Complex Forms of Natural Selection

- **Most of the treatment so far about natural selection involves a single population or constant (i.e., only one s) fitness. Although informative, these models are simplistic and may not represent even a rare condition in the natural world.**

I) Levene's Model of Spatially Varying Selection

A) Background:

- **Soft Selection versus Hard Selection**

OH 10.1A and 10.1B

- **Calculation and Interrelationship of Means**
  - **Arithmetic Mean** = $\frac{1}{n}\sum_{i=1}^{n} x_i$ **(AM)**
  - **Geometric Mean** = $\sqrt[n]{\prod_{i=1}^{n} x_i}$ **(GM)**
  - **Harmonic Mean** = $\frac{1}{\frac{1}{n}\sum_{i=1}^{n}\frac{1}{x_i}}$ **(HM)**
  - **In all cases (unless invariant):**

AM > GM > HM

B) Assumptions of Levene's Model

1) **Same as Classical Model**
2) **Populations are subdivided into niches**
3) **Different viability selection in each niche (i.e., s is niche specific)**
4) **Fraction of adults in each niche does not change over time**
5) **Zygotes genotype frequencies are in HWE**
6) **Specific Generational Cycles**

OH 10.2

C) Levene's Model of Spatially Varying Selection

For each niche:

(all models have equal niche contribution, i.e., $c_1 = c_2 = c_2 \ldots$)

Genotype	A_1A_1	A_1A_2	A_2A_2
Frequency in Zygote	P^2	$2pq$	q^2
Viability	W_{11}	W_{12}	W_{22}

For Niche 1:

$$p' = \frac{p^2 W_{11,h} + pqW_{12,h}}{\overline{W}_h}$$

$$= \frac{p(pW_{11,h} + qW_{12,h})}{\overline{W}_h}$$

$$= \frac{pW_{1,h}}{\overline{W}_h}$$

As shown previously:

$$\Delta p = p' - p$$

$$= \frac{pq(W_1 - W_2)}{\overline{W}}$$

$$= \frac{pq[p(W_{11} - W_{12}) + q(W_{12} - W_{22})]}{\overline{W}}$$

For each niche then:

$$\Delta p_h = \frac{p_h q[p(W_{11,h} - W_{12,h}) + q(W_{12,h} - W_{22,h})]}{\overline{W}_h}$$

Simplify:

Assume $W_{12,h} = 1.0$

Then:

$$\Delta p_h = \frac{pq[p(W_{11,h} - 1) + q(1 - W_{22.h})]}{\overline{W}_h}$$

There are m niches such that the proportion of individuals contributed to the mating pool from each niche (c):

$$\sum_{h=1}^{m} c_h = 1.0$$

Over all m niches the average change is:

$$\Delta p = \sum_{h=1}^{m} c_h \Delta p_h$$

$$= pq \sum_{h=1}^{m} c_h \frac{[p(W_{11,h} - 1) + q(1 - W_{22,h})]}{\overline{W}_h}$$

Define a function h(p):

$$h(p) = \sum_{h=1}^{m} c_h \frac{[p(W_{11,h} - 1) + q(1 - W_{22,h})]}{\overline{W}_h}$$

$$\Delta p = p(1 - p)\, h(p)$$

Then $\Delta p = 0.0$ and Levene's model is in equilibrium when:

- **$p = 0.0$**
- **$q = 0.0$**
- **$h(p) = 0.0$**

In previous models we were able to determine explicitly where $\Delta p = 0.0$ because of the simplicity of the system. Here, we have many niches each with their own selection coefficients and models (not all niches have to be directional or underdominant or overdominant). It is too complicated to mathematically solve this for equilibrium points.

Define:

A Protected Polymorphism (PP) exists if:

1) **neither allele can be lost from the system. This will happen in Levene's Model if:**
   a) **the frequency of an allele increases (i.e., $\Delta p > 0.0$ when p nears 0.0 or $\Delta p < 0.0$ when p nears 1.0)**
   b) **Fixation equilibrium are unstable**
2) **a PP does not mean that equilibrium exists, just that alleles are maintained in populations.**
   a) **a PP is sufficient but not necessary to maintain variation**

Does a PP exist in the Levene's Model?

