

Similarity of General Population Matrices and Pseudo-Leslie Matrices

João F. Alves and Henrique M. Oliveira*

Center of Mathematical Analysis, Geometry and Dynamical Systems, Departamento de Matemática, Instituto Superior Técnico, Universidade de Lisboa, Av. Rovisco Pais, 1049-001 Lisbon, Portugal

Received: 5 Jan. 2015, Revised: 6 Apr. 2015, Accepted: 7 Apr. 2015

Published online: 1 Sep. 2015

Abstract: A similarity transformation is obtained between general population matrices models of the Usher or Lefkovitch types and a simpler model, the pseudo-Leslie model. The pseudo Leslie model is a matrix that can be decomposed in a row matrix, which is not necessarily non-negative and a subdiagonal positive matrix. This technique has computational advantages, since the solutions of the iterative problem using Leslie matrices are readily obtained. In the case of two age structured population models, one Lefkovitch and another Leslie, the Kolmogorov-Sinai entropies are different, despite the same growth ratio of both models. We prove that Markov matrices associated to similar population matrices are similar.

Keywords: Population dynamics, Leslie matrix, Lefkovitch matrix, Kolmogorov Sinai entropy, Markov matrices.

AMS Classif.: 37N25, 15A21, 92D25

This paper is dedicated to the memory of Professor José Sousa Ramos.

1 Introduction

This article deals with classic discrete structured models for linear population dynamics [2, 8] such as Leslie matrices and Lefkovitch or Usher matrices. Given A , a non negative $n \times n$ matrix and a population vector \mathbf{x}_k which components are the fractions of the population at each age or stage, the dynamical system that gives the population vector at any positive time $k + 1$ is given by

$$\mathbf{x}_{k+1} = A\mathbf{x}_k, \text{ with initial condition } \mathbf{x}_0.$$

Obviously the solution is given by the powers of A

$$\mathbf{x}_k = A^k \mathbf{x}_0.$$

In this paper we prove that there is a similarity transform that converts the complicated dynamics of the so called Usher or Lefkovitch matrices to the simpler study of matrices which are Leslie matrices or pseudo-Leslie matrices, a concept that we introduce in this paper.

The paper is organized in three sections, in the second we introduce pseudo-Leslie matrices and prove the main theorem. In the third section we present some consequences of interest in population dynamics, namely on the similarity of Markov matrices associated to similar population dynamics matrices and obtain transformation rules for corresponding stationary distributions.

2 Main theorem

In age structured population dynamics one divides the population in classes [2, 7]. When we consider size classes or stage classes instead of pure age classes we have a structured population model with dynamics given by the linear equation

$$\mathbf{x}_{n+1} = \mathcal{L}\mathbf{x}_n, \quad (1)$$

where \mathbf{x}_n is a non negative structured absolute population vector, or a proportion of individuals in each class and \mathcal{L}

* Corresponding author e-mail: holiv@math.tecnico.ulisboa.pt

is a matrix such that

$$\mathcal{L} = \begin{bmatrix} f_1 & f_2 & f_3 & \cdots & f_{n-1} & f_n \\ b_1 & c_1 & 0 & \cdots & 0 & 0 \\ 0 & b_2 & c_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & c_{n-2} & 0 \\ 0 & 0 & 0 & \cdots & b_{n-1} & c_{n-1} \end{bmatrix},$$

usually called Usher (in the classic reference [2]) or Lefkovitch matrix in [7]. The coefficient f_j is called the fertility rate of class $j > 1$, the coefficient $b_k > 0$, for any $k = 1, \dots, n - 1$, is the transition rate from class $k - 1$ to class k and the c_l the rate of individuals that remain in class l . Along this paper we assume that $f_n > 0$, assuring that \mathcal{L} is irreducible [2].

The coefficient f_1 can be decomposed in $\hat{f}_1 + c_0$, i.e., a fertility rate and a permanency rate. Since this decomposition has no influence on the similarity transformation we do not split f_1 . One must keep in mind the biological meaning of this coefficient.

