Elgersburg Summer School, March 2014
Mathematical Biology
Exercise Sheet 2– Positive matrices and matrix PPMs

(1) **Positive matrices:**

(i) Suppose that $A \in \mathbb{R}_+^{n\times n}$ is irreducible and has a nonnegative eigenvector w with corresponding eigenvalue λ. Prove that necessarily $\lambda > 0$ and w is componentwise positive.

(ii) Prove the following parts of the Perron–Frobenius Theorem for primitive matrices A:

(a) The dominant eigenvalue λ, also known as the Perron–Frobenius eigenvalue, is simple (that is, has algebraic and thus geometric multiplicity one).

Consequently, the eigenspace associated to λ is one–dimensional and thus the same is true for the left eigenspace, that is, the eigenspace for A^T. Let v^T and w denote positively scaled positive eigenvectors of A corresponding to λ respectively.

(b) There are no other positive (moreover nonnegative) eigenvectors except positive multiples of w or v^T. In particular, all other eigenvectors must have at least one negative or non–real component.

(c) The limit

$$\lim_{k\to\infty} \lambda^{-k} A^k = \frac{wv^T}{v^T w},$$

holds. Moreover, the matrix wv^T is the projection onto the eigenspace corresponding to λ (the so–called Perron projection).

(iii) Suppose that $A \in \mathbb{R}_+^{n\times n}$ has dominant eigenvalue $\lambda > 0$. Prove that if either all of the row sums of A, or all the column sums of A are less than ρ, then $\lambda < \rho$.

(iv) If $A, B \in \mathbb{R}_+^{n\times n}$ denote primitive matrices with dominant eigenvalues $\lambda > 0$ and $\mu > 0$ respectively. If $A - B$ is componentwise nonnegative show that $\lambda \geq \mu$. If additionally $A - B$ is non–zero, show that $\lambda > \mu$.

(2) **Population Projection Models:** For $A \in \mathbb{R}_+^{n\times n}$, consider the matrix (P)opulation (P)rojection (M)odel

$$x(t+1) = Ax(t)\,, \quad x(0) = x^0\,, \quad t \in \mathbb{N}_0\,. \tag{1}$$

(i) Draw and label life–cycle graphs for the matrix PPMs (1) with A given by

$$A_1 = \begin{bmatrix} 0 & 0 & 0 & 20 \\ 0.9 & 0 & 0 & 0 \\ 0.1 & 0.1 & 0 & 5 \\ 0.2 & 0 & 0.2 & 0.5 \end{bmatrix}, \; A_2 = \begin{bmatrix} 0 & 1 & 2 & 3 \\ 0.5 & 0 & 0 & 0 \\ 0 & 0.2 & 0 & 0 \\ 0 & 0 & 0.4 & 0 \end{bmatrix}, \; A_3 = \begin{bmatrix} 0.5 & 0 & 0.4 & 0 \\ 0.1 & 0.5 & 0 & 0 \\ 0 & 0.2 & 0.5 & 0 \\ 0 & 0 & 0.4 & 0.5 \end{bmatrix}.$$

(ii) Make a best match between the projection matrices A_1, A_2 and A_3 and population models of

- an age–structured animal;
- a stage–structured plant;
- a stage–structured reptile.

(iii) Show that A_1 models a growing population and that A_2 declines. Does A_3 grow or decline? Note that you do not need to compute eigenvalues.

(iv) Assuming that A is primitive, show that

$$\lim_{t\to\infty} \lambda^{-t} x(t) = \frac{v^T x^0}{v^T w} w \,, \tag{2}$$

and letting $N := \|x\|_1$ so that $N(t) = \sum_{j=1}^n x_j(t)$ for $t \in \mathbb{N}_0$, show also that for $N(0) \neq 0$

$$\frac{\min_i(v_i)}{\max_i(v_i)} \lambda^t \leq \frac{N(t)}{N(0)} \leq \frac{\max_i(v_i)}{\min_i(v_i)} \lambda^t \,, \quad t \in \mathbb{N}_0 \,.$$

(v) The *reactivity* of a nonnegative matrix A (or of the PPM model (1)) is given by $\|A\|_1$.

(a) Convince yourself that the reactivity of A is equal to the largest column sum of A.

(b) Noting that $\lambda \leq \|A\|_1$ (make sure you know why this is true), convince yourself that A can have arbitrarily large reactivity, even when $\lambda < 1$. Give such an example.

