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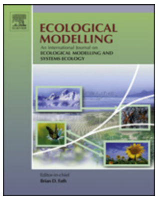

Calamagrostis model revisited: Matrix calibration as a constraint maximization problem

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ABSTRACT

A matrix model for age-stage-structured population dynamics of *Calamagrostis canescens*, a perennial grass species colonizing forest clear-cut areas, was calibrated before from a type of data called 'identified individuals with unknown parents' (Logofet, 2008) in order to estimate λ_1, the dominant eigenvalue of the projection matrix. A number of methods were applied to tackle the 'reproductive uncertainty' in data, and the output variety contained λ_1 both greater and less than 1 (Logofet, 2008), leaving the estimation uncertain. An 'adaptation conjecture' was then proposed that reduced the calibration to a nonlinear constraint maximization problem and provided for a satisfactory outcome.

Two reasons have now caused revisiting. First, the maximization technique has been theoretically comprehended. In particular, an existence-uniqueness theorem has been proved that requires the maximizing solution to be reached at a vertex of the polyhedral of constrains. To facilitate searching for the solution in practice, I use the notion of potential-growth indicator and prove R_0 and R_1, the known indicators, to be certain linear functions of the uncertain fertility rates in a general class of projection matrix patterns. To solve a conjugate linear maximization problem under the same constraints as for λ_1 is both theoretically and technically simpler, and this causes a practical benefit from the indication along with calculation.

Second, the former uniform (non-specific) estimate of the upper bounds for the status-specific fertility rates has now conceded to the age-stage-specific estimates inferred from a special case study. These more sophisticated constraints produce respectively more accurate calibration, hence a more reliable estimation of λ_1 as the growth potential inherent in the population in a certain environment at a given time.

1. Introduction

Calamagrostis model was developed as a matrix model (Logofet, 2002) for the population dynamics of *Calamagrostis canescens*, a perennial herbaceous plant dominating the grass layer of felled forest areas in the temperate zone due to fast vegetative propagation (Ulanova et al., 2002; Logofet et al., 2006; Logofet, 2008). Individual plants were classified by age and stage – the chronological age in years and the stage of ontogenesis along an *ontogenetic scale* developed earlier (Zhukova and Ermakova, 1985; Ulanova and Demidova, 2001). The *life cycle graph* (LCG) was correspondingly defined on a finite two-dimensional lattice of age-stage-specific *statuses* (Fig. 1). The LCG features what is called *polyvariant ontogeny*,[1] i.e., 'the realization of diverse pathways in the ontogenesis' (Zhukova and Komarov, 1990, p. 451). In the terms of LCG, it means alternative transitions from a graph node, i.e., more than one outgoing arrows, excepting the reproductive ones, at a node. It was shown in a number of case studies that 'polyvariant ontogeny can be regarded as the most important, population-level mechanism of adaptation contributing to coenopopulation heterogeneity and providing for its persistence in the changing environment' (Zhukova and Komarov, 1990, p. 459, and references therein).

Given an LCG, it defines both the components in the vector, $\boldsymbol{x}(t)$, of *population structure* and the *pattern* of nonzero elements allocation in the *projection matrix* $\boldsymbol{L}$. The matrix projects the current structure one time-step further according to the traditional, vector-matrix equation

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

of the *matrix population model* (see, e.g., Caswell, 2001). Matrix elements represent *vital rates* or *demographic parameters* (Caswell, 2001).

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[1] The term was first articulated *as multivariant ontogeny* in a monograph on plant physiology by Sabinin (1963); it was thereafter used by Russian botanists in its present form (Zhukova, 1986).

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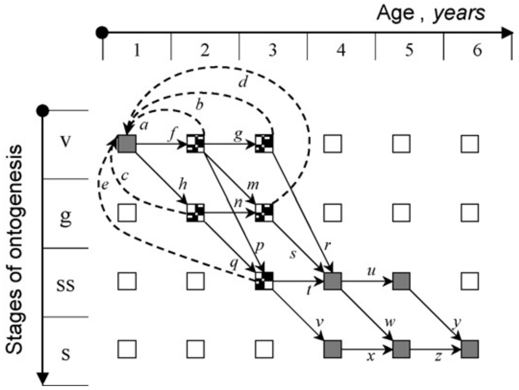

Fig. 1. The woodreed (*Calamagrostis canescens*) LCG (life cycle graph) accounting for stages of ontogeny and chronological age for the vegetative mode of reproduction. The stages are: v, *virginal*; g, *generative*; ss, *subsenile*; s *senile*; the shorter initial, *plantule* and *immature*, stages are incorporated into the 1-year virginal one. Empty boxes designate the age-stage states not observed in the field study, patterned boxes indicate the states participating in reproduction; solid arrows represent ageing and ontogenetic transitions in one year, dashed arrows correspond to reproduction; Latin letters associated with arrows denote the age-stage-specific rates (Logofet, 2008).