The solution of the problem is given by the powers of \mathcal{L} , given the non-negative initial condition \mathbf{x}_0

$$\mathbf{x}_n = \mathcal{L}^n \mathbf{x}_0.$$

A Leslie matrix is a matrix of the type

$$L = \begin{bmatrix} \phi_1 & \phi_2 & \cdots & \phi_{n-1} & \phi_n \\ b_1 & 0 & \cdots & 0 & 0 \\ 0 & b_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & b_{n-1} & 0 \end{bmatrix},$$

where all the entries ϕ_j are non-negative and all b_j are strictly positive. The Leslie matrix can be decomposed in two matrices

$$L = R + B,$$

where

$$R = \begin{bmatrix} \phi_1 & \phi_2 & \cdots & \phi_{n-1} & \phi_n \\ 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & 0 \end{bmatrix} \text{ and } B = \begin{bmatrix} 0 & 0 & \cdots & 0 & 0 \\ b_1 & 0 & \cdots & 0 & 0 \\ 0 & b_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & b_{n-1} & 0 \end{bmatrix}.$$

When the entries ϕ_n of the first row of R are real numbers, not restricted to the non-negative case, we say that L is a pseudo-Leslie matrix. Obviously this class of matrix does not have an immediate biological correspondence when some of its entries are negative. That poses no problem in the framework of this article, since L is merely used as a computational instrument.

To state the main theorem we define the sums of products of p factors Γ_i^p , where $i = 1, \dots, n$ denotes the row index of a given $n \times n$ Lefkovitch matrix \mathcal{L}

$$\Gamma_i^p =$$

$$\begin{cases} (-1)^p \sum_{n-1 \geq i_p > \cdots > i_2 > i_1 \geq i} c_{i_1} c_{i_2} \cdots c_{i_p} & \text{if } 0 < p \leq n - i \\ 1 & \text{if } p = 0 \\ 0 & \text{if } n - i < p \end{cases}.$$

For the products of the transition rates b_1, \dots, b_{n-1} of \mathcal{L} we use the notation

$$\Lambda_i^j = \begin{cases} \prod_{k=i}^j b_k & \text{if } i \leq j \leq n - 1 \\ 1 & \text{if } j = i - 1 \end{cases}.$$

Now we introduce an upper triangular matrix S and a pseudo-Leslie matrix L defined by

$$S = \begin{bmatrix} 1 & s_{1,2} & s_{1,3} & \cdots & s_{1,n-1} & s_{1,n} \\ 0 & 1 & s_{2,3} & \cdots & s_{2,n-1} & s_{2,n} \\ 0 & 0 & 1 & \cdots & s_{3,n-1} & s_{3,n} \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & 1 & s_{n-1,n} \\ 0 & 0 & 0 & \cdots & 0 & 1 \end{bmatrix},$$

with

$$s_{i,j} = \frac{\Gamma_i^{j-i}}{\Lambda_i^{j-1}}, \text{ for } j \geq i$$

and

$$L = \begin{bmatrix} \phi_1 & \phi_2 & \phi_3 & \cdots & \phi_{n-1} & \phi_n \\ b_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & b_2 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & \cdots & b_{n-1} & 0 \end{bmatrix},$$

with

$$\phi_j = -\frac{\Gamma_1^j}{\Lambda_1^{j-1}} + \sum_{k=1}^j \frac{\Gamma_k^{j-k}}{\Lambda_k^{j-1}} f_k, \text{ for } j = 1, \dots, n.$$

We are now in position to state the main result of this work.

Theorem 1. For any Lefkovitch matrix, \mathcal{L} , one has $S^{-1} \mathcal{L} S = L$ where S and L are the matrices defined above.

The following lemma is used in the proof of theorem 1.

Lemma 1. If \mathcal{L} is a $n \times n$ Lefkovitch matrix, then $\Gamma_i^{p+1} = c_{i-1} \Gamma_i^p + \Gamma_{i-1}^{p+1}$, for all $p \geq 0$ and $n \geq i > 1$.

Proof. As $\Gamma_i^0 = 1$, $\Gamma_i^1 - \Gamma_{i-1}^1 = c_{i-1}$ and $\Gamma_i^p = \Gamma_i^{p+1} - \Gamma_{i-1}^{p+1} = 0$ for $p > n - i$, the proof is obvious for $p = 0$ or $p > n - i$. So we may assume $0 < p \leq n - i$.

