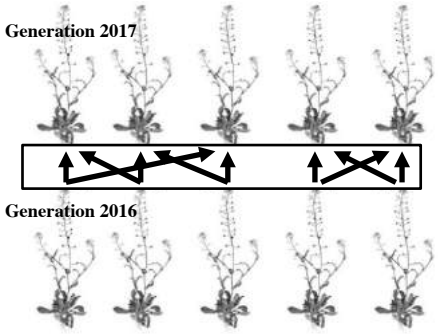
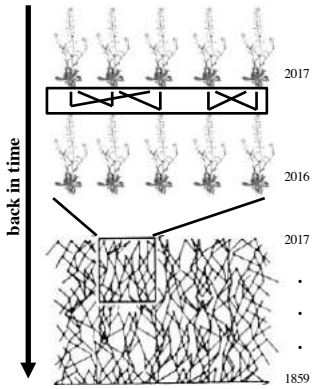
Evolution

To understand historical biogeography, we will examine the evolution of life from the level of populations and the formation of species, of relationships of species and higher taxonomic levels, and of extinction.



In outcrossing diploid organisms such as shepherd's purse, each offspring of the next generation receives a copy of genetic material from two parents, who in turn had received their copies of genes from two parents of the preceding generation

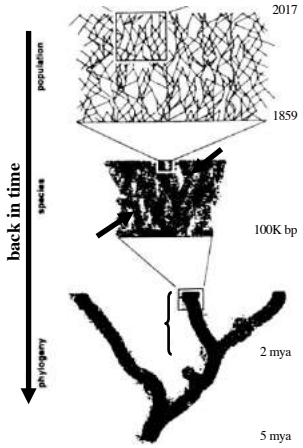
Evolution



As you go back in time to earlier generations, the genetic connections appear as a network within the population of interbreeding individuals

1 Population

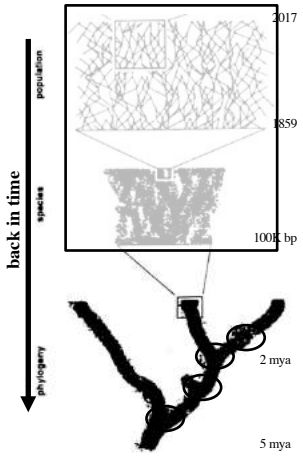
Evolution



As you go back even further in time, the genetic connections appear as a braided rope within a species

- discernible populations of interbreeding individuals are recognized within a species, these populations may be genetically isolated to varying degrees depending on gene flow and geography
- anagenesis can occur within a species lineage through time

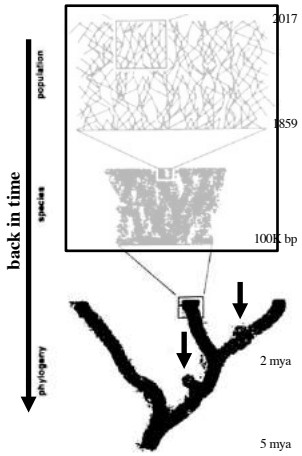
Evolution



As you go back even further in time in this tree or phylogeny, the formation of species and the extinction of species (fossils?) are seen

- cladogenesis or speciation occurs when there is complete genetic isolation between groups of once connected populations

Evolution

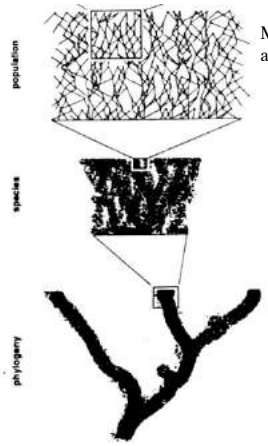


As you go back even further in time in this tree or phylogeny, the formation of species and the extinction of species (fossils?) are seen

• cladogenesis or speciation occurs when there is complete genetic isolation between groups of once connected populations

• extinction can occur when a species lineage fails to move its genetic material to a new generation

Geographical Variation



Morphological or physiological variation within a species is often geographically based

Geographical Variation

Morphological or physiological variation within a species is often geographically based

• a pioneer in understanding this geographical variation was Swedish botanist Göte Turesson

• he was interested in understanding the nature of geographical variation in plant species

- is it Environmental Variation? — differences in morphology resulting from differences in environmental conditions, or
- is it Genetic Variation? — differences in morphology from differences in genes possessed by these populations

Geographical Variation

The beach pea or *Lathyrus maritimus* or *L. japonicus* var. *maritimus* (indicating the messy taxonomic situation due to geographical variation) is widespread in circumboreal seashores and Great Lakes shores.

The plant shows considerable variation in leaf size, texture, and thickness throughout its range.

Baltic sea

Lake Michigan

Geographical Variation

Turesson transplanted different looking individuals from different areas into the same beach location (one set of environmental conditions).