In the *Calamagrostis* model, the vector $\boldsymbol{x}$ represents the *age-stage* structure consisting of the 11 components:

$$\boldsymbol{x}(t) = [v^1, v^2, v^3, g^2, g^3, ss^3, ss^4, ss^5, s^4, s^5, s^6]^{\mathrm{T}}, \tag{2}$$

and following the LCG of Fig. 1, the projection matrix takes on the form (Logofet, 2002, 2008).

$$\boldsymbol{L} = \begin{bmatrix} \boldsymbol{L}' & \boldsymbol{O} \\ \boldsymbol{N} & \boldsymbol{P} \end{bmatrix}, \tag{3}$$

with submatrix $\boldsymbol{L}'$:

$$\boldsymbol{L'} = \begin{bmatrix} 0 & a & b & c & d & e \\ f & 0 & & & & \\ 0 & g & 0 & & 0 & \\ h & 0 & 0 & 0 & & \\ 0 & m & 0 & n & 0 & \\ 0 & p & 0 & q & 0 & 0 \end{bmatrix}, \tag{4}$$

corresponding to the *reproductive core* of the LCG (Logofet et al., 2006), and submatrix $\boldsymbol{P}$:

$$\boldsymbol{P} = \begin{bmatrix} 0 & & & & \\ u & 0 & & 0 & \\ 0 & 0 & 0 & & \\ w & 0 & x & 0 & \\ 0 & y & 0 & z & 0 \end{bmatrix}, \tag{5}$$

corresponding to transitions among the post-reproductive groups.

The dominant eigenvalue, $\lambda_1(\boldsymbol{L}) > 0$, of the projection matrix has long been recognized, both in theory and practice, as the analogue to the scalar intrinsic growth rate to apply for multidimensional population growth (recent survey in Salguero-Gómez and de Kroon, 2010). When a projection matrix is reliably calibrated from data in situ, its λ_1 can be calculated by a standard computer routine. As a matter of mathematical fact (expression (8), Section 2), λ_1 shows the rate at which the population vector increases along its asymptotic direction (given by the corresponding eigenvector), i.e., after a great enough number of time steps under the constancy of the matrix. At the same time, λ_1 is determined in a unique algebraic way by the matrix entries, namely, by those transitions and reproductions that occurred for the short calibration period. This is why the dominant λ, in spite of its asymptotic nature, does determine the growth potential that the population possessed in a particular environment on a certain interval of time. In this sense, it does measure how the population adapts to its environment.

The data collected in the *Calamagrostis* case study were of the 'identified individuals' type (Caswell, 2001, p. 134), yet with unknown parents (Logofet, 2008). It means that the fate of each individual plant was monitored within a permanent sample plot through successive years, but the parent plant could not be determined for any recruit without destroying the plot or having recourse to genetic analysis. This brought uncertainty into the calibration of matrix $\boldsymbol{L}$, hence into the estimation of $\lambda_1(\boldsymbol{L})$, from the data. In this paper, the calibration problem is reformulated for the general case of "reproductive uncertainty" and reduced to a kind of constraint nonlinear maximization problem under an assumption that adaptation maximizes λ_1; the problem has a unique theoretical solution.

This method was used, among several other alternatives, to calibrate the *Calamagrostis* matrix on the field data for two successive years of observation (Logofet, 2008). The solution appeared to depend essentially on the upper-bound constraint on fertility rates. The constraint was assumed uniform for all the rates as an ad hoc expert estimation in that study, although the method itself did not require any uniformity in the constraints. The uniform estimation has invoked a fare critique (Salguero-Gómez, 2012), and, in this paper, it concedes to the status-specific upper bounds (Section 5) ensuing from a profound case study on vegetative propagation in *C. canescens* (Demidova, 2004).

In the next three sections, I address the calibration problem for a general class of matrix population models and formulate an extremal principle to eliminate the uncertainty in fertility rates. It does so when a unique global solution exists to the constraint nonlinear maximization problem. The corresponding theorem is established for a general class of projection matrices.

In practice, however, checking the theorem conditions for a given matrix and data may face technical obstacles, while the irrespective search for solution by means of a computer routine faces one more kind of uncertainty: whether a local extremum returned by the routine provides for the global one too, the issue requiring further nontrivial study. I propose an auxiliary way to tackle the problem that makes use of a scalar function of matrix elements called a *potential-growth indicator* (*PGI*, Logofet and Klochkova, 2002; Logofet and Belova, 2008). Given a matrix $\boldsymbol{L}$, this function indicates, by its own value, the principal property of $\lambda_1(\boldsymbol{L})$ being greater or less than 1, without calculating the λ_1 itself. The net reproductive rate R_0 is a well-known example of PGI, and I propose another one, R_1. These functions turn out to be linear with regard to unknown fertility rates in a wide class of projection matrices. To solve a linear extremal problem under the same constraints as for $\lambda_1(\boldsymbol{L})$ is both theoretically and technically simpler, and this causes a practical benefit from the indication along with calculation.

2. General pattern of the projection matrix and its potential-growth indicators

Since Leslie (1945) and Lefkovitch (1965) times, a vast variety of *patterns* have appeared in the allocation of nonzero elements