If $0 < p < n - i$, then

$$\begin{aligned} \Gamma_{i-1}^{p+1} &= (-1)^{p+1} \sum_{n-1 \geq i_{p+1} > \dots > i_2 > i_1 \geq i-1} c_{i_1} c_{i_2} \dots c_{i_{p+1}} \\ &= (-1)^{p+1} \sum_{n-1 \geq i_{p+1} > \dots > i_2 > i_1 \geq i} c_{i_1} c_{i_2} \dots c_{i_{p+1}} \\ &\quad - (-1)^p \sum_{n-1 \geq i_{p+1} > \dots > i_2 \geq i} c_{i-1} c_{i_2} \dots c_{i_{p+1}} \\ &= \Gamma_i^{p+1} - c_{i-1} \Gamma_i^p. \end{aligned}$$

Finally, assume that $0 < p = n - i$. In this case, as $\Gamma_i^{p+1} = 0$, one gets

$$\begin{aligned} c_{i-1} \Gamma_i^p + \Gamma_{i-1}^{p+1} &= \\ &= c_{i-1} (-1)^p c_i c_{i+1} \dots c_{n-1} + (-1)^{p+1} c_{i-1} c_i \dots c_{n-1} \\ &= 0 = \Gamma_i^{p+1}. \square \end{aligned}$$

We are now in position to prove the main result.

Proof of theorem 1. In order to prove the equality $\mathcal{L}S = SL$, we begin by computing SL . As $s_{i,i} = 1$ and $s_{i,j} = 0$ for $i > j$, one has

$$\begin{aligned} (SL)_{i,j} &= \begin{cases} s_{i,1} \phi_n & \text{if } j = n \\ s_{i,1} \phi_j + s_{i,j+1} b_j & \text{if } j < n \end{cases} \\ &= \begin{cases} \phi_n & \text{if } i = 1, j = n \\ \phi_j + s_{1,j+1} b_j & \text{if } i = 1, j < n \\ b_j & \text{if } i = j + 1 \\ s_{i,j+1} b_j & \text{if } n > j \geq i > 1 \\ 0 & \text{otherwise} \end{cases}. \end{aligned}$$

As $\Gamma_1^n = 0$ and $\Lambda_1^j = \Lambda_1^{j-1} b_j$ one has

$$\begin{aligned} \phi_n &= -\frac{\Gamma_1^n}{\Lambda_1^{n-1}} + \sum_{k=1}^n \frac{\Gamma_k^{n-k}}{\Lambda_k^{n-1}} f_k \\ &= \sum_{k=1}^n \frac{\Gamma_k^{n-k}}{\Lambda_k^{n-1}} f_k, \end{aligned}$$

and

$$\begin{aligned} \phi_j + s_{1,j+1} b_j &= -\frac{\Gamma_1^j}{\Lambda_1^{j-1}} + \sum_{k=1}^j \frac{\Gamma_k^{j-k}}{\Lambda_k^{j-1}} f_k + \frac{\Gamma_1^j}{\Lambda_1^j} b_j \\ &= -\frac{\Gamma_1^j}{\Lambda_1^{j-1}} + \sum_{k=1}^j \frac{\Gamma_k^{j-k}}{\Lambda_k^{j-1}} f_k + \frac{\Gamma_1^j}{\Lambda_1^{j-1}} \\ &= \sum_{k=1}^j \frac{\Gamma_k^{j-k}}{\Lambda_k^{j-1}} f_k, \text{ for } j < n, \end{aligned}$$

finally we get

$$s_{i,j+1} b_j = \frac{\Gamma_i^{j+1-i}}{\Lambda_i^j} b_j = \frac{\Gamma_i^{j+1-i}}{\Lambda_i^{j-1}}, \text{ for } n > j \geq i.$$

Thus, we may write

$$(SL)_{i,j} = \begin{cases} \sum_{k=1}^j \frac{\Gamma_k^{j-k}}{\Lambda_k^{j-1}} f_k & \text{if } i = 1 \\ b_j & \text{if } i = j + 1 \\ \frac{\Gamma_i^{j+1-i}}{\Lambda_i^{j-1}} & \text{if } n > j \geq i > 1 \\ 0 & \text{otherwise} \end{cases}.$$

Notice that since $\Gamma_i^{n+1-i} = 0$ for all i , we finally arrive at

$$(SL)_{i,j} = \begin{cases} \sum_{k=1}^j \frac{\Gamma_k^{j-k}}{\Lambda_k^{j-1}} f_k & \text{if } i = 1 \\ b_j & \text{if } i = j + 1 \\ \frac{\Gamma_i^{j+1-i}}{\Lambda_i^{j-1}} & \text{if } j \geq i > 1 \\ 0 & \text{otherwise} \end{cases}. \quad (2)$$

