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. **Sympathy**

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) **Parapathy** 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 parapartic 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 parapaty.

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**

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 ⇒ 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, $\sigma$, of the dispersal distribution.

A population "neighbourhood": group of individuals who come from an area $2\sigma$ 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:

$$w = 1.7 \frac{\sigma}{\sqrt{s}}$$  \[What does this mean?\]

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

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

$$w = 2.8 \frac{\sigma}{\sqrt{s'}}$$  \[where $s'$ is average of $s$ & $t$.\]

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.

⇒ No tendency for a cline to remain stationary. If \( s \neq t \), cline will move.

\[ \text{gene frequency} \]
\[ \downarrow \text{selection, } t \]
\[ \vdash \text{moving cline} \]
\[ \downarrow \text{maximum gradient} \]

\( s \)

\( t \)

\( \downarrow \text{distance} \)

\( \uparrow \)

\( \text{gene frequency} \)

\( \downarrow \text{selection, } t \)

\( \vdash \text{moving cline} \)

\( \downarrow \text{maximum gradient} \)

\( \downarrow \text{distance} \)

\( s \)

\( t \)

\( \uparrow \)

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\( \vdash \text{moving cline} \)

\( \downarrow \text{maximum gradient} \)

\( \downarrow \text{distance} \)

\( s \)

\( t \)

\( \uparrow \)
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**

© Boris I. Tomofeev; see http://elib.cs.berkeley.edu/

### The Bombina hybrid zone

<table>
<thead>
<tr>
<th></th>
<th>Bombina bombina</th>
<th>Bombina variegata</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Habitat</strong></td>
<td>Lowland</td>
<td>Hilly</td>
</tr>
<tr>
<td><strong>Water bodies</strong></td>
<td>Lakes, ponds</td>
<td>Temporary ponds, puddles</td>
</tr>
<tr>
<td><strong>Skin thickness</strong></td>
<td>Thin</td>
<td>Thick</td>
</tr>
<tr>
<td><strong>Eggs (spawn)</strong></td>
<td>Small, many</td>
<td>Large, fewer</td>
</tr>
<tr>
<td><strong>Belly warning colour</strong></td>
<td>Red and black</td>
<td>Yellow &amp; black</td>
</tr>
</tbody>
</table>

**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

\[
   w = 2.8 \sigma^2 \sqrt{a/b} 
\]

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

Barton, used linkage disequilibrium.

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

Using his formula \( R = k \sigma^2 \), where \( k \) is a constant, Barton showed that \( \sigma = 0.99 \) km / gen.

\( w = 6.05 \) 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