(c) For $t \in \mathbb{N}_0$, let $\underline{\rho}_t$ and $\overline{\rho}_t$ denote the minimum and maximum column sum of A^t respectively. Prove that $N := \|x\|_1$, where x is given by (1), satisfies

$$\underline{\rho}_t \|x^0\|_1 \leq N(t) \leq \overline{\rho}_t \|x^0\|_1 \quad t \in \mathbb{N}_0 \,.$$

(d) Reactivity is used in the ecology literature (see, for example, [1, 2, 3]) as a measure of *transient* growth (or decline) of a population. Explain verbally why a large reactivity is indicative of transient growth.

(vi) The *inertia* of the PPM model (1) from $x^0 \neq 0$ is defined as

$$\frac{v^T x^0 \|w\|_1}{v^T w \|x_0\|_1} \,. \tag{3}$$

(a) What is the inertia of (1) from $x^0 = w$?

(b) Using your answer to 2(vi)a and (2), give a verbal explanation of what inertia from x_0 is.

(c) Prove that for any non–zero $x^0 \in \mathbb{R}^n_+$,

$$\frac{\min_i(v_i)}{v^T w} \leq \frac{v^T x^0 \|w\|_1}{v^T w \|x_0\|_1} \leq \frac{\max_i(v_i)}{v^T w} \,, \tag{4}$$

and that the bounds in (4) are attained for certain x^0 that you should determine.

(d) Use (2) and (4) to verify that if w is normalised so that $\|w\|_1 = 1$ then for any non–zero $x_0 \in \mathbb{R}^n_+$

$$\frac{\min_i(v_i)}{v^T w} \leq \lim_{t\to\infty} \frac{\lambda^{-t} N(t)}{N(0)} \leq \frac{\max_i(v_i)}{v^T w} \,.$$

(3) **Leslie matrices:** For $N \in \mathbb{N}$, consider a general, age–structured Leslie [4] matrix

$$L = \begin{pmatrix} f_1 & f_2 & \dots & f_{N-1} & f_N \\ s_1 & 0 & \dots & 0 & 0 \\ 0 & \ddots & 0 & \dots & 0 \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ 0 & \dots & \dots & s_{N-1} & 0 \end{pmatrix} \,, \tag{5}$$

where $0 \leq f_i$ for all $i \in \{1, 2, \dots, N\}$ and $0 \leq s_j \leq 1$ for all $j \in \{1, 2, \dots, N-1\}$.

(i) Describe in words the biological interpretation of the f_i and s_j.

(ii) Prove that L is irreducible if, and only if,

$$f_N > 0 \quad \text{and} \quad \forall\, j \in \{1, 2, \ldots, N-1\}, \quad s_j > 0\,. \tag{6}$$

(iii) Show that condition (6) is *not* sufficient for L to be primitive in general. Find a sufficient condition on the f_i of a Leslie matrix that ensures that L is primitive.

(iv) Suppose that at least one of the f_i are positive. As a componentwise nonnegative matrix, a Leslie matrix always has a nonnegative eigenvalue λ.

  (a) Use the Perron–Frobenius Theorem to show that λ is in fact positive.

  (b) Demonstrate that there is a corresponding (right) eigenvector that is strictly positive. [Hint: Try an eigenvector w with $w_N = 1$].

  (c) What are the eigenvalues of L if $f_i = 0$ for every $i \in \{1, 2, \ldots, N\}$? You do not need to compute them.

(v) Assuming that L has a positive eigenvalue λ, show that $\lambda > 1$ if, and only if,

$$R := f_1 + f_2 s_1 + f_3 s_1 s_2 + \ldots + f_N s_1 \ldots s_{N-1} > 1\,. \tag{7}$$

What is the biological interpretation of R?

(vi) Most matrix PPMs are irreducible and primitive [5]. Do you think that these are reasonable assumptions? Describe some of the problems faced when either of these assumptions fail to hold.

(4) **Perturbations– theory:** Throughout this question we consider $A \in \mathbb{R}^{n\times n}$ for $n \in \mathbb{N}$ (generally specifying a matrix projection model (1), so that additionally $A \in \mathbb{R}_+^{n\times n}$).

By perturbation theory we mean studying the effect of (usually "small") changes on the entries of A on some property of A (or of (1)), such as the spectral radius, here denoted by λ throughout.

An approach to perturbation theory prevalent in the existing ecology literature is to consider the *sensitivity* [6] of λ to small changes in A. By considering "small" changes $A \mapsto A + \delta A$ we seek formulae for the resulting small change $\delta\lambda$ in $\lambda \mapsto \lambda + \delta\lambda$.

