Original Research Article

Averaging the population projection matrices: Heuristics against uncertainty and nonexistence

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ABSTRACT

In matrix population models, the process of population "projection" through a number of time steps is fundamentally multiplicative, hence the arithmetic mean of the consecutive matrices is of doubtful meaning, while the geometric mean quite corresponds to the multiplication principle. The geometric mean of positive numbers does not bear any problem, but that of matrices does. The "population projection matrices" (PPMs) are rather nonnegative than positive, with the allocation of non-zeros that is predetermined by the life cycle graph (LCG) reflecting the development biology of a given species, and this graph is principally incomplete. The average matrix A should logically have the same fixed pattern of zeros as those to be averaged, and this causes the averaging matrix equation to be overdetermined as a system of element-wise algebraic equations for the unknown positive elements. Therefore, the exact solution to the problem of *pattern-geometric* averaging does generally not exist, while the classical (least-squares) approximation leads to a significant error. My heuristic approach to finding a better approximate A for the PPMs in the form of $L = T$(transition) $+ F$(fertility) is to solve the problem in a combined way: the pattern-geometric approximation for the T part and the exact arithmetic mean for F (as population recruitment is an additive process). As a result, the approximation error decreases drastically due to matrix T being always substochastic, while the combined, *TF-averaging*, method turns out efficient even under 'reproductive uncertainty' in data, i.e., for the whole families of feasible matrices F in the sum $L = T + \{F\}$. I illustrate the method of *TF*-averaging with 5 matrices $L(t)$ calibrated for each pair of consecutive years from a 6-year period of observation in a case study of *Eritrichium caucasicum,* a short-lived perennial herbaceous species. The approximate *TF*-average enables gaining the 'age-specific traits from stage-specific models' (Caswell, 2001, p. 116) that are characteristic of the entire period, and I discuss other motivations/advantages for/of pattern-geometric means in matrix population models.

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1. Introduction

The population projection matrix (PPM) is an $n \times n$ nonnegative matrix L that governs the discrete-time dynamics in a single-species population structured into n stage-specific groups. The *stage* is understood in a generalized sense, as any discrete (or discretized) characteristic that can be used to classify the status of individuals in the population (Caswell, 2001), such as *age*, *size*, or *stage* of ontogeny, etc. The *population structure* is then represented by vector $x(t) \in \mathbb{R}^n_+$ whose components are the (absolute or relative) numbers of individuals in the corresponding stage-specific groups at time moment t. These moments are normally associated with consecutive (e.g., annual) censuses of the population and with the basic model equation,

$$x(t+1) = L(t)x(t), \ t = 0, 1, 2, \ldots, \tag{1}$$

where the elements of matrix $L(t)$, or the *vital rates* (Caswell, 2001), depend generally on t and may also depend on the population density or the densities of some status-specific groups.

However, in a growing number of practical applications (MPIDR, 2017), the PPM represents a linear transformation of the vector space. When considered as an operator in a vector space, an $n \times n$ matrix A is called a *projection matrix* if $AA = A$. The meaning of this definition is obvious: once projected to a subspace, any

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Abbreviations: LCG, life cycle graph; PPM, population projection matrix.
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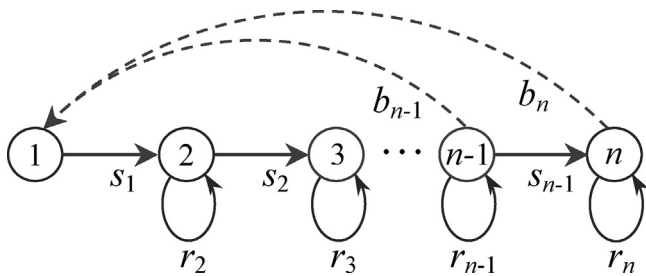*E-mail address:* daniLaL@postman.ru (D.O. Logofet).

Fig. 1. An example of the LCG for a hypothetical stage-structured population with n stages, of which the $(n-1)$-th and the n-th stages are reproductive.

vector $\boldsymbol{x} \in \mathbb{R}^n$ can no longer be changed by the same operator $\boldsymbol{A}$, but this matrix property could hardly be motivated in model (1). Therefore, the "Projection Matrices" in the title are not quite legal, though well-established among the *matrix models* of population dynamics (Caswell, 1989, 2001), following the idea that the matrix "projects" the current population structure for one time step further.

When the knowledge of species biology is expressed as a *life cycle graph* (*LCG*, Caswell, 2001) reflecting the transitions among structural groups that may occur for one time step and the population recruitment that may appear for the same period (Fig. 1), the *pattern* of matrix $\boldsymbol{L}$ (i.e., the allocation of its positive and zero elements) is determined by the LCG as the directed graph associated formally to the matrix (Harary et al., 1965). For example, the LCG in Fig. 1 generates a so-called Lefkovitch (1965) matrix

$$\boldsymbol{L} = \begin{bmatrix} 0 & \cdots & b_{n-1} & b_n \\ s_1 & r_2 & 0 & 0 \\ \vdots & \ddots & \ddots & \vdots \\ 0 & \cdots & s_{n-1} & r_n \end{bmatrix} \tag{2}$$

with positive *survival rates* $s_i > 0$ ($i = 1, 2, \ldots, n-1$) on the first subdiagonal, nonnegative[1] stage *delay rates* $r_j \geq 0$ ($j = 1, 2, \ldots, n$) on the principal diagonal, two positive *reproduction rates* b_{n-1}, $b_n > 0$ in the first row, and zeroes elsewhere. The actual quantitative meanings of these rates follow evidently from Eq. (1) explicated for each vector component (Caswell, 2001, Ch. 4). Other LCGs may generate matrices with more complicated patterns (see, e.g., Logofet, 2008).

