MORAN'S ISLAND MIGRATION MODEL

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P A. P. MORAN (1959) considers two Mendelian populations between which there is migration. He discusses the case of no dominance in both populations combined with equal migration rates. The results are interesting because it is possible to obtain stable polymorphisms in the two populations without fixation of either gene. MORAN establishes the result when the amount of selection is the same in both populations but selection acts in different directions. MORAN's discussion can be extended to cover different selection patterns. In this paper, firstly no dominance is assumed but the restrictions on the parameters are relaxed. A more general condition for the existence of stable polymorphisms is obtained. Secondly, for the general model, sufficient conditions are given for the existence of genetic polymorphisms.

§1. THE GENETIC MODEL

Consider two populations consisting of diploid individuals AA, Aa and aa such that in population I gene A has frequency p_1 and in population II, gene A has frequency p_2. The next generation is formed by random mating and selection within each population followed or preceded by migration between the populations. If, in population I, the relative viabilities of the zygotes are AA: $1+a_1$, Aa: 1, aa: $1+b_1$ and in population II, AA: $1+a_2$, Aa: 1, aa: $1+b_2$, then the new gene frequencies p'_1, p'_2 are

$$p'_1 = p_1 + m_1 (p_2 - p_1) + p_1 q_1 (a_1 p_1 - b_1 q_1) + E$$
$$p'_2 = p_2 + m_2 (p_1 - p_2) + p_2 q_2 (a_2 p_2 - b_2 q_2) + E$$

where m_1 is the proportion of migrants from population II in population I and m_2 is the proportion of migrants from population I in population II and E is used to denote a function of higher powers of the parameters. We will assume that E can be neglected, that is, the parameters are in this sense "small".

§2. THE EQUILIBRIA

The equilibria are solutions of the simultaneous equations $p'_1 = p_1$ and $p'_2 = p_2$. The homozygous states, $p_1 = p_2 = 0$ and $p_1 = p_2 = 1$ always satisfy these equations.

When there is no dominance in both populations the equilibrium equations are simpler, namely,

$$p_2 = p_1 (1 - \alpha_1 q_1) \text{ and } p_1 = p_2 (1 - \alpha_2 q_2)$$

where the viabilities of AA, Aa, aa are $1+a_i$: 1: $1-a_i$ in the ith population, and where $\alpha_1 = a_1/m_1$ and $\alpha_2 = a_2/m_2$. To find the remaining equilibria, substitute $p_1 (1-\alpha_1 q_1)$ for p_2 in the second equation. Then p_1 is a solution of the quadratic equation

$$\alpha_1 + \alpha_2 (1-\alpha_1 q_1)(1+\alpha_1 p_1) = 0.$$

We are only interested in solutions such that $0 < p_1 < 1$. This equation has at most one root between 0 and 1. A necessary and sufficient condition for such a root to exist is that the quadratic expression takes opposite signs at $p_1 = 0$ and $p_1 = 1$, that is either

$$\alpha_1 + \alpha_2 (1-\alpha_1) > 0 \text{ and } \alpha_1 + \alpha_2 (1+\alpha_1) < 0 \text{ , or}$$
$$\alpha_1 + \alpha_2 (1-\alpha_1) < 0 \text{ and } \alpha_1 + \alpha_2 (1+\alpha_1) < 0 \text{ .}$$

If $\alpha_1 \alpha_2 > 0$, we must have $-\alpha_1 \alpha_2 < \alpha_1 + \alpha_2 < \alpha_1 \alpha_2$.
If $\alpha_1 \alpha_2 < 0$, we must have $\alpha_1 \alpha_2 < \alpha_1 + \alpha_2 < -\alpha_1 \alpha_2$.
Elimination of p_1 leads to the same condition.

The roots of the quadratic equation are

$$p_1 = 1/2 - 1/\alpha_1 \pm S/2$$
$$\text{where } S^2 = 1 - 4/\alpha_1 \alpha_2 .$$

If $\alpha_1 \alpha_2 > 0$, and one root lies between 0 and 1, the corresponding value of p_2 is negative. If $\alpha_1 > 0$ and $\alpha_1 \alpha_2 < \alpha_1 \alpha_2 < -\alpha_1 \alpha_2$, the root between 0 and 1 is $p_1 = 1/2 - 1/\alpha_1 + S/2$ and the corresponding value of p_2 is $1/2 - 1/\alpha_2 - S/2$ which lies between 0 and 1.