Hypothesis: if differences persist among populations in the same environment, then they are due to genetic differences among populations.

Baltic sea

Lake Michigan

Geographical Variation

Turesson transplanted different looking individuals from different areas into the same beach location (one set of environmental conditions).

Result: most plants changed leaf size, texture, and thickness to reflect variation at that site — Environmental Variation only — he suggested saltiness of the water

Baltic sea

Lake Michigan

Geographical Variation

The round-leaved harebell/bellflower or *Campanula rotundifolia* is widespread in circum-temperate regions and mountains.

The plant shows considerable variation in height, flowering time, flowers, and leaves.

Lake Michigan

Scotland

Geographical Variation

Turesson collected individuals from 9 different sites (latitudinal & elevational gradients) and put them in a common garden.

Lake Michigan

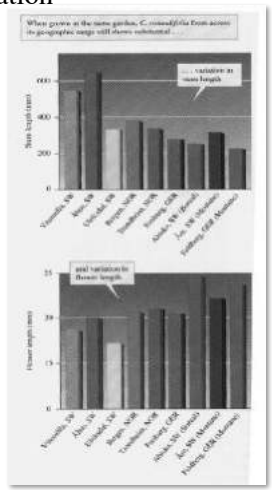
Scotland

Geographical Variation

Turesson collected individuals from 9 different sites (latitudinal & elevational gradients) and put them in a common garden.

Result: when grown in the same garden, *Campanula rotundifolia* from across the geographic range still showed substantial variation in stem length, flowering time, floral length, and leaf length — Genetic Variation!

Turesson called these different populations, exhibiting genetically fixed characters (adaptations) to local environmental conditions, **ecotypes**.



Geographical Variation

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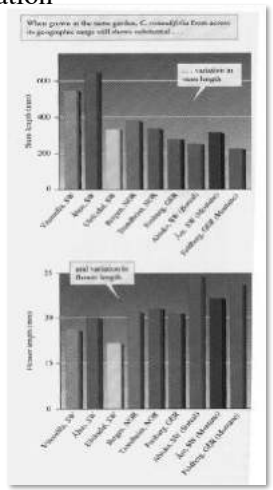
Ecotype Concept
(Turesson 1922)

A segment or group of populations of a more widely distributed species arising through selection as a genotypic response to a particular environmental condition



Geographical Variation

Turesson repeated these experiments with many other widespread and variable species — then generalized . . .

"It should not be thought that the differentiation of a species-population into hereditary habitat types is a phenomenon peculiar to the species discussed above. *The same will very likely be found to hold true for the majority of common plant species*. It is in fact to be assumed that *the rarity of certain species is in great measure due to a decreased power of genotypical response to habitat differences, climatic and edaphic, within their area of distribution*."

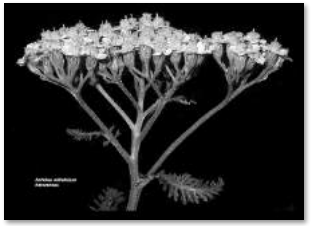
Göte Turesson 1922
The Genotypical Response of the Plant Species to the Habitat

Geographical Variation

Three American botanists (taxonomists and ecologists) pushed the ecotype concept further with their studies on a variety of plant species in California during 1940-1950s

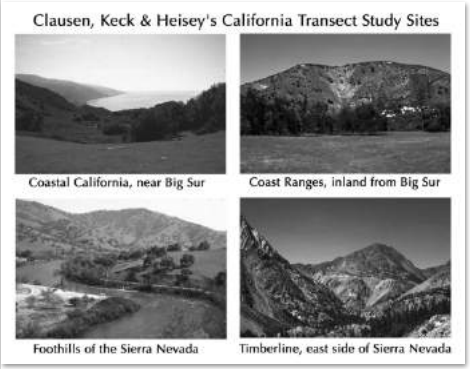
Their work on the *Achillea millefolium* (yarrow) complex and *Potentilla glandulosa* (sticky cinquefoil) are the best known

Jens Clausen, William Hiesey, David Keck



Geographical Variation

Clausen, Keck, and Hiesey used a reciprocal transplant design by setting up common garden sites across an elevation gradient from coastal California, through the Coast Range, and up and over the Sierra Nevada



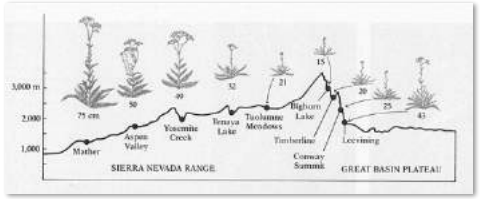
Common garden at Stanford

Common garden at Mather

Geographical Variation

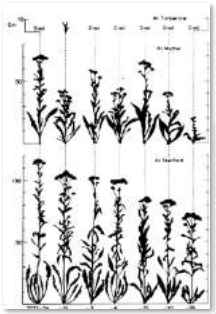
Achillea lanulosa
- wooly yarrow

Achillea lanulosa exhibits clinal variation in natural populations across this gradient – is it genetic or is it environmentally induced?