When matrix $\boldsymbol{L}(t) = \boldsymbol{L}$ remains constant over time, we obviously have

$$\boldsymbol{x}(t) = \boldsymbol{L}^t \boldsymbol{x}(0) \, \forall \, t = 0, 1, \ldots.$$

Perron–Frobenius theorem for nonnegative matrices, the mathematical ground of matrix population models, provides for the existence of the dominant eigenvalue coincident with the spectral radius, $\lambda_1(\boldsymbol{L}) = \rho(\boldsymbol{L}) > 0$, and guaranteeing, in the primitive case, the convergence

$$\boldsymbol{x}(t)/\lambda_1{}^t \to \boldsymbol{x}^* \text{ as } t \to \infty, \tag{3}$$

where $\boldsymbol{x}^*$ is a corresponding positive eigenvector whose length depends on the initial structure $\boldsymbol{x}(0)$ (Logofet, 1993; Cushing, 1998; Li and Schneider, 2002; Logofet and Belova, 2008). Thus, $\lambda_1(\boldsymbol{L})$ represents the *asymptotic growth rate* of the population, hence, in applications, i.e., whenever $\boldsymbol{L}$ has been calibrated from data, it serves as a *measure* at which the local population is adapted to the environment, or an efficient measuring tool in comparative demography (see, e.g., Klimas et al., 2012; Logofet, 2013b, 2016).

In addition, a number of 'age-specific traits' can be extracted 'from stage-specific models' (Caswell, 2001, p. 116), such as the *life*

expectancy and the mean *age at first reproduction* (Caswell, 2001, Ch. 5), by means of constructing some virtual absorbing Markov chains that can reach certain age-specific events in the life cycle of individuals for random times (random numbers of time steps), while the mean and variance of these random variables are amenable to calculation by known formulae (Kemeny and Snell, 1960), thus resulting in the estimates desired.

However, these age-specific traits, as well as the adaptation measure $\lambda_1(\boldsymbol{L})$, can only be relevant to quite a limited interval of real time, namely, to the period defined by the data used to calibrate the projection matrix $\boldsymbol{L}$. This period may often reduce to just one discrete-time step of the model, e.g., the interval between two consecutive censuses at time moment $t = 0$ and at $t = 1$. The situation is typical for the type of data called 'identified individuals' (Caswell, 2001, p. 134), where the 'individuals are marked and followed over time' (Caswell, 2001, p. 134).

When available is a *time series* of data for several time steps, it is logical to seek for the population characteristics that cover all the period of time. In terms of a matrix population model calibrated on several time steps, it means that we have a finite set of one-step matrices, $\boldsymbol{L}(t)$, each obeying Eq. (1) with the known data $\boldsymbol{x}(t)$, $t = 0$, 1, $\ldots$, $M-1$, where M denotes the final moment in the time series of data. In general terms, we are dealing with a *nonautonomous* matrix model and seeking for the population characteristics averaged over the time series. The nearest way to reveal those expanded characteristics is to extract them from a matrix $\boldsymbol{A}$ that represents an average of the calibrated one-step matrices, and the question is 'What kind of matrix averaging does correspond to the idea of time- averaged characteristics?'

Averaging issues get little attention in the literature on matrix population models, while authors use the *arithmetic mean* by default (Logofet, 2013a) since it poses no problems due to the linearity of matrices as operators in a vector space. In the present paper, I show, first, that the correct answer to the above question is *geometric mean* and, second, that it does typically not exist as an *exact solution* to the system of averaging equations for the PPMs of matrix population models. An *approximate solution* remediates the situation, and I illustrate this in Section 3, where a nonautonomous matrix model of stage-structured dynamics in a local population of a short-lived perennial plant species is reported as a case study. The field data were of the 'identified individuals with uncertain parents' type (Logofet, 2010, p. 33), and the uncertainty in data complicated the task to average five calibrated annual projection matrices $\boldsymbol{L}(t)$. Their own $\lambda_1(\boldsymbol{L})$s were localized differently with regard to 1, thus depriving the model of the ability to forecast the population dynamics in terms of asymptotic increase, steady state, or decline. Averaging has enabled the forecast to be certain as well as a certain answer to 'How specifically short does the short-lived perennial live?' Finally, I discuss more motivations to seek for the geometric mean of the time-specific PPMs.

2. How to average a nonautonomous matrix model

Suppose we have a nonautonomous matrix model for stage-structured population dynamics in the form of Eq. (1), where vector $\boldsymbol{x}(t) \in \mathbb{R}_+^n$ represents the population structure at a discrete time moment $t = 0, 1, \ldots$ If the empirical data are of the 'identified individuals with uncertain parents' type (Logofet, 2010, p. 33), then the vectors $\boldsymbol{x}(t)$ should be known for a finite number $M + 1 \geq 3$ of consecutive moments $t = 0, 1, \ldots, M$ in spite of the 'uncertain parents' (Caswell, 2001, Ch. §6.1.1).

If we have managed to calibrate the matrices $\boldsymbol{L}(t)$ at M those moments, then it follows from Eq. (1) that

$$\boldsymbol{x}(M) = \boldsymbol{L}(M-1)\boldsymbol{L}(M-2) \ldots \boldsymbol{L}(1)\boldsymbol{L}(0)\boldsymbol{x}(0) \tag{4}$$

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[1] Shown is the case where $r_1 = 0$ and all the rest $r_j > 0$.