INTRODUCTION TO MATHEMATICAL BIOLOGY

HOMEWORK SOLUTIONS

November 14, 2016

Exercise 7.1

(a) Divide the population in two states according to the habitats. Then, the projection matrix is

$$\mathbf{A} = \begin{pmatrix} (1-m)\rho_1 & sm\rho_2 \\ sm\rho_1 & (1-m)\rho_2 \end{pmatrix}$$

Notice that $\mathbf{A} = \mathbf{MF}$ where $\mathbf{M}$ is the dispersal matrix and $\mathbf{F}$ is the reproduction matrix:

$$\mathbf{M} = \begin{pmatrix} (1-m) & sm \\ sm & (1-m) \end{pmatrix}, \qquad \mathbf{F} = \begin{pmatrix} \rho_1 & 0 \\ 0 & \rho_2 \end{pmatrix}$$

(b) In the limit $s \to 0$, the projection matrix becomes

$$\mathbf{A}_0 = \begin{pmatrix} (1-m)\rho_1 & 0 \\ 0 & (1-m)\rho_2 \end{pmatrix}$$

Hence, the population is viable if and only if

$$\max_{i=1,2} (1-m)\rho_i \geq 1.$$

Exercise 7.2

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.

The projection matrix corresponding to the states (seedlings, intermediate, adult) is

$$\mathbb{A} = \begin{pmatrix} 0 & 0 & S \\ s_1 & s_2(1-p) & V \\ 0 & s_2 p & s_3 \end{pmatrix}$$

Exercise 7.3

Consider the Leslie matrix

$$\mathbf{L} = \begin{pmatrix} 0.6 & 1.1 \\ 0.5 & 0 \end{pmatrix}$$

The eigenvalues of $\mathbf{L}$ are

$$\lambda_1 = 1.1, \quad \lambda_2 = -0.5$$

with corresponding eigenvectors

$$u_1 = \begin{pmatrix} 1 \\ 5/11 \end{pmatrix} \qquad u_2 = \begin{pmatrix} 1 \\ -1 \end{pmatrix}$$

Denote

$$U = \begin{pmatrix} u_1 & u_2 \end{pmatrix} = \begin{pmatrix} 1 & 1 \\ 5/11 & -1 \end{pmatrix}$$

Then, we can write

$$\mathbf{L} = U^{-1} \begin{pmatrix} 1.1 & 0 \\ 0 & -0.5 \end{pmatrix} U$$

and hence

$$\mathbf{L}^{10} = U^{-1} \begin{pmatrix} 1.1 & 0 \\ 0 & -0.5 \end{pmatrix}^{10} U = U^{-1} \begin{pmatrix} 1.1^{10} & 0 \\ 0 & 0.5^{10} \end{pmatrix} U$$

Since $0.5^{10} \ll 1$, the matrix $\mathbf{L}^{10}$ is almost singular. This happens because in the long term the structure of the population tends to align along the eigenvector corresponding to the leading eigenvalue.

Exercise 7.4

Graph	Example	Irreducible	Primitive
1	age structure with pre- and post-reproductive state	no	no
2	dispersal between two patches	yes	yes
3	growth and dispersal	yes	no
4	three patches and dispersal cloud (where the individual stay for one full year)	yes	yes

Notice that the first example can be made irreducible (and hence primitive), by eliminating the last state.

Exercise 7.5

(a) Let $\mathbf{v}^T$ be the leading left eigenvector, i.e.,

$$\mathbf{v}^T \mathbf{A} = \lambda \mathbf{v}^T,$$

where λ is the leading eigenvalue of $\mathbf{A}$. Let v_j be the reproductive value of an individual in class j and let $\mathbf{e}_j$ be the j-th element of the canonical basis. Then,

$$v_j = \mathbf{v}^T \mathbf{e}_j = \frac{1}{\lambda}(\mathbf{v}^T \mathbf{A})\mathbf{e}_j = \frac{1}{\lambda}\mathbf{v}^T(\mathbf{A}\mathbf{e}_j) = \frac{1}{\lambda}\sum_{i=1}^{n} v_i(\mathbf{A}\mathbf{e}_j)_i$$

and notice that the vector $\mathbf{A}\mathbf{e}_j$ contains exactly the number of descendants of an individual in class j the next year.

The term $1/\lambda$ takes into account the fact that the descendants next year have one year less for reproducing: their effective contribution is given by their reproductive value v_i (which is relative to the initial time) divided by λ, which is the growth factor of the population in one year.

(b) Let $\mathbf{v}$ be the vector of reproductive values (i.e., the left eigenvector corresponding to the leading eigenvalue), let $\mathbf{u}$ denote the dominant right eigenvector, which describes the asymptotic population structure, and let $\mathbf{U}$ be the matrix of right eigenvectors. At the stable state distribution, $\mathbf{Au} = \lambda\mathbf{u}$, and u_j denotes the fraction of individuals of the population which are in state j. Hence, the expected reproductive value v is

$$v = \sum_{j=1}^{n} v_j u_j = \mathbf{v}^T \mathbf{u} = 1,$$

from the standard normalization.

(c) As before, the probability of picking an individual in state j is u_j. Next year, the descendants of this individuals are $\mathbf{Ae}_j$, and their reproductive values are given by the vector $\mathbf{v}^T$. Hence, the expected reproductive value $\tilde{v}$ of the descendant of a random individual is

$$\tilde{v} = \sum_{j=1}^{n} \mathbf{v}^T (\mathbf{Ae}_j) u_j = \mathbf{v}^T \mathbf{Au} = \lambda.$$