Hence we have

(2.1) If gene A is advantageous in both populations, that is, $\alpha_1 > 0$, $\alpha_2 > 0$, there are two equilibria, namely $p_1 = p_2 = 0$ and $p_1 = p_2 = 1$.

(2.2) If gene a is advantageous in both populations, that is, $\alpha_1 < 0$, $\alpha_2 < 0$, there are two equilibria, namely $p_1 = p_2 = 0$ and $p_1 = p_2 = 1$.

(2.3) If gene A is advantageous in one population and disadvantageous in the other, that is, either $\alpha_1 > 0 > \alpha_2$ or $\alpha_1 < 0 < \alpha_2$, then

  a) there are two equilibria if $|\alpha_1^{-1} + \alpha_2^{-1}| \geqslant 1$
    namely $p_1 = p_2 = 0$ and $p_1 = p_2 = 1$

  b) there are three equilibria if $|\alpha_1^{-1} + \alpha_2^{-1}| < 1$
    namely $p_1 = p_2 = 0$, $p_1 = p_2 = 1$ and if
    $\alpha_1 > 0 > \alpha_2$,
    $p_1 = 1/2 - 1/\alpha_1 + S/2$, $p_2 = 1/2 - 1/\alpha_2 - S/2$
    and if $\alpha_1 < 0 < \alpha_2$,
    $p_1 = 1/2 - 1/\alpha_1 - S/2$, $p_2 = 1/2 - 1/\alpha_2 + S/2$.

§3. STABILITY OF THE EQUILIBRIA

It can be shown (EYLAND 1969; FALK and FALK 1969; LEWONTIN 1969) that a Liapounov stability condition is applicable. The advantage of the Liapounov condition is the simplicity of its application, particularly in the genetic models.

Suppose that we want to determine the stability of the equilibrium $(\hat{p}_1, \hat{p}_2)$. Then evaluate the first order partial derivatives of $(p'_1 - p_1)$ and $(p'_2 - p_2)$ at $p_1 = \hat{p}_1$ and $p_2 = \hat{p}_2$ and let

$$a = \frac{\partial}{\partial p_1}(p'_1 - p_1); \quad b = \frac{\partial}{\partial p_2}(p'_1 - p_1); \quad c = \frac{\partial}{\partial p_1}(p'_2 - p_2); \quad d = \frac{\partial}{\partial p_2}(p'_2 - p_2)$$

$\Delta = ad - bc$ and $I = a + d$.

If $\Delta < 0$, $(\hat{p}_1, \hat{p}_2)$ is semi-stable or neutral.

If $0 < 4\Delta < I^2$, $I > 0$, $(\hat{p}_1, \hat{p}_2)$ is unstable.

If $0 < 4\Delta < I^2$, $I < 0$, $(\hat{p}_1, \hat{p}_2)$ is stable.

In the model being discussed, I^2 is always greater than 4Δ.

Note that this only gives local stability. Global stability requires the elimination of cyclic behaviour. Applying these results to the present model, we have the following classification of the equilibria:

		$(0,0)$	$(1,1)$	(p_1, p_2)
(2.1)	$\alpha_1, \alpha_2 > 0$	U	S	
(2.2)	$\alpha_1, \alpha_2 < 0$	S	U	
(2.3) a)	$\alpha_1^{-1} + \alpha_2^{-1} \geq 1$	S	N	
	$\alpha_1^{-1} + \alpha_2^{-1} \leq -1$	N	S	
b)	$|\alpha_1^{-1} + \alpha_2^{-1}| < 1$	N	N	S

U = unstable equilibrium   S = stable   N = neutral or semi-stable.

The Liapounov conditions are applicable because the recurrence relations of §1 form the Euler algorithm of the differential equation

$$\frac{dp_1}{dp_2} = \frac{m_1(p_2 - p_1) + a_1 p_1 q_1}{m_2(p_1 - p_2) + a_2 p_2 q_2} \; .$$

Results relating to the solutions of this equation are therefore applicable. Hence the use of Liapounov conditions. Also, from a result due to VOROBEV (1960), cyclic behaviour of the solution curves is excluded; thus in each case, convergence to the stable equilibrium is certain.