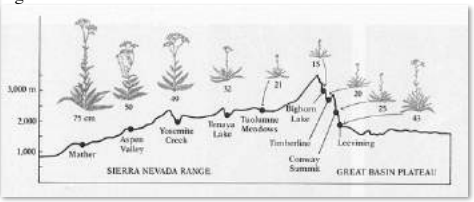
Clausen, Jens; Keck, David D.; Hiesey, William M. 1948. Experimental studies on the nature of species. III: Environmental responses of climatic races of *Achillea*. Publication 581; Washington, D.C.: Carnegie Institution of Washington.

Geographical Variation



Achillea lanulosa exhibited clinal variation in natural populations across this gradient – is it genetic?

Populations exhibited marked lowering of fitness and adaptation when placed at other sites — clinal genetic variation



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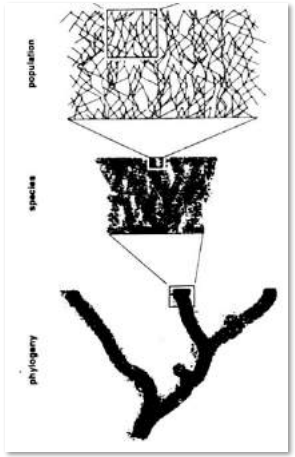
Geographical Variation

Geographical variation is naturally seen as you go back in time — in this case to recognized subspecies of an eastern North American milkweed species

Asclepias tuberosa - butterfly weed

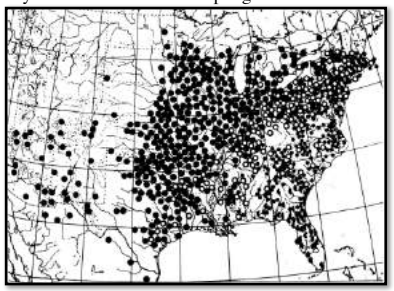


Geographical Variation

Geographical variation is naturally seen as you go back in time — in this case to recognized subspecies of an eastern North American milkweed species

Asclepias tuberosa - butterfly weed

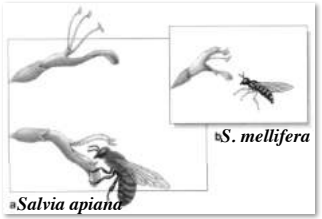
The three major subspecies differ in leaf shape and floral color, the variants show a clear geographical pattern, are largely separated genetically, although putative hybrids occur in the overlap region



Woodson, 1946

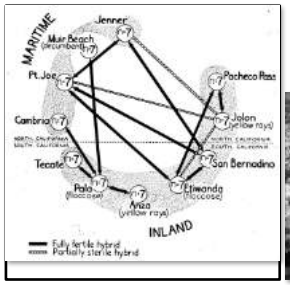
Geographical Variation

In any case, geographical correlates of reproductive isolating factors are important features in actively speciating groups — such as mechanical isolation via floral shapes and pollinators in *Salvia* (sage)



S. mellifera

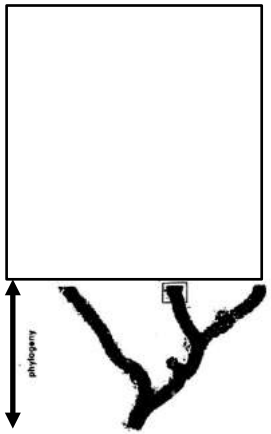
Salvia apiana



The degree of reproductive isolation among geographical sets of populations within an actively evolving species complex is often tested by crossing experiments — as in the tidy tips of California

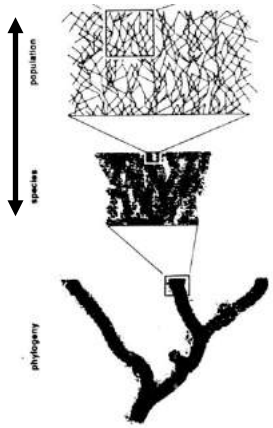
Layia platyglossa

Phylogeography — Historical Biogeography of the Species



Historical biogeography traditionally deals with relationships among species, genera, and higher taxonomic groups and the areas they occupy

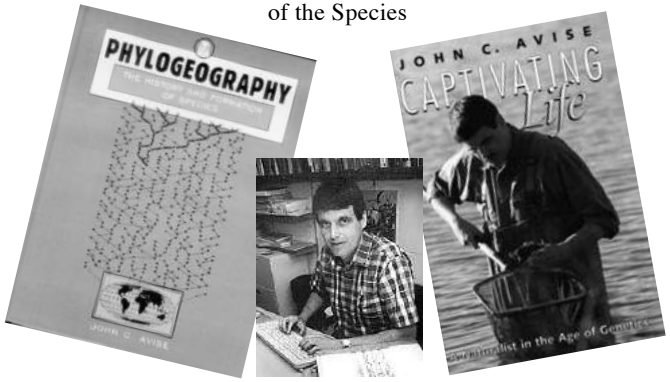
Phylogeography — Historical Biogeography of the Species