Next we compute $\mathcal{L}S$. As $s_{i,i} = 1$ and $s_{i,j} = 0$ for $i > j$, one has

$$\begin{aligned} (\mathcal{L}S)_{i,j} &= \begin{cases} \sum_{k=1}^n s_{k,j} f_k & \text{if } i = 1 \\ b_{i-1} s_{i-1,j} + c_{i-1} s_{i,j} & \text{if } i > 1 \end{cases} \\ &= \begin{cases} \sum_{k=1}^j s_{k,j} f_k & \text{if } i = 1 \\ b_j & \text{if } i = j + 1 \\ b_{i-1} s_{i-1,j} + c_{i-1} s_{i,j} & \text{if } j \geq i > 1 \\ 0 & \text{otherwise} \end{cases} \\ &= \begin{cases} \sum_{k=1}^j \frac{\Gamma_k^{j-k}}{\Lambda_k^{j-1}} f_k & \text{if } i = 1 \\ b_j & \text{if } i = j + 1 \\ b_{i-1} \frac{\Gamma_{i-1}^{j-i+1}}{\Lambda_{i-1}^{j-1}} + c_{i-1} \frac{\Gamma_i^{j-i}}{\Lambda_i^{j-1}} & \text{if } j \geq i > 1 \\ 0 & \text{otherwise} \end{cases}. \end{aligned}$$

As $\Lambda_{i-1}^{j-1} = b_{i-1} \Lambda_i^{j-1}$ for $j \geq i > 1$, one has

$$\begin{aligned} b_{i-1} \frac{\Gamma_{i-1}^{j-i+1}}{\Lambda_{i-1}^{j-1}} + c_{i-1} \frac{\Gamma_i^{j-i}}{\Lambda_i^{j-1}} &= \frac{\Gamma_{i-1}^{j-i+1}}{\Lambda_i^{j-1}} + c_{i-1} \frac{\Gamma_i^{j-i}}{\Lambda_i^{j-1}} \\ &= \frac{\Gamma_{i-1}^{j-i+1} + c_{i-1} \Gamma_i^{j-i}}{\Lambda_i^{j-1}} \end{aligned}$$

and consequently

$$(\mathcal{L}S)_{i,j} = \begin{cases} \sum_{k=1}^j \frac{\Gamma_k^{j-k}}{\Lambda_k^{j-1}} f_k & \text{if } i = 1 \\ b_j & \text{if } i = j + 1 \\ \frac{\Gamma_{i-1}^{j-i+1} + c_{i-1} \Gamma_i^{j-i}}{\Lambda_i^{j-1}} & \text{if } j \geq i > 1 \\ 0 & \text{otherwise} \end{cases}. \quad (3)$$

Now, using lemma 1 we see that (2) and (3) are the same, which completes the proof. \square

The dynamical system (1) can be solved using the easily computable powers of L

$$\mathbf{x}_n = \mathcal{L}^n \mathbf{x}_0 = S^{-1} L^n S \mathbf{x}_0.$$

Since \mathcal{L} and L are similar, they share the same spectrum and the Perron-Frobenius Theorem still holds for L in what concerns the existence of a simple dominant positive eigenvalue. Using a generating function and formal power series obtained in [1] or the classic Jordan canonical form, it is always possible to obtain the powers of L . The eigenvectors of \mathcal{L} will be studied in the next section.

3 Sinai Kolmogorov entropy, Markov matrices and stationary distributions

In this section, using a simple example, we show that the Kolmogorov-Sinai entropy [3,4,5,6] is not an algebraic invariant. We also establish that two Markov matrices associated [6] to population dynamics similar matrices¹ are similar. Finally, we establish a transformation rule for the two stationary distributions of Markov matrices associated with two similar population matrices.

Given two matrices, one of Lefkovitch type and the other of Leslie type², with the same growth rate, they can have different Sinai-Kolmogorov entropies as we see in the following example.

