



# Aggregation may or may not eliminate reproductive uncertainty



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## ARTICLE INFO

### Article history:

Received 10 April 2017

Received in revised form 5 August 2017

Accepted 7 August 2017

Available online 20 September 2017

### Keywords:

Discrete-structured population

Life cycle graph

Matrix population model

Dominant eigenvalue

Reproductive uncertainty

Generative stages

Aggregation

Frobenius theorem

## ABSTRACT

In matrix population models, there cannot be any ‘reproductive uncertainty’ when the life cycle graph contains only one reproductive stage. Otherwise, it is logical to expect that aggregating all the reproductive stages into a single one would exclude the very basis of uncertainty. However, can the aggregation change principally the model characteristics such as the dominant eigenvalue  $\lambda_1$  of the projection matrix, thus signifying the aggregation failure? I demonstrate that it can with the data mined in a case study on the dynamics of a local stage-structured population of *Eritrichium caucasicum*, a short-lived perennial plant species inhabiting an alpine lichen heath. Frobenius Theorem for nonnegative matrices specifies the upper and lower bounds for  $\lambda_1$  via the row (or column) sums of matrix elements, and the lower bound, when it exceeds the maximal possible  $\lambda_1$  of the original, disaggregated matrix, does explain why the aggregation may fail to eliminate reproductive uncertainty.

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## 1. Introduction

‘Reproductive uncertainty’ is a problem of the ‘identified individuals with uncertain parents’ type of population data (Logofet, 2013a), so typical for botanical case studies (Logofet, 2016). The studies were focused on developing matrix population models for the dynamics of local single-species stage-structured populations, where the *stage* can be determined for each individual plant on a permanent sample plot. The standard form of a discrete-structured population model is given by a vector-matrix equation

$$\mathbf{x}(t+1) = \mathbf{L}\mathbf{x}(t), t = 0, 1, \dots, \quad (1)$$

where  $\mathbf{x}(t)$  is an  $nD$  vector of the *population structure* at time moment  $t$  and an  $n \times n$  matrix  $\mathbf{L}$  is called the *projection matrix* (Caswell, 1989, 2001). The *pattern* of nonzero elements allocation in matrix  $\mathbf{L}$  can be represented as the *associated directed graph* (Harary et al., 1965; Horn and Johnson, 1990), which coincides with the *life cycle graph* (LCG, Logofet and Belova, 2008) for individuals in the population. The graph summarizes the knowledge of species biology in terms of status-specific groups of individuals, with their population sizes being represented by the components of vector  $\mathbf{x}(t)$ . It shows all the transitions among status groups that are pos-

sible for one time step; it also indicates which of the status groups are *reproductive*, i.e., provide for the population recruitment, and in which status groups the recruits may appear at the time  $t+1$ . Correspondingly, the projection matrix is considered as the sum,

$$\mathbf{L} = \mathbf{T} + \mathbf{F}, \quad (2)$$

of its *transition* and *fertility* parts (Cushing and Yicang, 1994; Li and Schneider, 2002).

The ‘identified individuals’ are the kind of ‘data in which individuals are marked and followed over time’ (Caswell, 2001, p. 134), and they enable calculating the elements  $\tau_{ij}$  of matrix  $\mathbf{T}$  directly from the data as the ‘observed transition frequencies’ (*ibidem*). However, the ‘unknown parents’ leave the stage-specific *reproduction rates* (nonzero elements of  $\mathbf{F}$  when there are two or more of them) uncertain, yet constrained to a ‘recruitment balance equation’ (Logofet, 2008, p. 220, left)

$$\mathbf{x}(t+1) - \mathbf{T}\mathbf{x}(t) = \mathbf{F}\mathbf{x}(t). \quad (3)$$

Here, the left-hand side is known from the data, as well the coefficients at the uncertain reproduction rates in the right-hand side. When the recruitment appears in the initial stage alone, matrix Eq. (3) has only one (the first one) nontrivial linear component-wise equation for more than one unknown rates. Such an equation can generally not have a *unique* solution, which serves as the mathematical reason of uncertainty.

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**Table 1**  
Structures of the local *E. caucasicum* population over the years of observation.

Stage	The sizes of stage groups in the year of observation					
	2009	2010	2011	2012	2013	2014
<b>j</b>	149	31	150	211	119	99
<b>v</b>	80	136	129	181	296	166
<b>g</b>	10	9	10	9	6	11
<b>gt</b>	4	1	3	7	1	4

adapted from Logofet et al., 2016

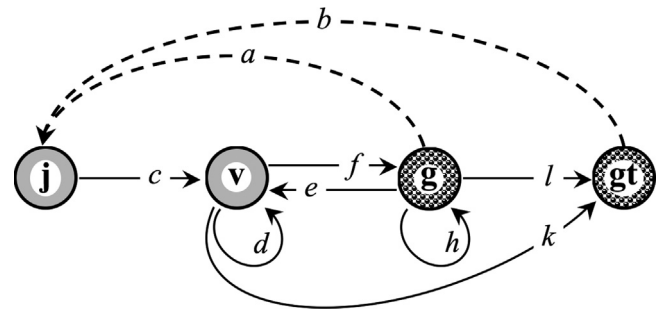
A number of tricks were proposed in the literature to cope with the reproductive uncertainty (see Logofet, 2008, and references therein). In particular, it was shown that the additional assumption of *maximal adaptation* (i.e., the maximal possible  $\lambda_1$  that conforms to the data) leads to a constraint maximization problem that has a unique solution (Logofet, 2013c). Whether the maximal-adaptation hypothesis can or cannot be accepted is a matter of theoretical discourse (Metz et al., 2008a,b; Gyllenberg and Service, 2011) and that of expert judgement in each practical case. However, without any additional hypotheses, matrix calibration results only in certain finite ranges for the unknown reproduction rates, hence in a certain range,  $[\lambda_{1\min}, \lambda_{1\max}]$ , for the adaptation measure  $\lambda_1(L)$  rather than an exact number. When the range lies entirely to the left or to the right of  $\lambda_1 = 1$ , it does give a certain answer whether the population declines or increases, but it does not when  $\lambda_1 = 1$  falls inside the range. Both cases did occur in modelling practice (Table 3 in Logofet et al., 2016), leaving the issue open for further studies.