Due to advances in DNA sequencing and fingerprinting methods, historical biogeography has recently begun to integrate relationships of populations within species and the areas they occupy

Historical biogeography traditionally deals with relationships among species, genera, and higher taxonomic groups and the areas they occupy

Phylogeography — Historical Biogeography of the Species



John Avise, animal geneticist at University of Georgia, coined the termed "phylogeography" to describe "the history and formation of species" from a geographical perspective

Phylogeography — Historical Biogeography of the Species

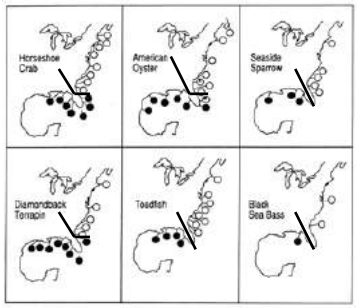
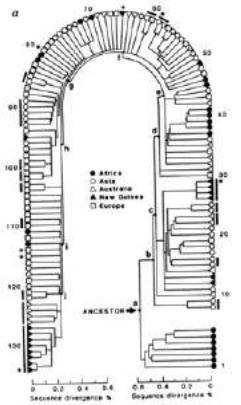


Figure 6.9. Geographic distributions of mtDNA genotypes within each of six maritime taxa (from Avise, 1992). Shown are pie diagrams summarizing frequencies of the two fundamental clades in populations of each species.

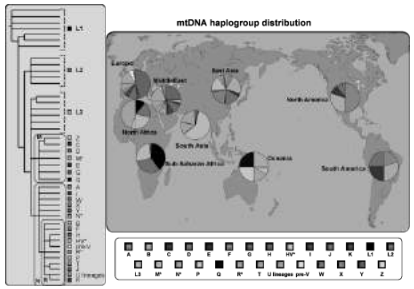
The classic phylogeographic analysis by Avise and his students involved the identification of a strong geographical signal within species separating populations from the Atlantic seacoast from the Gulf of Mexico seacoast.

The presence of two quite distinct genotypes within all these unrelated species has been explained by Pleistocene glacial and inter-glacial events

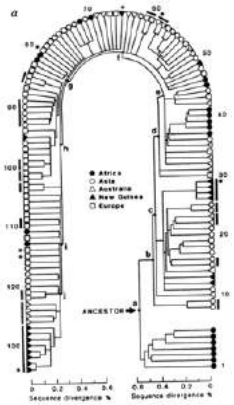
Phylogeography — Historical Biogeography of the Species



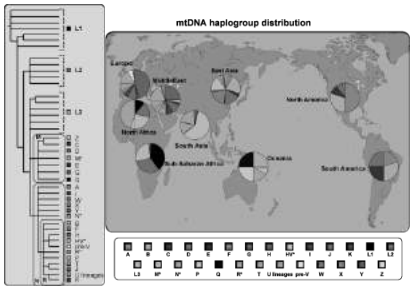
One of the most debated issues in phylogeography is the geographical origin of *Homo sapiens* - the "Eve hypothesis" as maternally inherited mitochondrial DNA (mtDNA) is often used



Phylogeography — Historical Biogeography of the Species

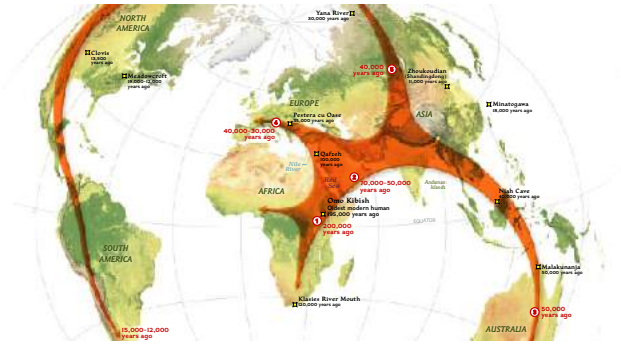


The "out-of-Africa" scenario is often supported - as shown here - and is consistent with the fossil record.



