

Types of evolution:

anagenesis (evolution within lineages vs. **cladogenesis** (splitting of lineages))

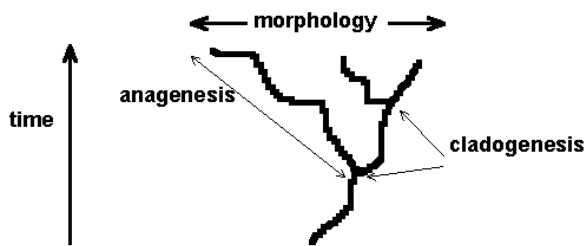


Diagram showing a phylogeny with anagenesis and cladogenesis

Similar to **microevolution** vs. **macroevolution**.

Can cladogenesis, macroevolution, be explained by the same principles as for the anagenetic, microevolutionary ideas we have covered so far?

In the next few weeks we shall discover...

Today: spatial evolution across the geographic range of a single species.

Subsequently: evolution of new species, or **cladogenesis**.

Finally: higher forms of evolution, **macroevolution**.

Genetic divergence of populations

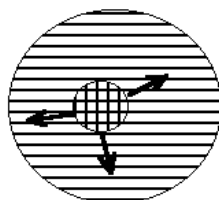
Genetic divergence under selection can be classified into two major geographic modes:

1. Sympatry

Populations are "sympatric" if within "cruising range", or dispersal range.

Examples: "Host races" of host-specialist parasites.

Or blackbirds and thrushes in London gardens.

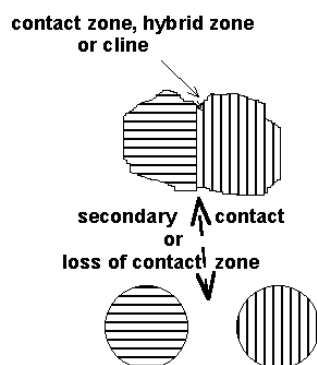


2. Geographic

a) Parapatry Populations in contact at edges.
Example: divergence in melanism of peppered moth between Liverpool and N. Wales.

b) Allopatry Populations are not in contact.

Example: island populations.



Geographic distributions can change:

Allopatric divergence may result in parapatric **distributions** via **secondary contact**.

Reverse also possible; allopatric distributions could result from the **abolition of a contact zone** between parapatrically distributed forms.

One cannot tell much about **geographical mode of origin** from the **current distribution**.

Genetic divergence and speciation

Speciation involves genetic divergence; usually over a long time period.

Cannot usually study speciation directly; we only have access to present-day populations. But we *can* study spatial variation in gene frequencies.

Dispersal is spatially limited, so distant populations share ancestry less recently than adjacent populations

Spatial variation therefore related to temporal variation in gene frequencies.

By studying spatial variation, we may be able to come to some understanding of the time course of genetic divergence and speciation.

Many newly formed pairs of species have parapatric or allopatric distributions.

Spatial differences in gene frequencies may represent speciation in progress

Parapatric distributions and **hybrid zones** or **contact zones** within species represent a first step in speciation.

Many intermediates between slight genetic differentiation and separate species occur in parapatry.

The remainder of the lecture will concern parapatric distributions.

Genetic variation across a geographic area

Any **consistent** change in gene frequency heritable phenotype, across a geographical range -- known as a **cline**.

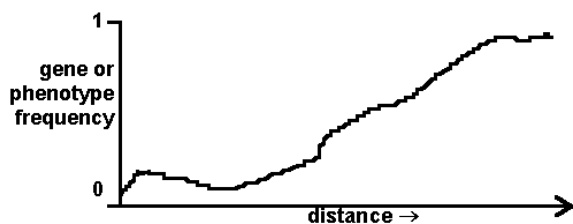
Clines occur because dispersal across a region is limited, because the whole geographical area does not form a single **panmictic population**.

(Population geneticists often call dispersal **migration**, but do not mean the kind where birds return after migration to near their parents nest!)

