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



back in time

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

1 Population



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

2019 population 1859 back in time species 100K bp phylogeny 2 mya 5 mya

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

2019 population 1859 species 100K bp phylogeny 2 mya 5 mya

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

Evolution

• 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

back in time



Morphological, physiological, or genetic variation within a species is often geographically based



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• 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

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.







Lake Michigan

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.







Lake Michigan

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







Lake Michigan

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

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



Lake Michigan



Scotland

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**.



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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



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



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



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

Clausen, Keck & Heisey's California Transect Study Sites



Coastal California, near Big Sur



Coast Ranges, inland from Big Sur



Foothills of the Sierra Nevada



Timberline, east side of Sierra Nevada



Common garden at Stanford



Common garden at Mather

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.



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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 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

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)







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



So far . . . looked at geographical variation (morphology, ecological) within species with genetic basis

• anagenesis can occur within a species lineage through time

Shortly . . . look at cladogenesis or speciation with complete genetic isolation between groups of once connected populations

But first . . . look at genetic relationships among populations within species - phylogeography