Phylogeography — Historical Biogeography of the Species

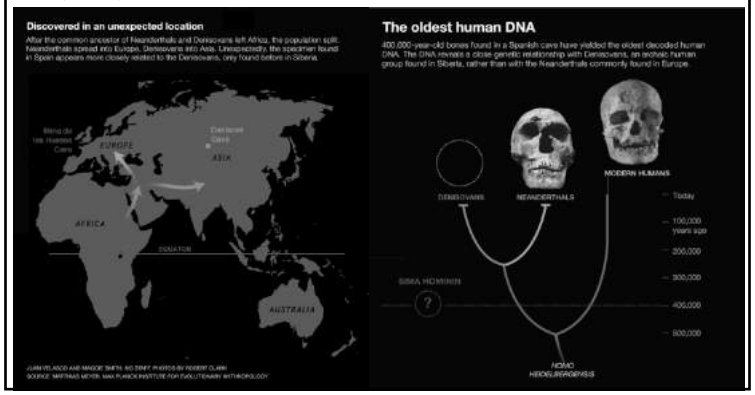
The "out-of-Africa" scenario is often supported - as shown here - and is consistent with the fossil record. However, different ways of analyzing DNA support an "out-of-Asia" scenario as well.



Phylogeography — Historical Biogeography of the Species

The "out-of-Africa" scenario vs. "multi-regional" hypothesis

Nature: November 2013



Phylogeography — Historical Biogeography of the Species

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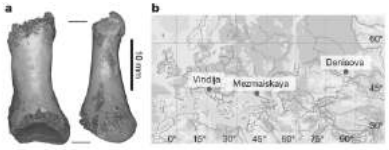
Nature: January 2014



The complete genome sequence of a Neanderthal from the Altai Mountains

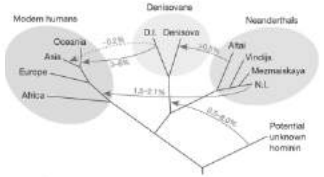
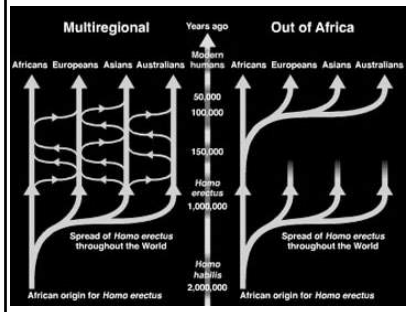
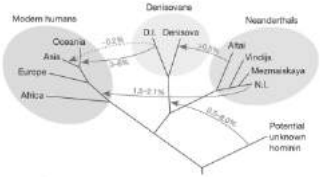


Figure 8 | A possible model of gene flow events in the Late Pleistocene. The direction and estimated magnitude of inferred gene flow events are shown. Branch lengths and timing of gene flows are not drawn to scale. The dashed line indicates that it is uncertain if Denisovan gene flow into modern humans in mainland Asia occurred directly or via Oceania. D.I. denotes the introgressing Denisovan, N.I. the introgressing Neanderthal. Note that the age of the archaic genomes precludes detection of gene-flow from modern humans into the archaic hominins.

Phylogeography — Historical Biogeography of the Species

The "out-of-Africa" scenario vs. "multi-regional" hypothesis





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Phylogeography — Historical Biogeography of the Species

Steps in a phylogeographic study

1. Sample populations widely across geographical range of species

2. Sample multiple individuals from each population to access levels of variation in cpDNA, mtDNA, or nuclear genes

3. Identify and quantify genotypes for each population [haplotypes if cpDNA or mtDNA]

Map of the populations and distribution of haplotypes of *Cedrela odorata* (Spanish cedar) across Mesoamerica (Cavers et al. 2003)

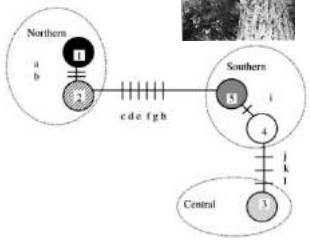
Phylogeography — Historical Biogeography of the Species

Steps in a phylogeographic study

4. Construct minimum spanning tree for the haplotypes

5. Overlay geographical distributions onto the tree (or use *Nested Clade Analysis* in complicated studies)

6. More recent Next Gen Sequence data allow for more sophisticated *Structure Analysis*



Minimum spanning tree of five haplotypes and their geographic locations for *Cedrela odorata* (Spanish cedar) (Cavers et al. 2003)

Phylogeography — Historical Biogeography of the Species

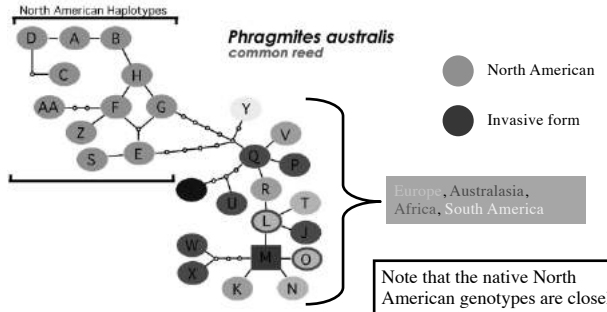
Example 1: Cryptic invasion of a non-native genotype of *Phragmites australis* (common reed) into North America (Saltonstall 2002)