Dispersal also called **gene flow**, though we usually mean **genotype flow**).

Causes of clines

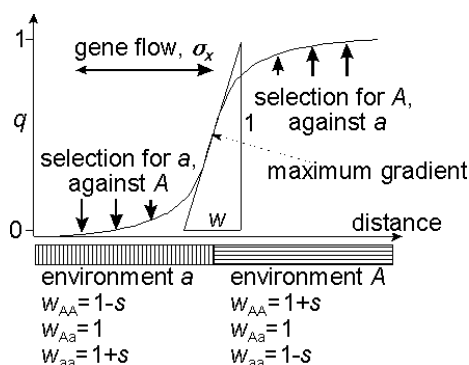
a) Clines produced by drift/migration balance



Random drift on its own will not produce consistent directional changes in gene frequency. (For details, see notes on [population structure and gene flow](#) and Futuyma 2005 Ch 9: 216-222, & 1998: pp 297-298, 315-320, but no longer be part of the course).

However, locally, drift may result in a temporary monotonic change.

b) Clines produced by selection/migration balance - **EXTRINSIC** selection



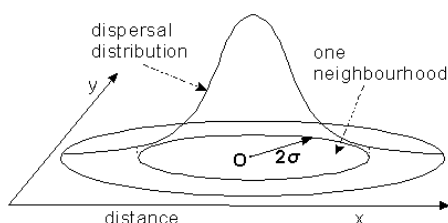
Selection favours different alleles in different areas; dispersal limited; frequencies may diverge \rightarrow **cline**.

Extrinsic or **environmental selection** is imposed by the environment directly.

If (1) environments favour different genes or phenotypes, (2) these environments are sufficiently widely spaced, and (3) if migration rates are not too high \Rightarrow **selection will set up a cline in gene or phenotype frequency**. Examples? (m, s, ir).

Measuring dispersal

If dispersal between birthplace and breeding site is random, equiv. to "drunkards walk". Same distribution as passive diffusion: a **two-dimensional normal distribution**.



Dispersal measure: standard deviation, σ , of the dispersal distribution.

A population **"neighbourhood"**: group of individuals who come from an area 2σ wide.

Theory of clines under extrinsic selection

At equilibrium, the width of a cline is proportional to dispersal divided by the sq. root of selection:

$$w = 1.7 \frac{\sigma}{\sqrt{s}} \quad \leftarrow \text{What does this mean?}$$

1) Width of cline should scale directly to dispersal distance; cline wider as dispersal increases

2) Stronger selection leads to narrower cline
i.e. $w \propto \frac{1}{\sqrt{s}}$ (selection)

So equation seems more or less sensible, though $\sqrt{1.7}$ comes out of the maths.

Why do we want such an equation?! Provides a way to understand evolution of clines.

Use of cline theory

Jim Bishop (1972) studied melanism in peppered moth between North Wales and Liverpool [OVERHEAD].

Bishop obtained expected cline by **computer simulation** rather than by **analytical theory**.

Used mark-release-recapture to estimate selection and dispersal along the transect. Compared actual cline in melanism with predicted cline.

Melanics reached further into rural N. Wales than expected. Due to selection on caterpillars?

c) Clines produced by selection- migration balance -- **INTRINSIC** selection

i) Heterozygous disadvantage

Heterozygous disadvantage creates a kind of **disruptive selection**. Equilibrium gene frequency, $\frac{t}{s+t}$ is unstable,

selection prevents polymorphism. Two peaks in mean fitness, known as **adaptive peaks**; fixation for A, and fixation for a.

Heterozygous disadvantage can cause clines?

Dispersal (or mixing) can be balanced by selection.

Intrinsic selection like this will cause clines with shape similar to those caused by **extrinsic selection**.

