**RESTRICTED MIGRATION: CLINES**

• Many evolutionary patterns result from limited dispersal

— E.g., "<u>clines</u>": graduated change in gene frequency or average phenotype from one place to another

• Clines are ubiquitous.

• Two questions we'll examine with respect to clines:

(1) *What determines the size, shape, and location of a cline?*

(2) *How does adaptation occur in connected patches?*

• **Stepping Stone model (linear habitat)**
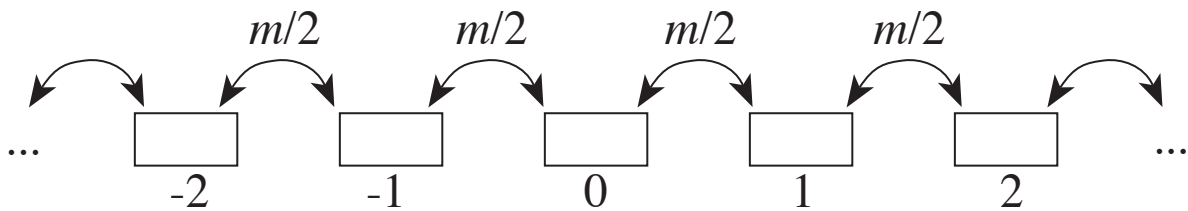
— Assumptions (2 alleles, *A* and *a*):

• ∞ number of equally-sized populations.

• Frequency of *A* in population *i*: p_i

• Each population exchanges a fraction *m*/2 adults with its neighbors; $(1 - m)$ remain.

— Implies "soft selection" since the number of migrants is independent of the local mean fitnesses: $w_{AA}(i)$, $w_{Aa}(i)$, $w_{aa}(i)$.

• Equations: (assumes adult migration)

$$p_i^* = p_i \frac{\overline{w}_A(i)}{\overline{w}(i)} ; \; p_i{}' = \frac{m}{2} p_{i-1}^* + (1 - m)p_i^* + \frac{m}{2} p_{i+1}^*$$

• Q: Given *m*, $w_{\bullet}(i)$'s, & initial p_i's what are p_i's in the future?

— Question has not been solved analytically.

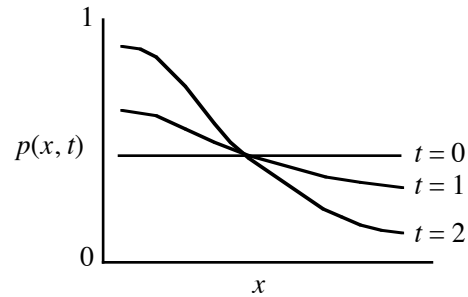— Haven't even been able to determine all the equilibria.

– Researchers have turned to computer simulations and "diffusion approximations" for answers.

– Diffusion Approximation

• New goal: find $p(x,t)$.

– define and show how $p(x,t)$ evolves: $p(x,0)$, $p(x,1)$, $p(x,2)$, etc. $\longrightarrow$

• Note: the frequency of a is $q(x,t) = 1 - p(x,t)$.

• A rough derivation of the diffusion approximation for the stepping stone model:

– Populations spaced closer together (spatial location described by continuous x).

– Assume $w_{\bullet}(i) \approx 1$ (weak selection), $m << 1$ (weak migration) so that allele frequencies change slowly.
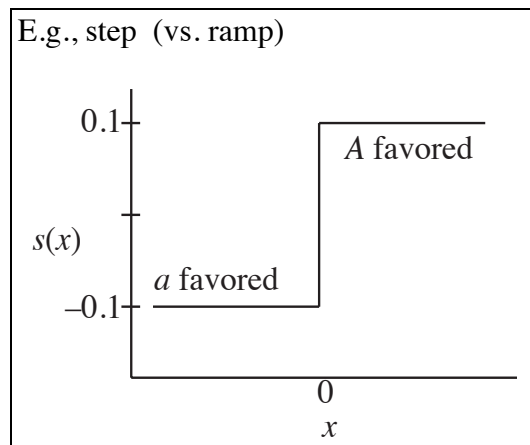
– Heuristic Derivation of allele frequency change:

• Basic relation:
$$\begin{bmatrix} \text{total } \Delta \text{ in } p \\ \text{at location } x \end{bmatrix} = \begin{bmatrix} \Delta \text{ in } p \text{ due} \\ \text{to migration} \end{bmatrix} + \begin{bmatrix} \Delta \text{ in } p \text{ due} \\ \text{to selection} \end{bmatrix}$$