Meanwhile, among the tricks to eliminate reproductive uncertainty there was a suggestion to deal with a single reproductive group only (Akçakaya and Burgman, 1999), i.e., with a single unknown to be found from the sole nontrivial element-wise equation of (3). Although this recipe looked like the wisdom to be healthy *but* reach, it has prompted an idea to aggregate the life cycle graph with a few reproductive stages to that with a single one. Thereafter, the  $\lambda_1$  of the aggregated matrix,  $L_{ag}$ , becomes calculable uniquely, and it would be logical to expect that  $\lambda_1(L_{ag})$  gets into the range of uncertainty for the original  $\lambda_1(L)$  values, thus finalizing the estimation.

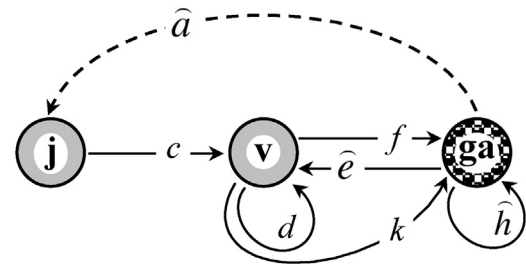
In the present communication, I report how this idea has been verified for a time series of the ‘identified individuals with uncertain parents’ data mined in a case study of a local stage-structured population of *Eritrichium caucasicum*, an herbaceous short-lived perennial species. The above expectation has turned out partially true: most of  $\lambda_1$ s for the aggregated matrices,  $L_{ag}(t)$ , have fallen pretty within the original ranges of uncertainty, but there has also been an exception, a  $\lambda_1(L_{ag}(t))$  beyond the original range  $[\lambda_{1\min}(t), \lambda_{1\max}(t)]$ . There is a mathematical reason for such an exception, and I propose an efficient condition to see a priori whether the aggregation would fail in eliminating the reproductive uncertainty.

**2. *Eritrichium caucasicum* case study**

Fig. 1 presents the LCG for a local population of *Eritrichium caucasicum*, a short-lived perennial plant inhabiting an alpine lichen heath. Seeds germinate each spring to seedlings, then mature successively to juvenile, virginal, and generative stages, where they produce seeds. Severe wintering conditions cause some of generative plants to not flower in the upcoming season, and this phenomenon causes the backward transition  $va \leftarrow g$  to appear in the LCG. Botanists can distinguish between the plants at the *generative* stage and those at the *terminal generative* stage, after which the plants die out. Thus, two generative stages provide for the population recruitment at the initial stage, but no method is available to distinguish between the progenies from those two stages. *Reproductive uncertainty* is therefore inevitable in this case, even for the



**Fig. 1.** LCG for a local population of *Eritrichium caucasicum*: **j** denotes young plants (seedlings and juveniles); **v** virginal plants and the adult non-flowering ones, **g** – generative plants; **gt** terminally generative plants. Solid arrows indicate ontogenetic transitions occurring for one year (the lack of transition, in particular); dashed arrows correspond to annual recruitment (Logofet et al., 2016).



**Fig. 2.** LCG for *E. caucasicum* with two generative stages aggregated to a single one, **ga**.

‘identified individuals’ type of data, which were mined by means of annual censuses on permanent sample plots in the period of 2009–2014 (Logofet et al., 2016).

The projection matrix takes on the following form:

$$L = T + F = \begin{bmatrix} 0 & 0 & 0 & 0 \\ c & d & e & 0 \\ 0 & f & h & 0 \\ 0 & k & l & 0 \end{bmatrix} + \begin{bmatrix} 0 & 0 & a & b \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}, \tag{4}$$

with two uncertain reproduction rates, *a* and *b*, constrained by the ‘recruitment balance equation’

$$j(t + 1) = a g(t) + b gt(t), t = 0, 1, \dots, 4, \tag{5}$$

where  $j(t + 1)$ ,  $g(t)$ , and  $gt(t)$  are all known from the data (Table 1). Known also are all the transition matrices  $T(t)$  calibrated in the rational numbers as the observed frequencies of transitions (Table 2).

Now, aggregating the generative stages into a single one, **ga**, results in the LCG shown in Fig. 2. The corresponding matrix  $L_{ag}$  reduces to

$$L_{ag} = \begin{bmatrix} 0 & 0 & 0 \\ c & d & \hat{e} \\ 0 & f + k & \hat{h} \end{bmatrix} + \begin{bmatrix} 0 & 0 & \hat{a} \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix},$$

and the vector,  $y(t)$ , of the aggregated population structure takes on the form of

$$y(t) = [j(t), v(t), ga(t)]^T, \tag{6}$$

where  $ga(t) = g(t) + gt(t)$  is evident from Table 1. The annual number of recruits remains obviously the same, hence  $j(t + 1) = \hat{a}[g(t) + gt(t)]$ , whereby the new reproduction rate is recalculated from Table 1 as

$$\hat{a}(t) = j(t + 1) / [g(t) + gt(t)], t = 0, 1, \dots, 4. \tag{7}$$

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