In particular, when $\alpha_1 \alpha_2 < 0$ and $|\alpha_1^{-1} + \alpha_2^{-1}| < 1$, the system results in genetic polymorphism in both populations, the stability being maintained by migration between the two populations. Such stable polymorphism is obtained from any initial state, provided of course that the system does not start with fixation of either gene in the two populations.

§4. OTHER SELECTION PATTERNS

The analysis of other patterns of selection is possible but more complicated. Details can be found in EYLAND (1969). The equilibrium equations are of a different order resulting in the possibility of more than three equilibria. The
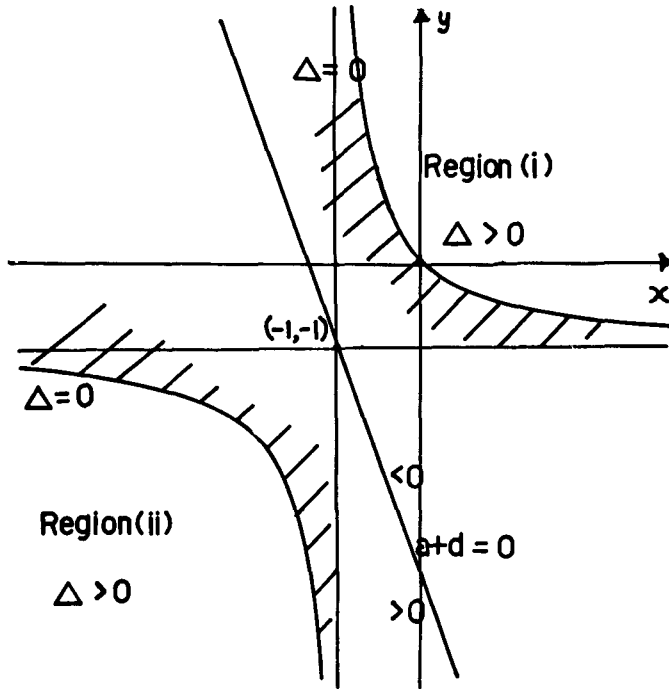
FIGURE 1.—Conditions for (0,0) and (1,1) to be stable, unstable and semistable.

differential equation theory does lead to some economy in establishing the results. Perhaps its most important use is in the discussion of convergence to stable equilibria.

General conditions for the existence of genetic polymorphism can be obtained by considering the nature of the trivial equilibria (0,0) and (1,1).

For the general model, the values of Δ and I at (0,0) and (1,1) take the same form, namely,

$$\Delta = m_1 m_2 \left[(1+x)(1+y)-1\right]; \quad I = -m_1(1+x)-m_2(1+y).$$
$$\text{At } (0,0), \; x = b_1/m_1, \; y = b_2/m_2$$
$$\text{At } (1,1), \; x = a_1/m_1, \; y = a_2/m_2 \; .$$

The conditions for (0,0) and (1,1) to be stable, unstable or semi-stable can be represented graphically. In Figure 1, the hyperbola $(1+x)(1+y) = 1$ and the line $m_1(1+x) + m_2(1+y) = 0$ are graphed. Points (x,y) in region (i) represent stable equilibria, points in region (ii) represent unstable equilibria and points in region (iii) represent semi-stable equilibria. A sufficient condition for the existence of genetic polymorphicm is that $(b_1/m_1, b_2/m_2)$ and $(a_1/m_1, a_2/m_2)$ lie in regions (ii) or (iii).

This condition is not necessary. In fact, in the case of heterozygote disadvantage in both populations, it is possible for (0,0) and (1,1) to be stable and for there to be further stable equilibria corresponding to situations of stable genetic polymorphism.

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SUMMARY

The analysis of Moran's Island Migration model can be extended to more general selection and migration patterns. In the simple model of no dominance in both populations, and provided that selection operates in opposite directions, it is possible to obtain stable polymorphisms in the two populations. With more general patterns of selection stable polymorphisms are still possible. The model suggests that the combined effects of migration and selection are important in maintaining genetic variability.

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