• Notation:
$$\begin{bmatrix} \text{total } \Delta \text{ in } p \\ \text{at location } x \end{bmatrix} \equiv \frac{\partial p(x,t)}{\partial t}$$

(1) Δ in p due to selection at location x:

Fitnesses:

$$\underline{w_{AA}(x) \qquad w_{Aa}(x)}$$
$$w_{aa}(x)$$
$$1 + s(x) \qquad 1 \qquad\qquad 1 - s(x)$$

E.g., step (vs. ramp)

$$\begin{bmatrix} \Delta \text{ in } p \text{ due} \\ \text{to selection} \end{bmatrix} = \Delta^s p(x,t) = p^*(x,t) - p(x,t) = p(x,t)q(x,t)\frac{\overline{w}_A(x) - \overline{w}_a(x)}{\overline{w}(x)}$$

$$= p(x,t)q(x,t)\frac{s(x)}{\overline{w}(x)} \approx p(x,t)q(x,t)s(x)$$

provided $s(x) << 1$ so that $\overline{w}(x) \approx 1$ for all x

(2) Δ in p due to migration:

- Stepping stone with no selection:

$$\Delta^m p = p' - p = \frac{m}{2}p(x-1,t) - mp(x,t) + \frac{m}{2}p(x+1,t)$$

$$= \frac{m}{2}\left\{\left[p(x+1) - p(x,t)\right] - \left[p(x,t) - p(x-1,t)\right]\right\} \approx \frac{m}{2}\frac{\partial^2 p(x,t)}{\partial x^2}$$

- In this context, m is the <u>variance</u> in dispersal distance/generation:
  - Mean dispersal distance: $\frac{m}{2}(-1) + (1-m)(0) + \frac{m}{2}(1) = 0$.
  - Var(dispersal distance): $\left[\frac{m}{2}(-1)^2 + (1-m)0^2 + \frac{m}{2}1^2\right] - 0^2 = m$

- "Derivation" assumes distance between patches = 1 and time is measured in generations.
  - In passing to diffusion approximation, space and time are "rescaled" so that a change by 1 is relatively small.

- Intuition for the 2nd derivative:
  - 2nd derivative (change in the rate of change)

$$\left.\begin{array}{ccc} 0.25 & 0.5 & 0.75 \\ p(x-1) \xrightarrow{m} & p(x) \xleftarrow{m} & p(x+1) \end{array}\right\} \Delta p(x) = 0$$

vs.

$$\left.\begin{array}{ccc} 0.25 & 0.5 & 1 \\ p(x-1) \xrightarrow{m} & p(x) \xleftarrow{m} & p(x+1) \end{array}\right\} \Delta p(x) > 0$$

(3) Combining Δp's due to migration and selection:

$$\frac{\partial p(x,t)}{\partial t} = \frac{m}{2}\frac{\partial^2 p(x,t)}{\partial x^2} + p(x,t)q(x,t)s(x)$$

– Data:
- Pattern of selection over space: $s(x)$
- Initial frequency of A over space: $p(x,0)$
- Variance in migration distance: m .

– Use diffusion approximation to determine:
- Allele frequencies at all locations at all future times.
- Equilibrium frequencies at all locations.

– Equilibria: What pattern of allele frequencies will eventually occur over space?
- Full solution is known for step selection $s(x) = \begin{cases} s & x > 0 \;\; (A \text{ favored}) \\ -s & x > 0 \;\; (a \text{ favored}) \end{cases}$
- Obtained by setting $\dfrac{\partial p(x,t)}{\partial t} = 0$ and solving for $p(x)$.
- Turns out:

$$\hat{p}(x) = \frac{1}{2} \mp \left\{ 1 - \tfrac{3}{2}\left[\tanh\left(\pm\sqrt{\frac{s}{2m}}\, x + 1.146 \right) \right]^2 \right\} \quad (-,+ \text{ for } x > 0 \text{ and } +,- \text{ for}$$

$x < 0$) where $\tanh(z) = \left(e^z - e^{-z}\right)\big/\left(e^z + e^{-z}\right)$.

– Conclude:

1) Pattern of allele frequencies will not fit the pattern of selection exactly.

2) Equilibrium depends only the ratio of s and m .

