Model 3, negative assortative mating (incl. 3.20 of EK)

Assumptions 2–4 again the same. The first is now

* female AA mate only male aa
* female aa mate only male AA
* female Aa mate male AA and aa with equal preference

Remark: one could make other assumptions and still call it neg. ass. mating, e.g., only exclude mating of the same genotype.

Mating table:

		Male AA u_n	Male Aa v_n	Male aa w_n
Female AA	u_n	0	0	u_n
Female Aa	v_n	$v_n \cdot \frac{u_n}{u_n+w_n}$	0	$v_n \cdot \frac{w_n}{u_n+w_n}$
Female aa	w_n	w_n	0	0

row sums must be u_n, v_n, w_n

← sum is v_n, elements are proportional to u_n, w_n (relative freq.)

Corresponding freq. of AA, Aa, aa:

–	–	$0,1,0$
$\frac{1}{2},\frac{1}{2},0$	–	$0,\frac{1}{2},\frac{1}{2}$
$0,1,0$	–	–

For the next generation:

$$\begin{cases} u_{n+1} = \frac{1}{2}\frac{u_n v_n}{u_n+w_n} \\ v_{n+1} = u_n + w_n + \frac{1}{2}v_n\left(\frac{u_n}{u_n+w_n} + \frac{w_n}{u_n+w_n}\right) = u_n + \frac{1}{2}v_n + w_n \\ w_{n+1} = \frac{1}{2}\frac{v_n w_n}{u_n+w_n} \end{cases}$$

non-linear system

Note: $v_{n+1} = \underbrace{u_n + w_n}_{1-v_n} + \frac{1}{2}v_n = 1 - \frac{1}{2}v_n \iff v_{n+1} + \frac{1}{2}v_n = 1$; can be solved

Homogeneous solution is $v_{n,h} = c\cdot\left(-\frac{1}{2}\right)^n$ (solves $v_{n+1} + \frac{1}{2}v_n = 0$),

a particular solution is $v_{n,p} = \frac{2}{3}$ $\left(\Rightarrow v_{n+1} + \frac{1}{2}v_n = \frac{2}{3} + \frac{1}{2}\cdot\frac{2}{3} = 1\right)$ $\Rightarrow$

$v_n = \frac{2}{3} + c\cdot\left(-\frac{1}{2}\right)^n$. $n=0 \Rightarrow v_0 = \frac{2}{3} + c \Rightarrow c = v_0 - \frac{2}{3}$ and $v_n = \frac{2}{3} + \left(v_0 - \frac{2}{3}\right)\left(-\frac{1}{2}\right)^n$ (*)

Observe $v_n \to \frac{2}{3}$, $n \to \infty$, independent of v_0 (and u_0, w_0)!

One could now use $u_{n+1} = \frac{1}{2}\frac{u_n v_n}{u_n+w_n} = \frac{1}{2}u_n \frac{v_n}{1-v_n}$ and plug in (*) for v_n, to get a linear but not constant coefficient equation for u_n, not easy to solve.

Instead, we use $w_n = 1 - v_n - u_n$ and analyze the 2D system for u_n and v_n:

$$\begin{cases} u_{n+1} = \frac{1}{2}\frac{u_n v_n}{1-v_n} \\ v_{n+1} = 1 - \frac{1}{2}v_n \end{cases}$$

Steady states: $\begin{cases} \bar{u} = \frac{1}{2}\frac{\bar{u}\bar{v}}{1-\bar{v}} \\ \bar{v} = 1-\frac{1}{2}\bar{v} \end{cases} \Rightarrow \bar{v} = \frac{2}{3} \Rightarrow \bar{u} = \underbrace{\frac{1}{2}\frac{\bar{u}\cdot 2/3}{1/3}}_{=\bar{u}}$ always satisfied

$\Rightarrow (\bar{u}, \frac{2}{3})$ are steady states for all $\bar{u}$. For the 3D system $\bar{w} = 1-\bar{u}-\bar{v} = \frac{1}{3}-\bar{u}$

so $(\bar{u}, \frac{2}{3}, \frac{1}{3}-\bar{u})$ are steady states.