$$h(p) = \sum_{h=1}^{m} c_h \frac{\left[p\left(W_{11,h} - 1\right) + q\left(1 - W_{22,h}\right)\right]}{\overline{W}_h}$$

$$h(0.0) = \sum_{h=1}^{m} c_h \left[\frac{1 - W_{22,h}}{W_{22,h}}\right]$$

$$= \sum_{h=1}^{m} c_h \left[\frac{1}{W_{22,h}} - 1\right]$$

= W_{12}

this is the AM of the fitness

h(0.0) is positive (as is Δp and the p = 0.0 fixation equilibrium is unstable) when:

$$\sum_{h=1}^{m} c_h \frac{1}{W_{22,h}} > 1.0$$

AM

OR When

$$\frac{1}{\sum_{h=1}^{m} c_h \left[\frac{1}{W_{22,h}}\right]} < 1.0$$

HM

Similarly, h(1.0) must be negative for the fixation equilibrium to be unstable:

$$= \sum_{h=1}^{m} c_h \left[1 - \frac{1}{W_{11,h}}\right]$$

this is the AM of the fitness

h(1.0) is negative when:

$$\sum_{h=1}^{m} c_h \frac{1}{W_{11,h}} < 1.0 \qquad \text{AM}$$

OR When

$$\frac{1}{\sum_{h=1}^{m} c_h \left[\frac{1}{W_{11,h}}\right]} > 1.0 \qquad \text{HM}$$

So, a PP exists if the AM of both homozygotes is greater than the heterozygote OR the HM is less.

Conclusions:

1) **PP are not equilibrium points but do indicate conditions under which polymorphisms can be maintained in populations even when:**
   a) **heterozygotes are not overdominant in ANY niche**
   b) **heterozygotes are not overdominant on AVERAGE (AM)**
2) **Even with dominant polymorphisms where $W_{11} = W_{12} = 1.0$ (i.e., the 1 allele is favored and dominant and should results in F(2) => 0.0), a PP will exist if:**
   a) **HM W_{22} < 1.0 < AM W_{22}**
3) **In Levene's spatially varying model of selection the geometric mean of the average population fitness ($\overline{W}_h$) is maximized (as shown by Prout 1968 Am. Natur. 102:493-496).**

II) Haldane and Jayakar's Temporally Varying Model of Selection (1963 J. Genet. 58:237-242).

A) Background

1) **Same as in Classical Model.**
2) **Fitness changes over time (i.e., generation to generation)**
3) **Changes in fitness are caused by changes in climate, coevolution, coinhabitations, epidemic, etc.**

Can Temporally Varying Selection maintain polymorphisms?

B) No Dominance:

Genotype	AA	Aa	aa
Frequency at time t	P^2	2pq	q^2
Fitness at time t	$W_{11,t}$	1.0	$W_{22,t}$

$$p_{t+1} = \frac{p(pW_{11,t} + qW_{12,t})}{\overline{W}_t}$$

$$= \frac{p(pW_{11,t} + q)}{\overline{W}_t}$$

Where: $\overline{W}_t = p^2W_{11,t} + 2pqW_{12,t} + q^2W_{22,t}$

Define: $U_t = \frac{p_t}{q_t}$ **and note:**

if A is rare (i.e., p ≈ 0.0) then $U_t \approx 0.0$ (very small)

if a is rare (i.e., q ≈ 0/0) then U_t is very large

So:

as A increases, p increases, and U increases
as a increases p decreases, and U decreases

if U is increasing over generations, then allele A is also increasing

consider that A is initially rare (i.e., $p \approx 0.0$). Then there is a net increase from one generation to the next if:

$$U_n > U_0 \ (U_0 \approx 0.0 \text{ so it must also be true that) } \frac{U_n}{U_0} > 1.0)$$

p_{t+1} can be rewritten:

$$U_{t+1} = \frac{U_t\left(1 + U_t W_{11,t}\right)}{U_t + W_{22,t}}$$

Note:

$$U_n = U_0 \frac{U_1}{U_0} \frac{U_2}{U1} \frac{U_3}{U_2} \cdots \frac{U_n}{U_{n-1}}$$