Constant of proportionality is different, but the equations will be very similar. Under heterozygous disadvantage,

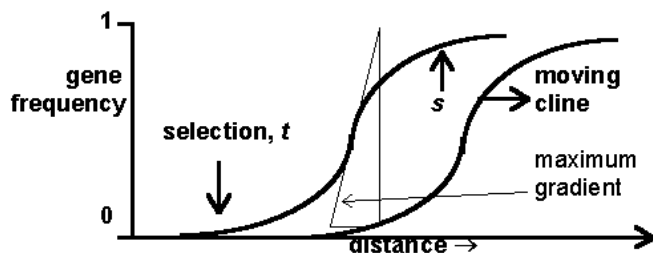
$$w = 2.8 \frac{\sigma}{\sqrt{s'}} \quad \dots \text{ where } s' \text{ is average of } s \text{ \& } t.$$

Again, stronger selection, $s \Rightarrow$ narrower cline; greater dispersal distance, $\sigma \Rightarrow$ broader cline.

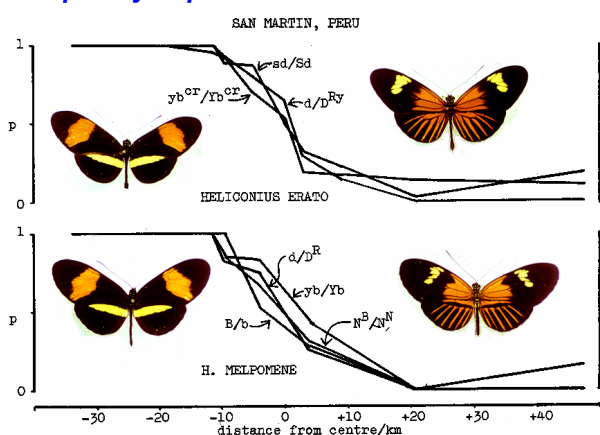
Moving clines

But there is a big difference: *Intrinsic selection* does not depend on the outside environment.

Depends only on "internal environment" of each population, that is, the local gene frequency.



ii) Frequency-dependent selection



For example, warning colour: rare forms non-adaptive because predators learn to avoid the commoner colour pattern.

iii) Epistatic and disruptive selection

Disruptive selection; a kind of *intrinsic selection* caused by the *environment*.

Selection can favour a **bimodal phenotypic distribution**, or two **adaptive peaks** simultaneously.

e.g. Darwin's finches have available large, tough seeds, and small soft seeds which are hard to get out of their pods or off grass stems.

One type of seed selects for stout, deep beaks; the other for narrow pincer-like beaks.

Disruptive selection for different adaptive peaks also produces epistasis

Bimodal or disruptive selection implies *epistasis*, must be due to non-additive interactions in selection between genes.

Sexual selection

Also may cause epistatic/disruptive selection: genes for mate choice strongly epistatic with genes for the traits being chosen.

Evolutionary result of disruptive selection

Bimodal phenotypic distribution virtually impossible to maintain in randomly mating population.

(mendelian inheritance → phenotypes ~ normally distributed - see QUANTITATIVE GENETICS)

Specialization on the second type of seed ruins adaptation to the first, and vice versa.

Causes stresses which multiple loci cannot easily resolve. There are three possible outcomes:

Polymorphism. A single locus or "supergene" polymorphism could evolve.

Speciation. In two populations of different species, easy to evolve bimodality. Competition ensures bimodal pattern of habitat use. Selection against intermediates (or hybrids) within a species causes reproductive isolation. Speciation may result from disruptive selection (see SPECIATION in a few days).

Loss of one adaptive peak. The population may evolve towards better adaptive peak.

Evolution of clines

Any type of *intrinsic* selection -- heterozygote disadvantage, frequency-dependent selection, or disruptive/epistatic selection -- can stabilize clines.

Under Ernst Mayr's "biological species concept, species are reproductively isolated.

Intrinsic and even extrinsic selection across clines gives a degree of "reproductive isolation": hybrids are poorly adapted.

Knowing about spatial evolution and cline theory is therefore important for understanding speciation.