Stability:

$$J(u,v) = \begin{pmatrix} \frac{1}{2}\frac{v}{1-v} & \frac{u}{2(1-v)^2} \\ 0 & -\frac{1}{2} \end{pmatrix} \Rightarrow J(\bar{u}, \tfrac{2}{3}) = \begin{pmatrix} 1 & \frac{9\bar{u}}{2} \\ 0 & -1/2 \end{pmatrix} \Rightarrow \underbrace{\lambda_1 = 1}_{\text{critical}}, \ \underbrace{\lambda_2 = -1/2}_{\substack{\text{OK for stability} \\ |\lambda_2|<1}}$$

Observe:

$$\frac{u_{n+1}}{w_{n+1}} = \frac{\frac{1}{2}\frac{u_n v_n}{u_n + w_n}}{\frac{1}{2}\frac{v_n w_n}{u_n+w_n}} = \frac{u_n}{w_n} \Rightarrow \frac{u_n}{w_n} = \text{constant} = \frac{u_0}{w_0} = \alpha$$

For steady state $\frac{\bar{u}}{\bar{w}} = \frac{\bar{u}}{\frac{1}{3}-\bar{u}} = \alpha \Rightarrow \frac{\bar{u}}{\alpha} = \frac{1}{3}-\bar{u} \Rightarrow \bar{u} = \frac{1}{3(1+\frac{1}{\alpha})} = \frac{1}{3(1+\frac{w_0}{u_0})} = \frac{u_0}{3(u_0+w_0)}$

and $\bar{w} = \frac{1}{3} - \bar{u} = \frac{w_0}{3(u_0+w_0)} \Rightarrow$

$$(\bar{u}, \bar{v}, \bar{w}) = \left(\frac{u_0}{3(u_0+w_0)}, \frac{2}{3}, \frac{w_0}{3(u_0+w_0)}\right)$$, steady states for all u_0, w_0

Small changes in u_0, w_0 give small (but non-zero) changes in $\bar{u}$ and $\bar{w}$
$\Rightarrow$ steady states ~neutral.
(Compare discrete SIR model which also has $\lambda_1 = 1$)

Tests	n=0	1	2	3	∞	n=0	1	2	∞
u_n	1/3	1/12	5/24	7/48	… → 1/6	0.2	0.1	0.15	… → 2/15
v_n	1/3	5/6	7/12	15/24	… → 2/3	0.5	0.75	0.625	… → 2/3
w_n	1/3	1/12	5/24	7/48	… → 1/6	0.3	0.15	0.225	… → 3/15

Note: p_n and q_n are not constant in this model
$p_0 = 0.2 + \frac{0.5}{2} = 0.45$, $p_1 = 0.1 + \frac{0.75}{2} = 0.475$, … $p_n \to \frac{2}{15} + \frac{1}{3} = \frac{7}{15} \approx 0.467$

Age structures of populations and Leslie matrices

Suppose there are m age classes in a population with $p_{1,n}, p_{2,n}, \dots, p_{m,n}$ individuals in the classes at time n (n could be year for humans, $m \sim 100$, or each class could be a 10-year interval).

Let α_j = number of births per unit time from each individual in class j, $\alpha_j \geq 0$

σ_j = fraction of class j that survives to class $j+1$, $0 < \sigma_j \leq 1$ assumed.

At time $n+1$ we have

newborns $\quad p_{1,n+1} = \alpha_1 p_{1,n} + \alpha_2 p_{2,n} + \dots + \alpha_m p_{m,n}$

survivors $\quad p_{j,n+1} = \sigma_{j-1} p_{j-1,n}, \quad j = 2, \dots, m$

Write $\bar{P}_n = \begin{pmatrix} p_{1,n} \\ \vdots \\ \vdots \\ p_{m,n} \end{pmatrix}$ and $A = \begin{pmatrix} \alpha_1 & \alpha_2 & \dots & \alpha_{m-1} & \alpha_m \\ \sigma_1 & 0 & \dots & 0 & 0 \\ 0 & \sigma_2 & \dots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \dots & \sigma_{m-1} & 0 \end{pmatrix}$ ($m \times m$ matrix)

$\Rightarrow$ we have the linear discrete system

$$\bar{P}_{n+1} = A \bar{P}_n \qquad A \text{ is called a } \underline{\text{Leslie matrix}}$$

