INTRODUCTION TO MATHEMATICAL BIOLOGY

HOMEWORK SOLUTIONS

November 21, 2016

Exercise 8.1

(a) At the stable age distribution, after one year we know that (1) every class grows of a factor λ, (2) for $i > 1$, individuals in class i are those survived from class $i-1$. Hence, for any class $i > 1$ we can write

$$u_i = \frac{1}{\lambda}P_{i-1}u_{i-1} = \frac{1}{\lambda^2}P_{i-1}P_{i-2}u_{i-2} = \cdots = \frac{1}{\lambda^i}l_i u_1$$

Hence, $u_i = cl_i/\lambda^i$ for $c = u_1$.
(b) Since v is the left eigenvector and from the special structure of the Leslie matrix,

$$v_i = \frac{1}{\lambda}(\mathbf{v}^T\mathbf{A})_i = \frac{1}{\lambda}(F_i v_1 + P_i v_{i+1}).$$

(i) Let j such that $F_i = 0$ for all $j \leq i \leq n$. Thanks to (b),

$$v_i = \frac{1}{\lambda}(F_i v_1 + P_i v_{i+1}) = \frac{1}{\lambda}(P_i v_{i+1}) = \frac{1}{\lambda^2}(P_{i+1}v_{i+2}) = \cdots = \frac{1}{\lambda^{(n-i+1)}}(P_n v_{n+1}) = 0$$

since $P_n = 0$.

(ii) Assume $\lambda \geq 1$. Using (a) and the fact that $P_i < 1$ for all i, for all $i > 1$ we can write

$$x_i = c\frac{l_i}{\lambda^i} = c\frac{P_i}{\lambda}\frac{l_{i-1}}{\lambda^{i-1}} < c\frac{l_{i-1}}{\lambda^{i-1}} = x_{i-1}$$

(iii) Let $1 \leq i < k$. Then we use (b)

$$v_i = \frac{1}{\lambda}(F_i v_1 + P_i v_{i+1}) = \frac{P_i}{\lambda}v_{i+1} < v_{i+1}.$$

Exercise 8.2

$$\sum_{i,j} e_{ij} = \frac{1}{\lambda}\sum_{i,j} v_i u_j a_{ij} = \frac{1}{\lambda}\mathbf{v}^T\mathbf{A}\mathbf{u} = 1$$

Exercise 8.3

The projection matrix of the turtles population is

$$\mathbf{A} = \begin{pmatrix} 0 & 0 & 60 \\ 0.6 & 0.7 & 0 \\ 0 & 0.001 & 0.8 \end{pmatrix}$$

with leading eigenvalue $\lambda \approx 0.95$.

To compute elasticities, we (numerically) compute the left and right eigenvectors normalized such that $\mathbf{v}^T\mathbf{u} = 1$:

$$\mathbf{u} \approx \begin{pmatrix} 35.8494 \\ 85.7315 \\ 0.5682 \end{pmatrix} \qquad \mathbf{v} \approx \begin{pmatrix} 0.0025 \\ 0.0040 \\ 1.0000 \end{pmatrix}$$

Now we can compute the elasticities corresponding to the effect of increasing fecundity, a_{13}, and the effect of increasing adult survival, a_{33}

$$e_{13} = \frac{1}{\lambda} v_1 u_3 a_{13} \approx 0.0897$$
$$e_{33} = \frac{1}{\lambda} v_3 u_3 a_{33} \approx 0.4785$$

Hence increasing adult survival has a much stronger relative effect in the conservation of the turtles population. Notice that if A_{ij} is the cost of an the 1% increase of the entry a_{ij}, the aim is to minimize the quantity A/e.

Exercise 8.4

Let S and V be the number of seedlings and of propagules produced by an adult plant, respectively. Let s_1, s_2, s_3 be the survival probability of seedlings, juveniles and adults, respectively, from one census to the next. Let p be the probability of a juvenile plant to grow adult, if it survived.

(a) $\mathbf{A} = \mathbf{F} + \mathbf{T}$ where

$$\mathbf{F} = \begin{pmatrix} 0 & 0 & S \\ 0 & 0 & V \\ 0 & 0 & 0 \end{pmatrix} \qquad \mathbf{T} = \begin{pmatrix} 0 & 0 & 0 \\ s_1 & s_2(1-p) & 0 \\ 0 & s_2 p & s_3 \end{pmatrix}$$

The next generation matrix $\mathbf{K}$ is defined by

$$\mathbf{K} = \mathbf{F}(I - \mathbf{T})^{-1}.$$

Let $q = ps_2/(1 - s_2(1-p))$. Then we can write

$$(I - \mathbf{T})^{-1} = \begin{pmatrix} 1 & 0 & 0 \\ \frac{s_1}{1-s_2(1-p)} & \frac{1}{1-s_2(1-p)} & 0 \\ \frac{s_1 q}{1-s_3} & \frac{q}{1-s_3} & \frac{1}{1-s_3} \end{pmatrix}$$

For our purposes, we only consider the block $\mathbf{K}_1$ corresponding to the two state-at-births (seedlings and juveniles):

$$\mathbf{K}_1 = \begin{pmatrix} 0 & 0 & S \\ 0 & 0 & V \end{pmatrix} \begin{pmatrix} 1 & 0 \\ \frac{s_1}{1-s_2(1-p)} & \frac{1}{1-s_2(1-p)} \\ \frac{s_1 q}{1-s_3} & \frac{q}{1-s_3} \end{pmatrix} = \frac{q}{1-s_3} \begin{pmatrix} Ss_1 & S \\ Vs_1 & V \end{pmatrix}$$

with corresponding eigenvalues $\lambda = 0$ and $\lambda = \frac{(V+Ss_1)q}{1-s_3} > 0$. Hence,

$$R_0^{(a)} = \frac{(V+Ss_1)q}{1-s_3} > 0.$$

(b) Consider the only state-at-birth to be the the seedling state (V is not too large). We write $\mathbf{A} = \mathbf{F} + \mathbf{T}$ with

$$\mathbf{F} = \begin{pmatrix} 0 & 0 & S \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix} \qquad \mathbf{T} = \begin{pmatrix} 0 & 0 & 0 \\ s_1 & s_2(1-p) & V \\ 0 & s_2 p & s_3 \end{pmatrix}$$

In particular, for $\mathbf{T}$ to be an admissible transition matrix it is sufficient to assume that $V + s_3 \leq 1$. We compute the inverse

$$(I - \mathbf{T})^{-1} = \begin{pmatrix} 1 & 0 & 0 \\ \frac{s_1}{1-s_2(1-p)} - \frac{s_1 q}{1-s_3-qV} & \frac{1}{1-s_2(1-p)} - \frac{s_1 q}{1-s_3-qV} & -\frac{1}{1-s_3-qV} \\ \frac{s_1 q}{1-s_3-qV} & \frac{q}{1-s_3-qV} & \frac{1}{1-s_3-qV} \end{pmatrix}$$

R_0 is the number obtain by multiplying the first row of $\mathbf{F}$ times the first column of $(I-\mathbf{T})^{-1}$, hence

$$R_0^{(b)} = \frac{qSs_1}{1-s_3-qV}$$

(c)

$$R_0^{(a)} \gtreqless 1 \Leftrightarrow qV + qSs_1 \gtreqless 1 - s_3 \Leftrightarrow \frac{qSs_1}{1-s_3-qV} \gtreqless 1 \Leftrightarrow R_0^{(b)} \gtreqless 1$$