Example 1. Let

$$\mathcal{L} = \begin{bmatrix} 1 & 3 \\ 0.4 & 0.55 \end{bmatrix},$$

we have the similarity matrix

$$S = \begin{bmatrix} 1 & -1.375 \\ 0 & 1 \end{bmatrix},$$

and a Leslie matrix L similar to \mathcal{L} , which is

$$L = \begin{bmatrix} 1.55 & 1.625 \\ 0.4 & 0 \end{bmatrix}.$$

The Perron-Frobenius dominant eigenvalue is $\lambda = 1.89331$ both for L and \mathcal{L} . The Markov matrix P^A [6], corresponding to a population matrix A is obtained using the relations

$$p_{ij}^A = \frac{a_{ij} u_j}{\lambda u_i},$$

where λ is the dominant eigenvalue of A , and the column vector $\mathbf{u} = (u_i)_{i=1,\dots,n} > 0$ is the Perron-Frobenius right eigenvector of A . (The left eigenvector will be called the line vector $\mathbf{v} = (v_i)_{i=1,\dots,n}^T$). For the Lefkovitch matrix \mathcal{L} we get the associated Markov matrix

$$P^{\mathcal{L}} = \begin{bmatrix} 0.528175 & 0.471825 \\ 0.709504 & 0.290496 \end{bmatrix},$$

the stationary distribution of $P^{\mathcal{L}}$ is $\pi^{\mathcal{L}} = [0.600598 \ 0.399402]$. The population Sinai-Kolmogorov entropy [6] is

$$H_{\mathcal{L}} = - \sum_{i,j} \pi_i^{\mathcal{L}} p_{ij}^{\mathcal{L}} \log p_{ij}^{\mathcal{L}},$$

where $p_{ij}^{\mathcal{L}}$ are the entries of $P^{\mathcal{L}}$ and $\pi_i^{\mathcal{L}}$ are the components of the stationary distribution $\pi^{\mathcal{L}}$ of $P^{\mathcal{L}}$ (the left eigenvector associated with the Perron-Frobenius eigenvalue 1 of $P^{\mathcal{L}}$, such that $\pi^{\mathcal{L}} P^{\mathcal{L}} = \pi^{\mathcal{L}}$). Doing the same computation for L we have

$$H_L = - \sum_{i,j} \pi_i^L p_{ij}^L \log p_{ij}^L,$$

where P^L is the matrix with entries p_{ij}^L , the Markov matrix associated to L is

$$P^L = \begin{bmatrix} 0.818671 & 0.181329 \\ 1 & 0 \end{bmatrix}.$$

The stationary distribution of P^L is $\pi^L = [0.846504 \ 0.153496]$ and the entropies of \mathcal{L} and L are different, respectively $H_{\mathcal{L}} = 0.656027$ and $H_L = 0.400738$.

The Markov matrices P^L and $P^{\mathcal{L}}$ associated to L and \mathcal{L} are also similar, with the same eigenvalues as we will see below. This result can be stated in the general context of similar matrices³ under the following hypothesis, which are assumed until the end of the paper:

1. \mathcal{L} is non-negative and irreducible, therefore has the dominant eigenvalue λ , and associated left and right positive eigenvectors \mathbf{t} and \mathbf{w} , respectively.
2. L and \mathcal{L} are similar, related by the invertible similarity matrix S , such that $\mathcal{L}S = SL$.
3. L , not necessarily non-negative, has right and left eigenvectors, respectively \mathbf{u} and \mathbf{v} , associated to λ with all entries positive.

The right eigenvector of L associated to the dominant eigenvalue λ

$$L\mathbf{u} = \lambda \mathbf{u}$$

is related to the right eigenvector \mathbf{w} of \mathcal{L} by the transformation rule $\mathbf{w} = S\mathbf{u}$, since

$$\mathcal{L}S\mathbf{u} = \lambda S\mathbf{u} \Leftrightarrow \mathcal{L}\mathbf{w} = \lambda \mathbf{w}.$$

The same happens for the left eigenvector \mathbf{v} of L

$$\mathbf{v}L = \lambda \mathbf{v}$$

and the left eigenvector $\mathbf{t} = \mathbf{v}S^{-1}$ of \mathcal{L} , since

$$\mathbf{v}S^{-1}\mathcal{L} = \lambda \mathbf{v}S^{-1} \Leftrightarrow \mathbf{t}\mathcal{L} = \lambda \mathbf{t}.$$

³ Not necessarily Lefkovitch, Usher or Leslie matrices.

¹ Under very general conditions.
² We consider a true non-negative Leslie matrix to establish this conclusion.