Similarly:

$$\frac{U_n}{U_0} = \frac{U_0 \frac{U_1}{U_0} \frac{U_2}{U_1} \frac{U_3}{U_2} \cdots \frac{U_n}{U_{n-1}}}{U_0}$$

$$= \prod \frac{U_{t+1}}{U_t}$$

To protect A from being eliminated from the population when $F(A) \approx 0.0$, $\Delta F(A)$ must be positive (i.e., $\frac{U_n}{U_{n-1}} > 1.0$). When $F(A) \approx 0.0$ then $U_t \approx 0.0$ (well, small). If U_t is small then:

$$\frac{U_{t+1}}{U_t} = \left[\frac{U_t\left(1 + U_t W_{11,t}\right)}{U_t + W_{22,t}}\right] \times \frac{1}{U_t}$$

$$\approx \frac{1}{W_{22,t}}$$

$$\frac{U_n}{U_0} \approx \frac{1}{\prod W_{22,t}} \qquad \textbf{GM Fitness}$$

$$\frac{U_n}{U_0} > 1.0 \text{ if and only if } \prod W_{22,t} < 1.0$$

To protect a from being eliminated from the population when $F(a) \approx 0.0$, $\Delta F(a)$ must be positive. "a" is protected when if and only if $\prod W_{11,t} < 1.0$

Finally, a PP will exist at a locus without dominance when:

GM W_{11} AND GM W_{22} < 1.0

C) Complete Dominance

Genotype	AA	Aa	aa
Frequency at time t	P^2	2pq	q^2
Fitness at time t	1.0	1.0	$W_{22,t}$

Similar situation as with no dominance for when A is protected

if $GM(W_{22}) < 1.0$

and when rate "a" shows a net increase in frequency when:

if $AM(W_{22}) > 1.0$

So there will be a protected polymorphism at a locus with dominance (of any type – additive is also a "type" of dominance) if and only if:

$$GM(W_{22}) < 1.0 < AM(W_{22})$$

III) Frequency Dependent Selection

A) Background

1) **Fitness is a function of the genotype and/or allele frequencies**

2) **Two types: negative frequency dependence and pair-wise frequency dependent.**

B) Negative frequency dependence – rare male mating advantage, Batesian mimicry, etc.

1) **Fitness decreases as a function of allele frequency.**

OH 10.5.5

Genotype	AA	Aa	aa
Relative Fitness	$1 - s_1p$	$1 - \left[\frac{s_1p + s_2q}{2}\right]$	$1 - s_2q$
Fitness	$W_{11}p$	$W_{12}p$	$W_{22}p$

Note: $W_{12} = \frac{W_{11} + W_{12}}{2}$ **i.e., additive (codominant) only**

a) **Three equilibriums exist**

i) $\hat{p} = 0.0$
ii) $\hat{p} = 1.0$
iii) $\hat{p} = \frac{s_2}{s_1 + s_2}$

b) **i and ii are unstable and iii is stable (i.e., similar to overdominance situation).**

c) **At stable equilibrium, critical values of fitness are equal and mean population fitness is maximized.**

OH 10.6 – 10.9

2) **Fitness decreases as a function of genotype frequency**

Genotype	AA	Aa	aa
Relative Fitness	$1 - sp^2$	$1 - s2pq$	$1 - sq^2$

a) **Three equilibriums exist**

i) $\hat{p} = 0.0$
ii) $\hat{p} = 1.0$
iii) $\hat{p} = 0.5$

b) **i and ii are unstable for $0.0 < s < 1.0$ (i.e., protected polymorphism).**

c) **$\hat{p} = 0.5$ is a locally stable equilibrium.**

C) Pair-wise Interaction Model of Frequency Dependent Selection

	Individual 1		
Individual 2	**AA**	**Aa**	**aa**
AA	W_{22}	W_{21}	W_{20}
Aa	W_{12}	W_{11}	W_{10}
aa	W_{02}	W_{01}	W_{00}

W_{1j} where i is the number of "A" in the interaction contributed by individual 2 and j is the number of "A" contributed by individual 1.

