

Speciation

Overview

For convenience, we can analyze speciation as a three-step process: 1) an initial step that isolates populations; 2) a second step that results in the divergence of characteristics between populations; 3) a final step that results in reproductive isolation (re-enforcement)

Mechanisms of Isolation

The speciation process begins when populations become isolated and gene flow is reduced

One of the classical models of speciation is related to this phenomenon is **allopatric speciation** - the formation of a new species in isolated geographical areas

Populations can become isolated through dispersal and colonization

Populations can also become geographically isolated as the result of **vicariance**, including formation of mountains ranges, river formation, drying and the subsequent fragmentation of forests, lava flows, etc.

Geographic Isolation via Dispersal and Colonization

This often occurs as the result of founder events – when individuals of a population disperse to new habitats or islands

One consequence of founder events is that colonizing individuals are isolated from the original ancestral population

The isolated founding population experiences drift and differences in mutation and selection as the result of being in different environments

In the process of adapting to different environments, the populations undergo different genetic substitutions and gradually become genetically differentiated

As the result of accumulated genetic differences, distinguishable morphological and physiological differences arise (second stage of speciation)

It is when populations have changed enough to be recognizably different, but not to be reproductively isolated, they are usually referred to as **races** or **varieties**

This is the first recognizable step in allopatric speciation - the populations have become genetically differentiated in the process of adapting to different environments

Example: Hawaiian *Drosophila*

A good example of allopatric speciation via geographic isolation is divergence among Hawaiian *Drosophila*

Many of the Hawaiian *Drosophila* are endemic to particular islands of the archipelago
And the leading hypothesis for their diversification is the founder effect

Q. Is the hypothesis supported by evidence?

Based on the manner in which the islands were formed, the founder event hypothesis makes two predictions: 1) closely related species should be found on adjacent islands; 2) phylogenetic relations among the flies should correspond to the manner in which the islands were formed

Mitochondrial DNA sequence data for 4 species of flies supports these predictions
That is, the most recent species are found on the youngest islands and the sequence of branches for the phylogenetic hypothesis of flies is consistent with the order of island formation

Geographic Isolation through Vicariance

Populations can become isolated from one another via vicariance events, including mountain range formations, habitat fragmentation, etc.

A classic example of a vicariance event separating populations is the isthmus of Panama – the land bridge that developed between North and South America some 3 million years ago

A study was done examining the population genetics of snapping shrimp on either side of the isthmus (e.g., 7 pairs of closely related morphospecies, with one member of each pair found on either side of the isthmus)

A comparison of mitochondrial DNA sequences indicated that species pairs from either side of the land bridge are each other's closest relatives

Changes in Chromosomes as a Barrier to Gene Flow

Chromosomal mutations that lead to polyploidization can result in reproductive isolation between populations because if the incompatibilities between gametes with different number of chromosomes

Mechanisms of Divergence

The Role of Genetic Drift

Most species are thought to have originated as a consequence of small population sizes (during colonization events, in peripheral populations, etc.)

There is lots of work done examining the influence of small population size and therefore drift on the rapid differentiation of populations

Interestingly these findings suggest that the impact of drift on small populations is not always through a loss of overall genetic variation

In fact, when a population is reduced to a small size because of bottleneck, only the rare alleles are lost due to drift; for genetic diversity to be dramatically reduced the population would have to be extremely small

By contrast, most models show that genetic variation in the population can actually *increase* as a result of bottlenecks

The Role of Natural Selection

Research involving the apple maggot fly, *Rhagoletis pomonella*

Researchers were interested in determining whether the flies that parasitize hawthorn and apples host species were distinct species

Has NS based on host preference for different food created different races of flies?

Electrophoretic analysis indicates that the flies are genetically differentiated since they exhibit significant allele frequency differences at 6 enzyme loci

It appears that rather than being isolated by dispersal or vicariance, the flies are isolated on different host species

When given a choice flies show a strong preference for their original host

Because mating occurs on the plant, host preference results in strong nonrandom mating

These experiments seem to imply that NS has favored distinct habitat preferences in apple and hawthorn flies. *Why?*

Interestingly, individual fly larvae of both species do much better (in terms of growth and survival) when reared on hawthorn fruit

What fitness advantage do flies get from switching to apple trees?

There may be at least 3 advantages to switching to apple fruit

- Escape from parasitoids.
- Escape from intraspecific competition.
- Escape from interspecific competition.