Kristin Saltonstall

Native population in Great Lakes

Invasive population in Great Lakes

Phylogeography — Historical Biogeography of the Species



Minimum spanning tree for all genotypes

Note that the native North American genotypes are closely related and they are unrelated to the invasive form from the Old World

Phylogeography — Historical Biogeography of the Species

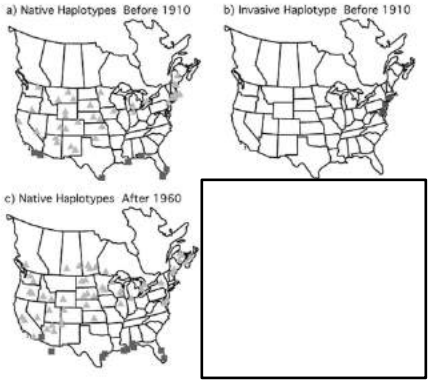
Genotyping of common reed from herbarium specimens *prior to 1910* indicates the widespread presence of 11 **native genotypes** and 1 **southern genotype** also seen in South America and Asia

Phylogeography — Historical Biogeography of the Species

Genotyping of common reed from herbarium specimens *prior to 1910* indicates the widespread presence of 11 **native genotypes** and 1 **southern genotype** also seen in South America and Asia

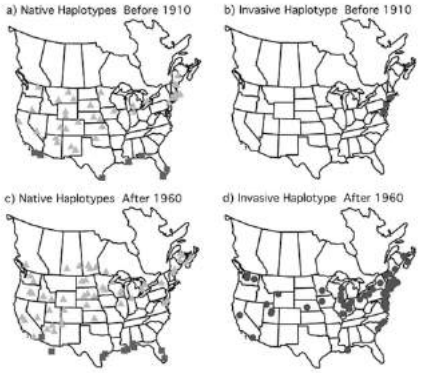
A few populations scattered from Connecticut to Maryland prior to 1910 also exhibited the **invasive genotype**

Phylogeography — Historical Biogeography of the Species



Genotyping of common reed from modern populations (both herbarium specimens *after 1960* and extant populations) indicates the same distributions of genotypes

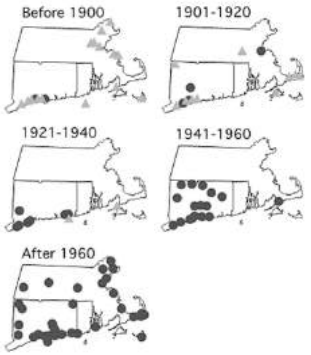
Phylogeography — Historical Biogeography of the Species



Genotyping of common reed from modern populations (both herbarium specimens *after 1960* and extant populations) indicates the same distributions of genotypes

However, the **invasive genotype** has dramatically spread across North America since 1910

Phylogeography — Historical Biogeography of the Species

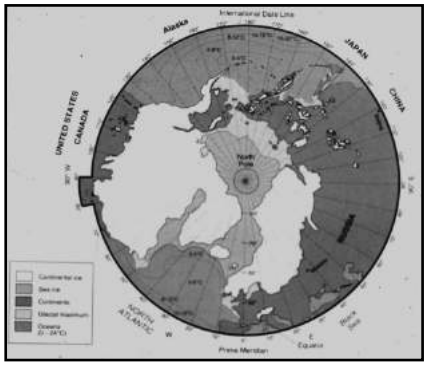


The "invasive" nature of the **introduced common reed** is more dramatically seen in the time sequence of genotyping of pre-1900 to modern populations

The **native North American** genotypes are systematically replaced by the invasive form along the eastern seaboard of Connecticut, Rhode Island, and Massachusetts

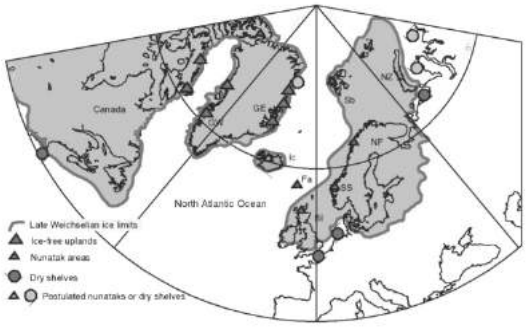
Phylogeography — Historical Biogeography of the Species

Example 2: History of the North Atlantic during the Pleistocene - differentiation in refugia (nunataks) or recent (Holocene) migration? (Brochmann et al. 2003)



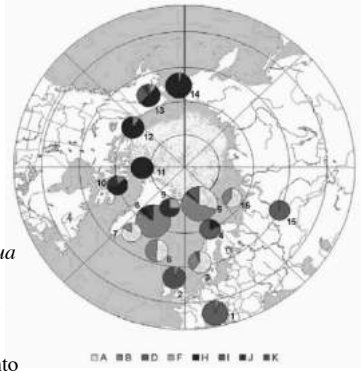
Phylogeography — Historical Biogeography of the Species