If A has eigenvalues $\lambda_1, \lambda_2, \dots, \lambda_m$ with eigenvectors $\bar{v}_1, \bar{v}_2, \dots, \bar{v}_m$, the solutions are

$$\bar{P}_n = c_1 \lambda_1^n \bar{v}_1 + c_2 \lambda_2^n \bar{v}_2 + \dots + c_m \lambda_m^n \bar{v}_m$$

(it is also possible to write down $\bar{P}_n$ in the case that A has $< m$ eigenvectors)

Suppose that λ_1 has the largest absolute value, $|\lambda_1| > |\lambda_j|$, $j = 2, \dots, m$. Then

$$\frac{1}{\lambda_1^n} \bar{P}_n = c_1 \bar{v}_1 + c_2 \underbrace{\left(\frac{\lambda_2}{\lambda_1}\right)^n}_{\to 0,\, n \to \infty} \bar{v}_2 + \dots + c_m \underbrace{\left(\frac{\lambda_m}{\lambda_1}\right)^n}_{\to 0,\, n \to \infty} \bar{v}_m \to c_1 \bar{v}_1, \quad n \to \infty \quad \Rightarrow$$

$$\bar{P}_n \approx c_1 \lambda_1^n \bar{v}_1 \quad \text{if } n \text{ large}$$

$\bar{v}_1$ is called the <u>stable age distribution</u>, its components show the number of individuals in each age class and can be used to predict future age distribution in a population. It should have all its components ≥ 0 and λ_1 real positive to be realistic.

Perron-Frobenius theory for matrices A with all elements $a_{ij}>0$ or $a_{ij}\geq 0$ can be applied (positive / non-negative matrices).

If $\alpha_m>0$ (maybe not the case for humans) and if, e.g., two consecutive α_j, α_{j+1} are >0, then A is an "irreducible" and "primitive" non-negative matrix and a theorem of Frobenius says:

> A has a real eigenvalue $\lambda_1>0$ with $\lambda_1>|\lambda_j|$ for $j=2,\dots,m$. The eigenvector $\bar{v}_1$ of λ_1 has all its components >0 (and no other eigenvector $\bar{v}_j$ has all components ≥ 0)

This theory fits our model, it is also the theory behind Google's PageRank and many results about Markov chains. If $\alpha_m=0$ theorems guarantee slightly weaker results.

Example with $m=4$

$$A=\begin{pmatrix} 0 & 0.5 & 0.7 & 0.1 \\ 0.9 & 0 & 0 & 0 \\ 0 & 0.9 & 0 & 0 \\ 0 & 0 & 0.8 & 0 \end{pmatrix}$$

Survival is 90% in first 2 steps, then 80%. Births: most (0.7) in class 3, 0.5 in class 2, few (0.1) in class 4, none in class 1.

One finds

$$\underbrace{\lambda_1\approx 1.03}_{\text{real positive}},\ \bar{v}_1\approx\underbrace{\begin{pmatrix}0.31\\0.27\\0.24\\0.18\end{pmatrix}}_{\substack{\text{all elements }>0\\ \text{scaled to have sum 1}}},\quad \lambda_2\approx -0.13,\ \bar{v}_2\approx\underbrace{\begin{pmatrix}0.00\\0.02\\-0.15\\0.99\end{pmatrix}}_{\text{mixed signs}},\ |\lambda_2|<\lambda_1$$

$$\lambda_{3,4}\approx -0.45\pm 0.54i,\quad \bar{v}_{3,4}\ \text{complex},\quad |\lambda_{3,4}|\approx 0.7<\lambda_1$$

Solutions to $\bar{P}_{n+1}=A\bar{P}_n$ are

$$\bar{P}_n=c_1(1.03)^n\bar{v}_1+c_2\underbrace{(-0.13)^n}_{\to 0\text{ fast}}\bar{v}_2+\underbrace{c_3\lambda_3^n\bar{v}_3+c_4\lambda_4^n\bar{v}_4}_{\substack{\text{can be written on real form}\\ \to 0\text{ quite fast}}}$$

For large n, $\bar{P}_n\approx c_1(1.03)^n\begin{pmatrix}0.31\\0.27\\0.24\\0.18\end{pmatrix}$, means that population grows by 3% per unit time, and there will be approx. 31%, 27%, 24%, and 18%, respectively, of the population in the different age classes.