(i) For primitive $A \in \mathbb{R}_+^{n\times n}$ with (simple) left and right eigenvectors v^T and w corresponding to λ respectively, show that

$$\frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{v^T w}\,, \quad \forall\, i, j \in \{1, 2, \ldots, n\}\,, \tag{8}$$

for each non–zero a_{ij}. Hence, by appealing to the chain rule, demonstrate that if a perturbation p simultaneously affects several vital rates a_{ij}, $(i, j) \in \mathcal{S}$ then the resulting sensitivity is

$$\frac{\partial \lambda}{\partial p} = \sum_{(i,j)\in\mathcal{S}} \frac{\partial \lambda}{\partial a_{ij}} \cdot \frac{\partial p}{\partial a_{ij}}$$

To accommodate for large variations in the relative sizes of λ or a_{ij}, *elasticities* [7] are sometimes used, which are given by

$$\frac{\partial \ln \lambda}{\partial \ln a_{ij}} = \frac{a_{ij}}{\lambda} \cdot \frac{\partial \lambda}{\partial a_{ij}}\,, \quad \forall\, i, j \in \{1, 2, \ldots, n\}\,. \tag{9}$$

Sensitivity or elasticity analyses are often used in the ecology and population management literature to guide or even direct conservation efforts. Examples include, but are by no means restricted to, [8]–[12].

(ii) What are the crucial assumptions used in deriving (8)? Why do you think that we believe that sensitivity and elasticity calculations should be used with caution?

A more analytic approach to perturbation theory uses structured perturbations of the form

$$A_\Delta := A + E\Delta F\,, \tag{10}$$

for $E \in \mathbb{R}^{n\times m}$, $F \in \mathbb{R}^{p\times n}$ and $\Delta \in \mathbb{R}^{m\times p}$ for some $m, p \in \mathbb{N}$. To determine the effect of the perturbation $E\Delta F$ on the spectral radius (that is, on stability) the crucial object is the (complex) *stability radius* $r(A; D, E)$ introduced, for continuous time systems, by Hinrichsen & Pritchard [13, 14]. Assuming that $r(A) < 1$, then

$$r(A; E, F) := \inf\{\|\Delta\|_2 \;:\; \Delta \in \mathbb{C}^{m\times p}\,,\; r(A + E\Delta F) = 1\}\,. \tag{11}$$

The complex stability radius admits the following characterisation:

$$r(A; E, F) = \begin{cases} \dfrac{1}{\|G\|_\infty}, & \|G\|_\infty > 0\,, \\ \infty, & \|G\|_\infty = 0\,, \end{cases} \quad \text{where} \quad s \mapsto G(s) := F(sI - A)^{-1}E\,, \tag{12}$$

(which you may derive for yourself if you wish). We first consider rank–one perturbations:

(iii) In the case that $A \in \mathbb{R}^{n\times n}_+$ and $E, F^T \in \mathbb{R}^n$ prove that

(a) for every $r > \lambda$, $r \in \rho(A)$ and $(rI - A)^{-1} \geq 0$ (that is, is componentwise nonnegative).

(b) if $E, F^T \in \mathbb{R}^n_+$ then $\|G\|_\infty = G(1)$, where G is as in (12),

(c) if A is irreducible or there exists $\rho > 0$ such that $A + \rho EF^T$ is irreducible then $G(1) > 0$.

(iv) Prove the following theorem from [15]: Suppose that $A \in \mathbb{R}^{n\times n}$ is a componentwise nonnegative, primitive matrix that can be written $A = A_0 + de^T$ where $A_0^{n\times n}$ is componentwise nonnegative and $d, e \in \mathbb{R}^n$ and at least one of them is nonnegative. If $\lambda > r(A_0)$ is an eigenvalue of A, then $\lambda = r(A)$.

(v) How does the above theorem allow us to describe the rank–one perturbations that give rise to $r(A) = 1$?

We now consider so–called multi–rank and multi–parameter perturbations:

(vi) Prove that $\mu \in \mathbb{C}$, $\mu \notin \sigma(A)$ satisfies $\mu \in \sigma(A_\Delta)$ if, and only if,

$$1 \in \sigma(G(\mu)\Delta)\,. \tag{13}$$

Simplify condition (13) if $G(\mu)\Delta$ is a scalar. In the case that $A_\Delta \in \mathbb{R}^{n\times n}_+$ is primitive, and $\mu > 0$ is its dominant eigenvalue, write down the eigenvectors of A_Δ corresponding to μ.

(vii) Consider the life–cycle graph in Figure 1(a). Write down the structured perturbation $E\Delta F$ that give rise to the perturbations in Figure 1(b) and 1(c) and factorise these into E, Δ and F so that only Δ depends on p or p_1 and p_2.