The Role of Mutation

For speciation, the primary role of point mutations, gene duplications, and chromosomal inversions is to provide the raw materials for drift and selection once gene flow is reduced

Sympatric and Parapatric Speciation

Sympatric speciation is the formation of new species in sympatry
You can think of it as reproductive isolation without geographic isolation

Thus, the difference between allopatry and sympatry may be a distance factor
Individuals in allopatric populations simply cannot travel far enough to mate, or otherwise interact, with each other

But, individuals in sympatric populations can; absolute distance is irrelevant

Genetic modeling suggests that populations can diverge with low to moderate gene flow provided that 2 conditions are satisfied: 1) selection for divergence is strong; and 2) mate choice must be correlated with the factor that is promoting divergence

Example of Sympatric Speciation using three-spined sticklebacks

Two different species of three-spined sticklebacks in each of five different lakes.
A large benthic species with a large mouth that feeds on large prey in the littoral zone
A smaller limnetic species - with a smaller mouth - that feeds on the small plankton in open water.

DNA analysis indicates that each lake was colonized independently, presumably by a marine ancestor, after the last ice age.

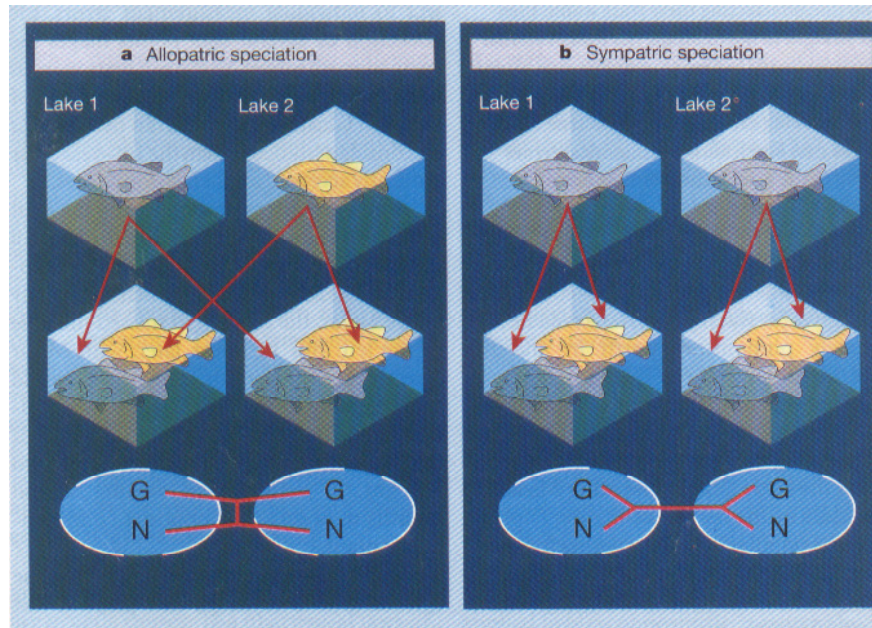
DNA analysis also shows that the two species in each lake are more closely related to each other than they are to any of the species in the other lakes.

Nevertheless, the two species in each lake are reproductively isolated; neither mates with the other.

However, aquarium tests showed that

- the benthic species from one lake will spawn with the benthic species from the other lakes and
- likewise, the limnetic species from the different lakes will spawn with each other.

These benthic and limnetic species even display their mating preferences when presented with sticklebacks from Japanese lakes; that is, a Canadian benthic prefers a Japanese benthic over its close limnetic cousin from its own lake.



Conclusion: in each lake, what began as a single population faced such competition for limited resources that **disruptive selection** coupled with **assortative mating** favored a divergence into two subpopulations exploiting different food in different parts of the lake.

The fact that this pattern of speciation occurred the same way on three separate occasions suggests strongly that ecological factors in a sympatric population can cause speciation.

Parapatric speciation is the establishment of reproductive isolation between adjacent populations; in other words, the formation of contiguous races and species
In this form of speciation, strong selection for divergence causes gene frequencies in the continuous population to diverge along the gradient

The formation of parapatrically distributed races could be accomplished by diversifying selection

If the dissimilar habitats that constitute diversifying selection are sharply delineated, then there could be strong selection against the transmission of genes responsible for the local adaptations across such a boundary

Hybrid individuals or their offspring would be ill adapted in either environment
Consequently, pre-zygotic isolation would be selected for to prevent this, resulting in speciation

A commonly cited example in support of parapatric speciation is the genetic divergence and reproductive isolation between mine tolerant and pasture populations of grasses in the face of gene flow

Reinforcement (reproductive isolating mechanisms)

The third stage in speciation may occur if diverged populations come back into contact and have an opportunity to interbreed

There are a number of possible fates of the hybrids: 1) they may survive and interbreed with the parental populations and eliminate the divergence; 2) may have new characteristics and become a distinct population