Example 2: History of the North Atlantic during the Pleistocene - differentiation in refugia (nunataks) or recent (Holocene) migration? (Brochmann et al. 2003)



Phylogeography — Historical Biogeography of the Species

Nodding saxifrage, *Saxifraga cernua*

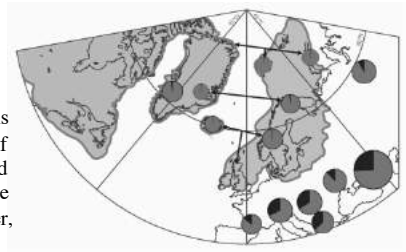


1. North Atlantic populations do not show endemic genotypes

2. Migration of several genotypes into (mixed) populations of North Atlantic regions

Phylogeography — Historical Biogeography of the Species

3. Lack of endemic genotypes is supported by the general lack of endemic species in the glaciated North Atlantic region. Genotype and species endemism, however, is high in "refugia" south of glaciated regions.



Levels of species endemism in the North Atlantic - **black** pie sections indicate proportion of endemism

Speciation

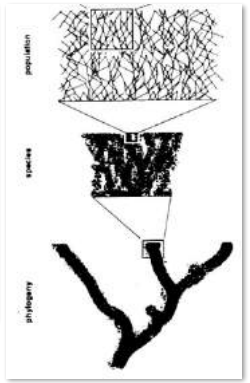
Although simple in concept, the recognition of species and thus the definition of what are species have been controversial — more than likely due to the continuum nature of the pattern resulting from the process of speciation

Biological Species Definitions

Species represent groups of populations reproductively & potentially reproductively isolated from other such groups

Phylogenetic Species Definitions

Species represent monophyletic clades of populations distinguished from other such clades by shared derived features



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Of the numerous species definitions that have been suggested, the Biological Species Concept and the Phylogenetic Species Concept are the most used

Speciation

Animal examples of speciation often show clear reproductive barriers - hence zoologists preference (as opposed to botanists) for the Biological Species Concept

Reproductive isolating mechanism — mating calls

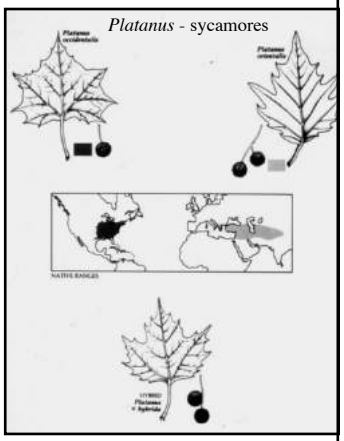
Rana pipiens - northern leopard frog in Wisconsin
Rana berlandieri - southern leopard frog in California

Speciation

Plant examples of speciation often show weak reproductive barriers - hence botanists' skepticism for the Biological Species Concept

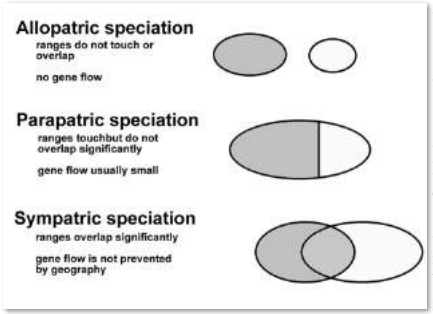
No reproductive isolation mechanism (except geography)— hybrid European plane tree

Platanus - sycamores



Speciation

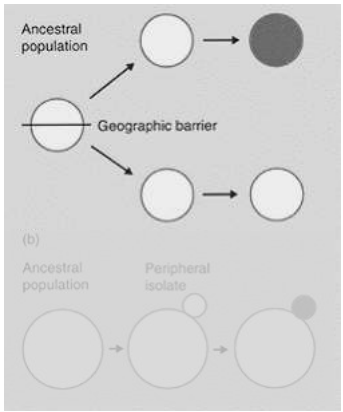
The different models of speciation are usually based on biogeography



- *-patry* refers to "fatherland" or "homeland"
- parapatric & sympatric speciation still debatable
- allopatric speciation refers to lineage splitting facilitated by complete geographical separation
- often called the geographical model of speciation — it is the best documented and most important

Speciation

In the conventional allopatric model of speciation, some type of barrier (desert, mountain, ocean, forest incursion) breaks up the ancestral area of a species



In isolation, one or both of the allopatric sets of populations slowly evolve on their own

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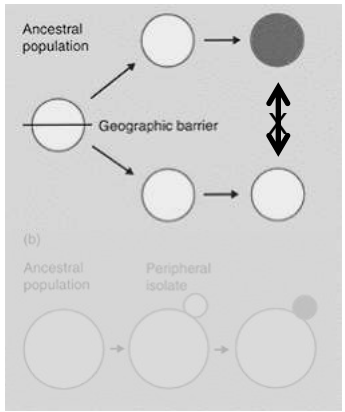


In isolation, one or both of the allopatric sets of populations slowly evolve on their own

Speciation is considered complete if the two resulting lineages maintain their differences even if they come back in contact (sympatry) . . .