3) Slope of the cline at its steepest point $(x = 0)$: $d\hat{p}/dx\big|_{x=0} = \sqrt{s/3m}$
   - Definition : "<u>Length of a Cline</u>" = 1/maximum slope = $\sqrt{3m/s}$.
   - This gives a distance over which allele frequency change is significant.

– <u>Effects of Dominance</u>

1) Increased heterozygote fitness lengthens clines.

2) Reduced heterozygote fitness shortens clines.

3) Underdominance can maintain a cline without any spatial variation in selection:
- I.e., for all x, $w_{AA}(x) = 1 + s$, $w_{Aa}(x) = 1$, $w_{aa}(x) = 1 + s$ where $s > 0$ is constant.
- Different regions may be fixed for different alleles.
- Short clines separate areas of alternate fixation

• May explain hybrid zone clines with no detectable environmental
    discontinuities.

– Adaptation to environmental patches

• When will a population respond to
    local selection in the presence
    of gene flow?

• Consider a patch of length L in
    which allele A is favored:
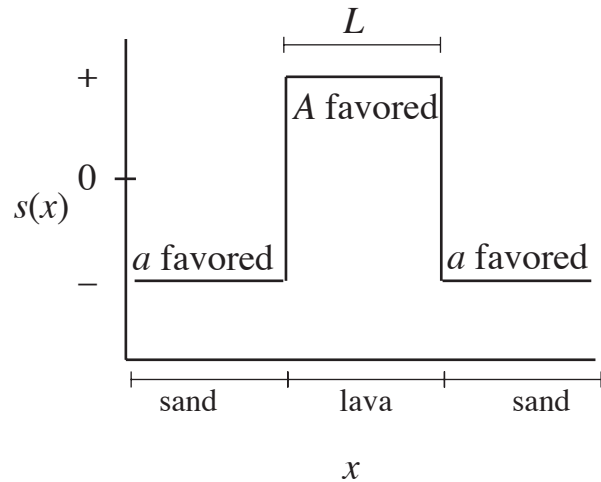
• The response or lack of response
    of allele frequencies depends
    the "characteristic length" of a
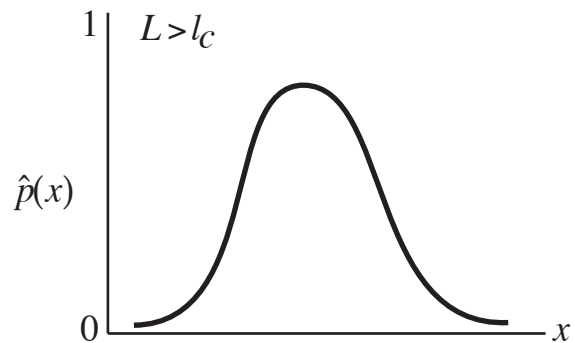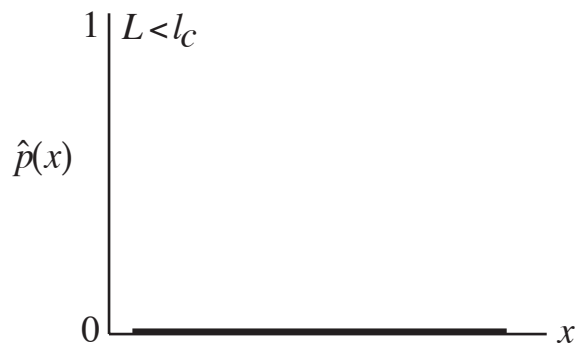   cline:

$$l_c = \sqrt{\frac{m}{s}} \quad (\approx 1/2 \text{ "length of cline")}$$

• Importance of the characteristic
    length:

– A locally favored allele will
    be lost if the size of the
    patch it is favored in (L) if
    smaller than l_c (or $2\,l_c$ is the
    patch is not completely
    surrounded).

• Conclude:

– Migration can swamp local
    adaptation.

– Selection that is strong
    relative to migration can
    maintain locally adapted
    alleles.

– <u>Wave of advance of a favorable allele</u>.

    • Suppose an allele is advantageous everywhere but initially appears in one place only.

    • How fast will it spread?

    • Use above models, $s(x) = s > 0$

       – Assume that a few copies of A are introduced in an area fixed for a

       – at equilibrium, A will be fixed everywhere.
          • i.e., $\hat{p}(x) = 1$ for every x.

       – turns out that the speed of spread of $A = \sqrt{2ms}$ per generation: