a **by-product of selection** for reproductive success in the new environment. Consider the following examples.

1. Successful reproduction in aquatic species may be tied to the water temperature in which the eggs develop. The peripheral population may be exposed to a different temperature regime than that found in the central populations. Consequently, selection can shift the optimum temperature for development in the peripheral population. Should individuals from this population invade the range of the central populations, they will have to breed at a different time of the year so that their eggs will develop at the same temperature to which they were adapted in the peripheral population. Thus, by adapting individuals to a new temperature regime in the peripheral locality, selection has incidentally produced a form of **seasonal isolation** and therefore a new species.
2. Suppose a number of flies are carried by the wind during a storm from a mainland locality to an island. The island is more exposed to severe

winds than the sheltered mainland habitat and this difference in wind velocity can act as a selective pressure to modify courtship pattern in these flies. Species-specific recognition cues in flies often involve the time the males spend hovering to attract females. Variation exists both in hovering times among the males and in response to hovering time by females. In this new environment long hovering times will be selected against because the longer the male spends hovering, the greater is the risk of being swept out to sea by the wind. The most successful reproducers will be males with short hovering times and females who respond only to short hovering time. Over the span of several generations the entire population will be characterized by a courtship pattern so different from that of the mainland populations that it constitutes a premating isolating mechanism (**ethological isolation**). When this occurs, the island population becomes a new species.

Note that in our discussion of speciation we included a role for each factor important in microevolution: (1) migration, (2) mutation, (3) genetic drift, and (4) natural selection, and showed how these interacted to produce new species. Be sure you understand how each fits into the overall process!

Most peripheral isolates will become extinct. A small minority of them will survive long enough to pass through the bottleneck of homozygosity successfully and undergo the genetic revolution. Most of these will not acquire species status. Rather, they will simply add to the level of interpopulational variation within the species. Some may remain allopatric and be classified as a subspecies, while others may invade the range of the central populations and hybridize with them forming a character gradient or cline.

Rarely will one of these peripheral isolates acquire a reproductive isolating mechanism during the genetic revolution and become a new species. When this does happen, the new species may remain separated geographically from populations in the species from which it speciated and be recognized as an allopatric, but related species. Alternatively, it may migrate into the range of its former parental species and become sympatric with it. This opens up the possibility for further differentiation between the two species through their interaction with one another - the subject of our next topic.

The Origin of Sympatric Species

Species that live together in the same area at the same time, i.e., that are **sympatric** and **synchronic**, tend to be clearly differentiated in morphology, ecology and reproductive behavior. **Congeneric species** (closely related species which are included in the same genus) which are always sympatric have led some biologists to suggest that they must

have evolved while part of the same species population (**sympatric speciation**). How they might have diverged genetically to the point of being reproductively isolated without being geographically isolated poses a severe problem for these theorists.

An alternative view of the origin of sympatric species relies on the theory of allopatric speciation wherein a **daughter species evolved** from a parental species **as an allopatric population and secondarily came into contact with the parental species through migration** into its home range.

Intergrades between subspecies where their ranges overlap suggests that secondary contact after isolation is rather common. In this instance a peripheral isolate might have differentiated genetically (evolved) but not acquired a reproductive isolating mechanism. Consequently, it interbred with other populations after differentiating and reinvading the range of central populations through migration.

Indirect effect of natural selection in producing a RIM

Only if the peripheral population had developed a RIM while in isolation would the two species not produce intergrades after range invasion by the new species. In this instance, natural selection only produced a RIM as an indirect by-product of adapting individuals while they were allopatric (see previous discussion of speciation). The acquisition of species status may prevent such sympatric species from interbreeding, but it will not prevent them from impacting on one another in an evolutionary relationship. Since the **daughter species** was once just a population of its **parent species**, the two species would be very similar. **Any differences between them would have resulted from evolutionary processes acting on them while they were geographically isolated**, but it is highly unlikely that these processes would have resulted in the usual level of differentiation observed among sympatric species. Further differentiation will result from the **direct action of natural selection acting against individuals in both species that are very similar**.

Due to individual variation and the fact that these two species are closely related, we would expect considerable overlap in morphological, ecological and reproductive characteristics. **Those individuals in both species outside of the area of overlap would not interact and so would be favored by natural selection; those in the area of overlap would interact and be eliminated from each population by the process of natural selection. This interaction could be either through competition for the same resources or in attempted mating. We will discuss the evolutionary significance of interspecific competition later in the course so will confine our discussion here to the effect of reproductive interaction between these two congeneric, sympatric species.**

Direct effect of natural selection in producing a RIM

Should a **pre mating** reproductive isolating mechanism evolve when daughter and parent species are allopatric (as was explained before) mutual range invasion would not result in any reproductive interaction between members of the two species. If, however, a **post mating** RIM evolved during allopatry, the ecological and ethological distinctions that serve to isolate well-differentiated sympatric species reproductively would not exist. These characters would be subjected to considerable overlap between the two species. Frogs, for example, use species-specific mating calls to facilitate successful reproduction. Male calls show some individual variation and female response to such calls also would be expected to vary. Each species would have a range of variation in both male call and female response to the call. **Individuals in the zone of overlap would on occasion make mistakes and breed with members of the wrong species**. Such mistakes would be fatal to the fitness of genes responsible for these phenotypic traits because successful reproduction would be prevented by the post mating RIM. These overlapping individuals would waste their gametes (no offspring would be produced). Thus, only those genes that allow males and females to correctly recognize their own species are passed on to the next generation. **Natural selection would directly weed out these overlapping traits and cause the evolution of a pre mating RIM to reinforce the post mating RIM(s) that evolved in allopatry**.

Character displacement as evidence

Evidence for this process can be seen in the phenomenon of character displacement. Allopatric species of frogs may overlap broadly in call characteristics without any selective penalty because the geographic separation prevents mistakes in mating. When these same two species are found in sympatry, call characteristics are sharply differentiated with no overlap. This differentiation is called **character displacement** because the mating call characters (visible on a sonograph) have been displaced where the two species are sympatric. By contrast, allopatric populations often show overlapping call characteristics.

Such comparisons between allopatric and sympatric species are only **patterns** observed at the same time but in different locations. **The mechanism by which they were produced is usually inferred, not directly observed**. Thus, the term "character displacement" is a description of the observed difference in pattern despite the suggestion of process indicated by the word "displacement."

The effect of natural selection in displacing characters in congeneric, sympatric species results in two completely different species distinguishable from one another morphologically, reproductively and ecologically. Once this process is over, the stage is now set for each species to speciate and produce a family of closely related species each

adapted to a different facet of the environment they share. This pattern is called **adaptive radiation** and is the means whereby species diversity is built in a given area.

Questions:

1. Distinguish between typology, BSC, and phylogenetic species. What is common to all? How is each an example of a scientific hypothesis?
2. Describe the process of range-splitting speciation.
3. Describe the types of reproductive isolating mechanisms and their significance to speciation.
4. Explain the difference between the processes of anagenesis and cladogenesis.
5. Distinguish between each of the following:
 - cladogenesis and anagenesis
 - evolution and speciation
 - central and peripheral populations (central and peripheral demes)
 - intrapopulation and interpopulation variation
 - biotic and abiotic selective pressures
 - role of selection in producing RIMs.
 - role of mutation and natural selection in the genetic revolution
 - premating (prezygotic) & postmating (postzygotic) isolating mechanisms
 - ecological, ethological & mechanical isolation
6. Identify each of the following:
 - allopatric (geographic speciation)
 - peripatric speciation
 - geographic isolate
 - founder effect
 - reproductive isolating mechanism