. . . indicating the origin of a reproductive isolating feature while in allopatry

Speciation

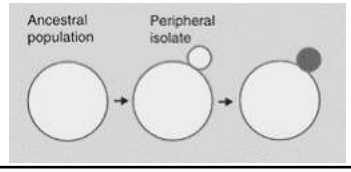
A more rapid type of allopatric speciation often occurs on "islands"

Hawaiian Islands — oceanic "islands"

Tepuis in Venezuela — continental "islands"

Speciation

A more rapid type of allopatric speciation often occurs on "islands"



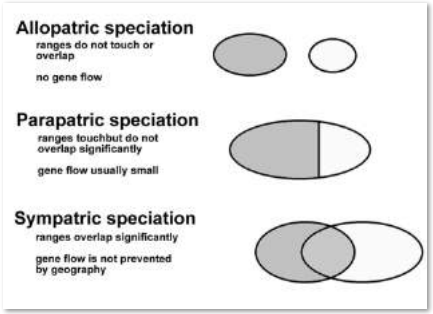
Often called the "peripheral isolate" or simply island model of allopatric speciation

A dispersal event ensures instant geographical/reproductive isolation

The founder event often involves a very small subset of the original genetic pool of the ancestral species — thus differences accumulate rapidly

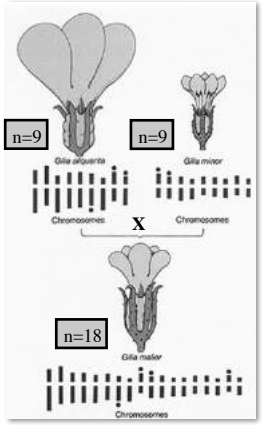
Speciation

A very common and instantaneous form of speciation in plants (and a few animals) is allopolyploidy.



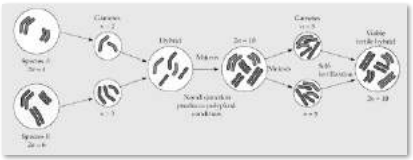
Allopolyploidy is a type of sympatric speciation as it occurs within the ranges of the original parental species.

Speciation



A very common and instantaneous form of speciation in plants (and a few animals) is allopolyploidy.

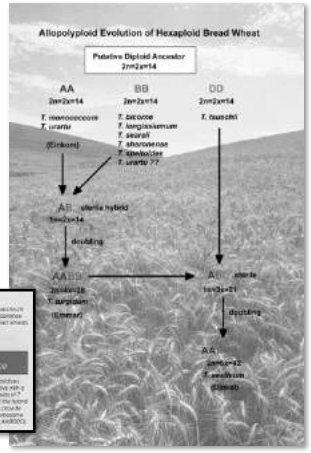
- hybridization occurs between two species
- meiotic incompatibilities makes hybrid sterile
- doubling of chromosomes occurs (polyploidy)
- allopolyploid is fertile and reproductively isolated from both parental species

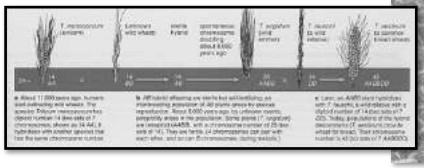


Speciation

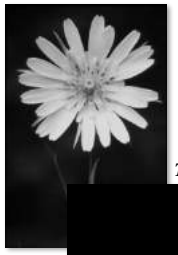
Under human selection in the Middle East, bread wheat (*Triticum aestivum*) has evolved in about 11,000 years.

Two successive rounds of hybridization followed by polyploidization have given bread wheat the genomes of three diploid species — it is a hexaploid (3 pairs of chromosomes, or 2 from each diploid parental species).



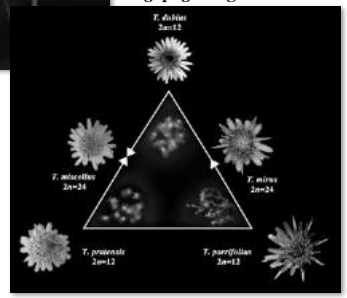


Speciation



Even more recent speciation has occurred in the goat's-beards in North America.

***Tragopogon* - goat's beard**



- Three diploid (2n=12) species were introduced into North America about 200 years ago.
- By early 1900s, these species had hybridized with each other and then formed two different allopolyploid (tetraploid) species.
- These two new allopolyploid species have evolved numerous times (!) in areas where the diploid species overlap in geographical range in North America