Hybrid zones: narrow zones of contact between divergent forms or even species.

Hybrid zones may include few hybrids or many, and the hybrids themselves may consist only of F_1 only, or of F_1 , F_2 and every kind of backcross.

Many species and/or races are distributed in parapatry, and have narrow hybrid zones between them.

Examples: chromosomal races of mammals, warningly coloured butterflies, sexually selected birds [manakins overhead]

The fire-bellied/yellow-bellied toads (*Bombina*)

Meet in a narrow east-west hybrid zone stretching over a large part of eastern Europe.

Bombina bombina



Bombina variegata



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The *Bombina* hybrid zone

	<i>Bombina bombina</i>	<i>Bombina variegata</i>
Habitat	Lowland	Hilly
Water bodies	Lakes, ponds	Temporary ponds, puddles
Skin thickness	Thin	Thick
Eggs (spawn)	Small, many	Large, fewer
Belly warning colour	Red and black	Yellow & black
Other differences	Male mating call Hybrids develop less successfully Immunological differences Multiple allozyme differences mtDNA differences	

Hybrid zones, then, are places **where narrow clines at multiple loci** occur together.

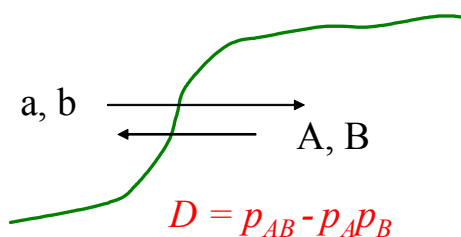
The use of gametic or “linkage” disequilibrium to measure selection and gene flow in hybrid zones

$$w = 2.8 \frac{\sigma}{\sqrt{s}}$$

A useful equation, but only gives ratio of gene flow to selection. To solve, we could find σ some other way.

Barton, used **linkage disequilibrium**.

In *Bombina*, $R (\sim D/D_{max}) = 0.22$ (i.e. 22% of maximum), Barton showed that the linkage disequilibrium is directly proportional to the amount of mixing (gene flow, σ^2).



Using his formula ($R = k \sigma^2$), where k is a constant, Barton showed that $\sigma \approx 0.99 \text{ km/gen}$.
 $w = 6.05 \text{ km wide}$, so, from the formula for w , $s = 0.21$.

Conclusions: space and time in evolution

Many definitions of species, but fundamentally, species differ genetically at multiple loci.

If two species occur together in space, this divergence is maintained;

To understand their speciation, we need to know about the events that took place in a past time.

Yet for most genetic studies, we only have the present; a thin film on the surface of time.

Space as a clue to time, speciation

Dispersal limited, so spatial separation proportional to time since separation. Spatially separated populations give an idea of divergence in time.

Spatially separated populations may be “incipient species”.

Spatial evolution and cline theory: important in “extrinsic” or environmental adaptation

Migration can swamp adaptation to a local area.

But wherever the cline width, w , is substantially smaller than environmental patch width, adaptation can occur in parapatry, in spite of gene flow.

Differently selected forms can evolve in parapatry. Populations separated by cline or hybrid zone.

Hybrid zones consist of multiple clines, so cline theory enables us to understand hybrid zones, too.

Spatial evolution and cline theory: understanding “intrinsic” selection

Intrinsic selected genes (heterozygous disadvantage, frequency-dependent selection, epistasis) will also evolve spatially Surprisingly similar clines to those in environmental adaptation.

Patchy structure of chromosomal races, mating types, and warning colours etc., similar to spatial evolution of genes for environmental adaptation.

FURTHER READING

FUTUYMA, DJ 2005. Evolution. Ch 6, Ch 9: 326-9
 FUTUYMA, DJ 1998. Evolutionary Biology. Geographic variation and clines: chapter 9 (pp. 257-262). Cline theory: chapter 13 (pp. 381-383). Hybrid zones: chapter 15 (pp. 454-456, 464-468).