(viii) Given a Leslie matrix L as in (5) of size $N \in \mathbb{N}$,

(a) write down a rank–one, multi–parameter perturbation that perturbs every fecundity f_i by a parameter p_i. Factorise such a perturbation into $E\Delta F$.

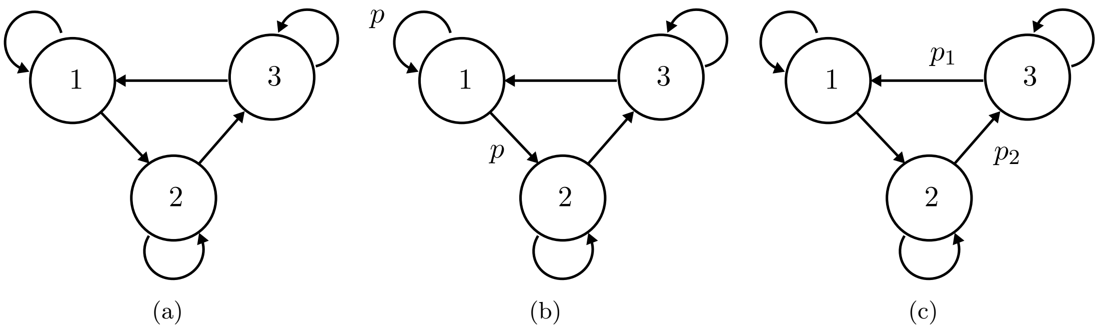

Figure 1: Three stage life–cycle with perturbations

(b) write down a multi–rank, one parameter perturbation that perturbs every survival rate s_i by a parameter p. Factorise such a perturbation into $E\Delta F$. What is the (minimal) rank of such a perturbation?

(5) **Perturbations– examples:** Here we apply the theory explored in question (4) to some worked examples.

(i) Consider the matrix PPM (1) with

$$A = \begin{bmatrix} 0.5 & 1.25 & 0.5 & 1.5 \\ 0.125 & 0 & 0 & 0 \\ 0 & 0.25 & 0 & 0 \\ 0 & 0 & 0.125 & 0 \end{bmatrix}.$$

(a) Find λ, v, w of A and $(I - A)^{-1}$.

(b) For each non–zero a_{ij}, compute the sensitivities as in (8) to **linearly extrapolate** the change in a_{ij}, δa_{ij} say, needed to achieve a perturbed dominant eigenvalue $\lambda_\delta := \lambda + \delta\lambda = 1$.

(c) Use the results of (4vi) and (4iv) to find the actual δa_{ij} needed to make $\lambda_\delta = 1$.

(d) For fecundities $a_{11}, a_{12}, a_{13}, a_{14}$ increased to $a_{11} + \delta a_{11}, a_{12} + \delta a_{12}, a_{13} + \delta a_{13}, a_{14} + \delta a_{14}$, find

$$(\delta a_{11}, \delta a_{12}, \delta a_{13}, \delta a_{14})$$

which results in $\lambda_\delta = 1$ and which minimises

$$\delta a_{11} + \delta a_{12} + \delta a_{13} + \delta a_{14}.$$

(ii) This question is about using perturbations to rank **managed conservation strategies**. A projection matrix for an endangered Blue Whale population is given by:

$$A = \begin{bmatrix} 0 & 0 & 0.50 & 0.50 & 0.75 & 0.75 & 0.40 \\ 0.69 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.67 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.65 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.65 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.70 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.60 & 0.72 \end{bmatrix}. \tag{14}$$

Transition rate	Sensitivity	Sensitivity–Predicted p	Actual p
a_{13}			
a_{14}			
a_{15}			
a_{16}			
a_{17}			
a_{21}			
a_{32}			
a_{43}			
a_{54}			
a_{65}			
a_{76}			
a_{77}			

Table 1: Whale perturbations

(a) Find the dominant eigenvalue λ and so verify that the PPM (1) with A given by (14) is indeed in asymptotic decline. Compute the stable stage structure w and reproductive value v of A (normalised so that each have first components equal to 1).

(b) We want to manipulate transition rates by increasing one a_{ij} by an amount p so that the geometric growth rate is equal to 1, i.e. **managed conservation** overcomes population decline.

(c) Compute $(I - A)^{-1}$ and the matrix of sensitivities S (with entries given by (8)).

(d) Complete Table 1.

Use the information gathered in the table to discuss appropriate conservation recommendations based on (i) *Sensitivity Calculations* (ii) *Actual Perturbations*.

In your discussion, refer to the three transitions as predicted to be most effective targets for conservation effort, and the three transitions as predicted to be least effective.

The techniques used in this question might be relevant for your group project.

References

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