The Markov matrix associated with L [6] is given by its entries

$$p_{ij}^L = \frac{L_{ij} u_j}{\lambda u_i}.$$

On the other hand, the Markov matrix associated with \mathcal{L} is given by

$$p_{ij}^{\mathcal{L}} = \frac{\mathcal{L}_{ij} w_j}{\lambda w_i}.$$

The stationary distribution [6] of P^L is

$$\pi^L = \frac{[v_1 u_1 \ v_2 u_2 \ \dots \ v_n u_n]}{\mathbf{v}\mathbf{u}},$$

where $\mathbf{v}\mathbf{u}$ is a compact notation for the inner product of the line vector \mathbf{v} and the column vector \mathbf{u} . The stationary distribution of \mathcal{L} is

$$\pi^{\mathcal{L}} = \frac{[t_1 w_1 \ t_2 w_2 \ \dots \ t_n w_n]}{\mathbf{t}\mathbf{w}}.$$

It is possible to prove that the Markov matrices P^L and $P^{\mathcal{L}}$ are similar.

Proposition 1. P^L and $P^{\mathcal{L}}$ are similar if L and \mathcal{L} are similar.

Proof. One defines the square matrices U and W such that

$$U = \begin{bmatrix} u_1 & & & \\ & u_2 & & \\ & & \ddots & \\ & & & u_n \end{bmatrix}, \quad W = \begin{bmatrix} w_1 & & & \\ & w_2 & & \\ & & \ddots & \\ & & & w_n \end{bmatrix}$$

with all $u_i \neq 0$ and $w_i \neq 0$, the inverses of U and W are

$$U^{-1} = \begin{bmatrix} \frac{1}{u_1} & & & \\ & \frac{1}{u_2} & & \\ & & \ddots & \\ & & & \frac{1}{u_n} \end{bmatrix}, \quad W^{-1} = \begin{bmatrix} \frac{1}{w_1} & & & \\ & \frac{1}{w_2} & & \\ & & \ddots & \\ & & & \frac{1}{w_n} \end{bmatrix}.$$

With this notation consider the transformations

$$P^L = \frac{1}{\lambda} U^{-1} L U \quad \text{and} \quad P^{\mathcal{L}} = \frac{1}{\lambda} W^{-1} \mathcal{L} W,$$

where $\lambda \neq 0$.

Now, it is straightforward to prove that P^L and $P^{\mathcal{L}}$ are similar

$$P^{\mathcal{L}} = \frac{1}{\lambda} W^{-1} \mathcal{L} W = \frac{1}{\lambda} W^{-1} S L S^{-1} W.$$

On the other hand

$$P^L = \frac{1}{\lambda} U^{-1} L U.$$

Therefore, λQ and λP are similar, since both are similar to L . Explicitly

$$L = \lambda S^{-1} W P^{\mathcal{L}} W^{-1} S = \lambda U P^L U^{-1}$$

or

$$P^L = U^{-1} S^{-1} W P^{\mathcal{L}} W^{-1} S U, \tag{4}$$

as desired. \square

We can prove that $\pi^{\mathcal{L}}$ is a stationary distribution of $P^{\mathcal{L}}$ [6] using matrix notation.

Proposition 2. The row vector $\pi^{\mathcal{L}}$ is a stationary distribution of $P^{\mathcal{L}}$.

Proof. Using the left eigenvector $\mathbf{t} = [t_1 \ t_2 \ \dots \ t_n]$ of \mathcal{L} , we define a diagonal matrix

$$T = \begin{bmatrix} t_1 & & & \\ & t_2 & & \\ & & \ddots & \\ & & & t_n \end{bmatrix}.$$

We have

$$\begin{aligned} \pi^{\mathcal{L}} P^{\mathcal{L}} &= \frac{1}{\lambda \mathbf{t}\mathbf{w}} [1 \ 1 \ \dots \ 1] T W W^{-1} \mathcal{L} W \\ &= \frac{1}{\lambda \mathbf{t}\mathbf{w}} [t_1 \ t_2 \ \dots \ t_n] \mathcal{L} W, \end{aligned}$$

since \mathbf{t} is a left eigenvector of \mathcal{L} we have

$$\begin{aligned} \pi^{\mathcal{L}} P^{\mathcal{L}} &= \frac{1}{\lambda \mathbf{t}\mathbf{w}} \lambda [t_1 \ t_2 \ \dots \ t_n] W \\ &= \frac{T W}{\mathbf{t}\mathbf{w}} \\ &= \pi^{\mathcal{L}}. \quad \square \end{aligned}$$

Using analogous techniques we obtain the relation between the two stationary distributions of P^L and $P^{\mathcal{L}}$.