Dobzhansky indicated that if populations diverged sufficiently while allopatric, they may no longer be compatible (e.g. the hybrids that are generated have markedly reduced fitness)

In this case populations have developed **post-zygotic isolating mechanisms**

He reasoned that selection should favor assortative mating, and that this **reinforcement** would finalize the speciation process

Selection would favor mutations in populations that would prevent mating from occurring – **prezygotic isolating mechanisms**

Post-zygotic Isolating Mechanisms

Isolating mechanisms that prevent hybrid zygotes from developing into viable, fertile adults

Fertilization occurs but subsequent development of the zygote is hindered

There are 3 general types:

i) Hybrid Mortality (Inviability)

The incompatibility in parental genes results in the breakdown of genetic and cellular mechanisms that regulate development

Results in the cessation of development and death before the individual reaches adulthood

ii) Hybrid Sterility

Post-zygotic reproductive isolation in which hybrid zygotes are sterile

Therefore, they cannot reproduce and their genes cannot flow from one species to the other

Probable causes include:

- a) abnormal development of the gonads
- b) failure of parental genes to produce gametes with correct numbers of homologous chromosomes (=polyploidy)

iii) Hybrid (F2) Breakdown

The F1 hybrids are normal, vigorous, and fertile, but the F2 contain inviable or sterile individuals (for same reasons as above)

Pre-zygotic Isolating Mechanisms

Under each of the above circumstances, selection would potentially favor or re-inforce assortative mating - some mechanism that would decrease the possibility of the 2 populations mating in the first place

There are 5 main types of **pre-zygotic isolating mechanisms**

i) Habitat Isolation

Two species may never come into contact with one another because they occur in different habitats in the same geographical area

ii) Temporal (Seasonal) Isolation

Potential mates do not meet because mating or cross fertilization takes place at different times of the year or different times of the day

iii) Ethological Isolation

Populations are isolated by different and incompatible behavior before mating (e.g., incompatible special signals or courtship displays that attract mates)

Also, species may come into contact with one another, but they never mate because there is no sexual attraction between males and females

iv) Mechanical Isolation

Closely related species may attempt to mate, but fail to consummate the act because they are anatomically incompatible

Common in plants - physical differences in the flowering parts

Also present in those plants that require insect pollination (e.g., differences in the anatomy of flowers results in only certain kinds of insects being)

Sometimes observed in animals, whereby differences in the genital structure of animals can also lead to unsuccessful mating

v) Gametic Isolation

In organisms with external fertilization, male and female gametes may not be attracted to one another

In organisms with internal fertilization, although mating occurs and the gametes may meet, they do not form a zygote due to gametic mortality (e.g., the sperm of one species may not survive in the environment of the female reproductive tract of another species)

Hybridization and Hybrid Zones

Hybridization

Reinforcement should occur when hybrids have reduced fitness, but what if they have increased fitness?

Example: If crop sorghum plants were transformed with a gene for herbicide resistance and these individuals hybridized with the weed johnsongrass

It is conceivable that some of the offspring would end up with a favorable combination of traits from each parent

e.g., an allele for herbicide resistance from the crop parent and a suite of genes that promote fast growth from the weedy parent

Hybrid Zones

A hybrid zone is a region where interbreeding between divergent populations occurs (after secondary contact or during parapatric speciation) and hybrids are frequent

Three possible outcomes dictate their size, shape and longevity

1. Under some circumstances, there may be *no measurable differences* in the fitness of hybrids and purebred lines

When this is the case, the hybrid zone is usually wide, with the hybrids having their highest frequency at the center of the zone and decreasing frequencies with increasing distance

The width of the zone is a function of: how far individuals from each population disperse and how long the zone has existed

Zones are wider if individuals disperse far and the populations are in contact for long periods

2. Under some circumstances, the resulting hybrids have *lower fitness* than the parental offspring

The fate of the hybrid zone under this scenario depends on the strength of selection against them

If selection is strong and reinforcement occurs then the hybrid zone is narrow and short lived; if selection is weak, then the zone is wider and longer-lived

3. Under other circumstances, the resulting hybrids can have a *higher fitness* than the purebred offspring in newly colonized environments or certain restricted habitats

When the hybrids are more fit, the fate of the hybrid zone depends on the extent of the environments in which hybrids have an advantage

If hybrids have higher fitness in environments outside the range of the parental species, then a new species may form

If hybrids have an advantage at the boundary of each parental species range, then a stable hybrid zone may form

The idea being that hybrid individuals have intermediate characteristics and have a fitness advantage in the transitional habitats (the ecotone between 2 habitats that the parental species occupy)