1) **Fitnesses of genotypes are based on pair wise interactions between individuals.**

Genotype	Relative fitness	Mean (net) Fitness
AA	W_2	$p^2W_{22} + 2pqW_{21} + q^2W_{20}$
Aa	W_1	$p^2W_{12} + 2pqW_{11} + q^2W_{10}$
aa	W_0	$p^2W_{02} + 2pqW_{01} + q^2W_{00}$

$$\overline{W} = p^2W_2 + 2pqW_1 + q^2W_0$$

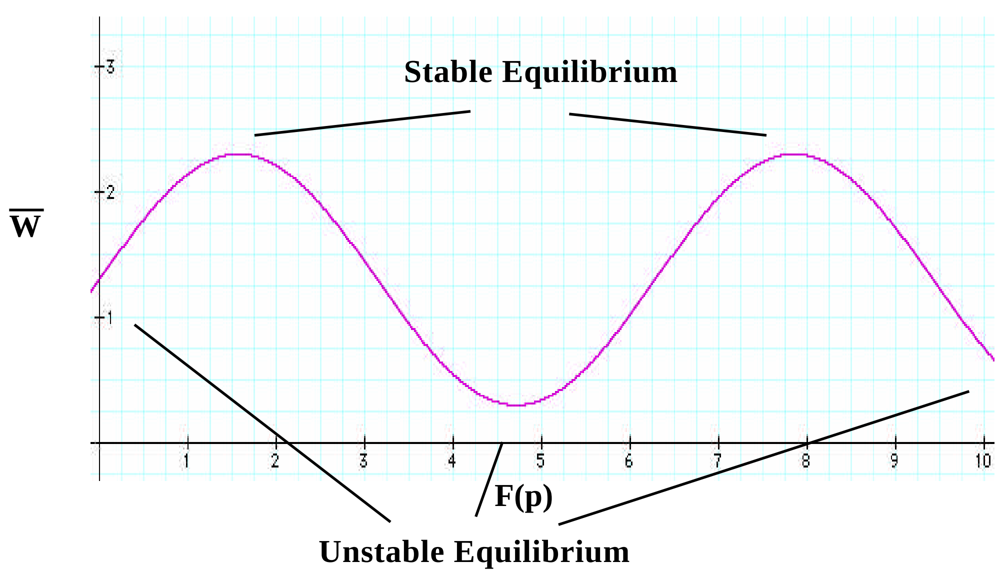
$$p' = \frac{p^2W_2 + pqW_1}{\overline{W}} = \frac{p(pW_2 + qW_1)}{\overline{W}}$$

$(pW_2 + qW_1)$ = **Marginal Fitness**

a) **Equilibrium are at:**

i) $\hat{p} = 0.0$
ii) $\hat{p} = 1.0$
iii) $\hat{p}$ = **Marginal Fitness A – Marginal Fitness a = 0.0**
(i.e., marginal fitness of alleles are equal)

These are complex, cubic equations. There can be more than three equilibriums where two can be simultaneously locally stable.



IV) Conclusions for Complex Forms of Selection

A) General

1) **More than 1 stable equilibrium possible**

2) **Mean fitness is not necessarily, globally maximized**

3) **Heterozygote advantage is not necessarily or even sufficient to maintain polymorphisms in populations (in Spatially and Temporally varying selection heterozygote advantage is sufficient but not necessary).**

B) Over-review:

1) **Spatially Varying Selection**

$$AM\left(\frac{W_{12}}{W_{22}}\right) > 1.0 \quad \text{OR} \quad HM\left(\frac{W_{22}}{W_{12}}\right) < 1.0$$

AND

$$AM\left(\frac{W_{12}}{W_{11}}\right) > 1.0 \quad \text{OR} \quad HM\left(\frac{W_{11}}{W_{12}}\right) > 1.0$$

Therefore a protected polymorphism exists if:

a) **heterozygotes are overdominant on average. i.e.,**

$$AM\left(\frac{W_{12}}{W_{22}}\right) > 1.0 \quad \text{and} \quad AM\left(\frac{W_{12}}{W_{11}}\right) > 1.0$$

b) **heterozygotes are not overdominant on average. e.g.,**

$$AM\left(\frac{W_{12}}{W_{22}}\right) < 1.0 \quad \text{but} \quad AM\left(\frac{W_{12}}{W_{11}}\right) > 1.0$$

$$\text{and} \quad HM\left(\frac{W_{22}}{W_{12}}\right) < 1.0$$

c) **Heterozygotes are not overdominat in any niche. i.e.,**

$HM(W_{11})$ and $HM(W_{22}) < HM(W_{12})$

d) **$GM(\overline{W})$ is maximized**

2) **Temporally Varying Selection**

a) **No Dominance: $GM(W_{22}) < 1.0$ AND $GM(W_{11}) < 1$**

b) **Dominance: $GM(W_{22}) < 1.0 < AM(W_{22})$**

e) References for Complex Selection Models

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