Proposition 3. The stationary distributions $\pi^{\mathcal{L}}$ and π^L are related by

$$\pi^L = \pi^{\mathcal{L}} W^{-1} S U$$

Proof. From (4) we have

$$P^L = Z^{-1} P^{\mathcal{L}} Z,$$

where $Z = W^{-1} S U$. In that case the stationary distribution π^L is given by the relationship

$$\pi^L P^L = \pi^L,$$

so

$$\pi^L Z^{-1} P^{\mathcal{L}} Z = \pi^L \iff \pi^L Z^{-1} P^{\mathcal{L}} = \pi^L Z^{-1},$$

which means that

$$\pi^{\mathcal{L}} = \pi^L Z^{-1},$$

as desired. \square

Remark. All the results in this section apply to the case of an irreducible Lefkovitch matrix \mathcal{L} and a similar pseudo-Leslie matrix L , since any matrix of the form

$$L = \begin{bmatrix} \phi_1 & \phi_2 & \cdots & \phi_{n-1} & \phi_n \\ b_1 & 0 & \cdots & 0 & 0 \\ 0 & b_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & b_{n-1} & 0 \end{bmatrix},$$

with positive coefficients b_j and with the dominant eigenvalue λ has the positive right eigenvector

$$\mathbf{u} = \begin{bmatrix} \frac{\Lambda_1^0}{\lambda} \\ \frac{\Lambda_1^1}{\lambda} \\ \frac{\Lambda_1^2}{\lambda^2} \\ \vdots \\ \frac{\Lambda_1^{n-1}}{\lambda^{n-1}} \end{bmatrix} = \begin{bmatrix} 1 \\ \frac{b_1}{\lambda} \\ \frac{b_1 b_2}{\lambda^2} \\ \vdots \\ \frac{b_1 b_2 \cdots b_{n-1}}{\lambda^{n-1}} \end{bmatrix}.$$

The similar Lefkovitch matrix

$$\mathcal{L} = \begin{bmatrix} f_1 & f_2 & f_3 & \cdots & f_{n-1} & f_n \\ b_1 & c_1 & 0 & \cdots & 0 & 0 \\ 0 & b_2 & c_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & c_{n-2} & 0 \\ 0 & 0 & 0 & \cdots & b_{n-1} & c_{n-1} \end{bmatrix}$$

is always irreducible if $f_n > 0$ and all the b_j are positive, [2]. Therefore, similar Lefkovitch and pseudo-Leslie matrices, \mathcal{L} and L , satisfy conditions 1, 2 and 3.

Acknowledgement

The authors were partially funded by FCT/Portugal through project PEst-OE/EEI/LA0009/2013.

References

- [1] Alves, J., Bravo, A., and Oliveira, H. (2014). Population Dynamics with Infinite Leslie Matrices - finite time properties. *Journal of Difference Equations and Applications* 20(14), 1307-1318.
- [2] Cushing, J. M. (1998). An introduction to structured population dynamics (pp. 133-139). Society Industrial and Applied Mathematics.
- [3] Demetrius, L. (1974). Demographic Parameters and Natural Selection. *Proceedings of the National Academy of Sciences* 71, 4645-4747.
- [4] Demetrius, L. (1976). Measures of Variability in Age-Structured Populations. *Journal of Theoretical Biology* 63, 397-404.
- [5] Demetrius, L. (1978). Adaptive Value, Entropy and Survivorship Curves. *Nature* 275, 231-232.

- [6] Demetrius, L. A. (2013). Boltzmann, Darwin and directionality theory. *Physics reports*, 530(1), 1-85.
- [7] Logofet, D. O., and Klochkova, I. N. (2002). Mathematics of the Lefkovitch model: the reproductive potential and asymptotic cycles. *Matematicheskoe Modelirovanie*, 14(10), 116-126. (Russian)
- [8] Pollard, J. H. (1973). *Mathematical models for the growth of human populations* (Vol. 10). Cambridge: Cambridge University Press.



João F. Alves prepared his PhD under the supervision of José Sousa Ramos in discrete dynamical systems. At the present time, he is an auxiliary professor with tenure at Lisbon University, Portugal. He has been publishing in topological dynamical systems, linear algebra and mathematical biology.



Henrique M. Oliveira, prepared his PhD under the supervision of José Sousa Ramos in discrete dynamical systems. At the present time, he is an "auxiliar professor" with tenure at Lisbon University, Portugal. He has been publishing in discrete dynamical systems, bifurcation theory and mathematical biology and supervised PhD and master students on discrete dynamical systems and mathematics of music.