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Complexity in matrix population models: Polyvariant ontogeny and reproductive uncertainty

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ABSTRACT

Linear matrix models of stage-structured population dynamics are widely used in plant and animal demography as a tool to evaluate the growth potential of a population in a given environment. The potential is identified with λ_1, the dominant eigenvalue of the projection matrix, which is compiled of stage-specific transition and fertility rates. Advanced botanical studies reveal *polyvariant ontogeny* in perennial plants, i.e., multiple different versions of individual development within a local population of a single species. This phenomenon complicates any standard, successive-stage, life cycle graph to a digraph defined on a 2D lattice in the age and stage dimensions, the pattern of projection matrix becoming more complex too. In a kind of experimental design, the transition rates can be calculated directly from the data for two successive time moments, but the age-stage-specific rates of reproduction still remain uncertain, adding more complexity to the calibration problem. Simple additional assumptions could technically eliminate the uncertainty, but they contravene the biology of a species in which polyvariant ontogeny is considered to be the major mechanism of adaptation. Given the data and expert constraints, the calibration can be reduced instead to a nonlinear maximization problem, yet with linear constraints. I prove that it has a unique solution to be attained at a vertex of the constraint polyhedral. To facilitate searching for the solution in practice, I use the net reproductive rate R_0, a well-known indicator for the principal property of λ_1 to be greater or less than 1. The method is exemplified with the calibration of a projection matrix in an age-stage-structured model (published elsewhere) for *Calamagrostis canescens*, a perennial herbaceous species with a complex (multivariant) life cycle that features unlimited growth when colonizing open areas.

1. Introduction

In spite of the fact that *nonlinearity* firmly settled in the most paradigms of modern theoretical population ecology, *linear* matrix models of discrete-structured population dynamics are widely used in the practice of plant and animal demography as a tool to evaluate the growth potential of a population in a given environment (Salguero-Gómez and de Kroon, 2010; Salguero-Gómez and Plotkin, 2010), the number of applications has been recently increasing world-wide (MPIDR, 2012). 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 a population (Caswell, 2001).

For a stage-structured population $\boldsymbol{x}$ governed by a constant matrix $\boldsymbol{L}$ of size $n \times n$:

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

the dominant eigenvalue (or the *Perron root*), λ_1, of the *projection* matrix $\boldsymbol{L}$ serves as the analogue to the scalar population growth rate for the case of vector growth. Matrix $\boldsymbol{L}$ consists of *survival* and *fertility rates*, which are *status-specific*, while the pattern of nonzero matrix entries is isomorphic to the *associated directed graph* (Harary et al., 1965; Svirezhev and Logofet, 1978; Horn and Johnson, 1990). The great advantage and practical appeal of matrix population models stem from the fact the digraph associated to the projection matrix coincides with the *life cycle graph* (Caswell, 1989, 2001), or the *LCG* (Logofet and Belova, 2008), a kind of biological knowledge related to the population under study.

The dominance of λ_1 ensues from the Perron–Frobenius theorem for nonnegative matrices provided that the matrix is indecomposable and primitive. These conditions can be verified for a given matrix $\boldsymbol{L}$ through its *associated digraph* (Horn and Johnson,

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Abbreviations: LCG, life cycle graph.

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1990; Logofet, 1993), or the LCG: the matrix being *indecomposable* (or *irreducible* in some texts) is equivalent to the LCG being *strongly connected* (Harary et al., 1965; Horn and Johnson, 1990), and primitivity ensues, for instance, from the LCG having at least one self-loop (Svirezhev and Logofet, 1978; Caswell, 1989, 2001; Logofet, 1993).

While the latter condition fails in the classical *Leslie* matrix for an age-structured population (as its principal diagonal consists exclusively of zeros unless the youngest age class produces offspring), the original *Lefkovitch* matrix for a stage-structured population (Lefkovitch, 1965; Caswell, 1989, 2001) always appears to be primitive due to its nonzero diagonal elements. For more complicated LCGs, hence more versatile patterns of the *projection* matrix $\boldsymbol{L}$ constructed for generalized stages (Caswell, 2001; Logofet, 2002), a criterion for the matrix to be primitive reduces to checking the lengths of all cycles in the LCG (Svirezhev and Logofet, 1978; Voyevodin and Kuznetsov, 1984; Logofet, 1993; Caswell, 2001; Logofet and Belova, 2008): those lengths must have a nontrivial common divisor for the matrix to be *imprimitive*. In the absence of 1-cycles (of nonzero diagonal elements), the divisor can only appear at a quite specific allocation of reproductive stages in the life cycle.

So, there is no obstacle in theory to define a measure of how a local population is adapted to its environment as $\lambda_1(\boldsymbol{L})$ where matrix $\boldsymbol{L}$ collects the vital rates evaluated in that specific environment. In practice, however, this concept encounters both general problems of model parameter estimation and specifically high sensitivity of $\lambda_1(\boldsymbol{L})$ to variations in fertility rates (Caswell, 1989, 2001; Li and Schneider, 2002; Logofet, 2008). However, there exists an experimental design where the data obtained enable quite rigorous calculation of the vital rates, rather than their approximation. This kind of data for a stage-structured population 'in which individuals are marked and followed over time' was called 'identified individuals' (Caswell, 2001, p. 134). Among several cases which Caswell cited as 'identified individuals', there are plants 'in a quadrat' where 'each individual is observed at each time' (Caswell, 2001, p. 134), and it is so in the case study I address as a typical example of the calibration problem.

The woodreed of *Calamagrostis canescens* (Web) Roth. is a perennial herbaceous plant able to colonize open forest areas (windfalls, clear-cuts, etc.) and to often prevent the forest from renewal in those areas (Ulanova, 2000). The species dominates in the grass layer of clear-cut areas of coniferous forests in European Russia. It was studied on permanent sample plots, where each individual plant, including recruits, was followed over time. The mark sensing was done once a year, in August (Ulanova and Demidova, 2001; Ulanova et al., 2002). The plants reproduce mostly through vegetative expansion by horizontal rhizome sprouts, so that the parent plant can hardly be determined without destroying the plot, hence the recruited plants can only be counted in total, rather than attributed to certain reproductive, status-specific groups of parent plants. Therefore, all identified individuals had unknown parents in that study. The unknown parents, in turn, bring uncertainty into the calculations of fertility rates for identified individuals. Nevertheless, the calibration of matrix $\boldsymbol{L}$ deserved no special attention in a number of plant case studies (Pfister, 1998; Ehrlén, 2000; Ehrlén and Lehtilä, 2002; Ramula and Lehtila, 2005) – perhaps, because it was provided by computer routines. Yet it remained unclear how the uncertainties were overcome in those routines.

It will be seen that *C. canescens* LCG features what motivates speaking of complexity in linear matrix models, namely, *polyvariant* (or *multivariant*) *ontogeny*, i.e., multiple different versions of individual development within a local population of a single species. This phenomenon complicates any standard, successive-stage, life cycle graph to a more complex digraph defined on a 2D lattice in the age and stage dimensions, the pattern of projection matrix becoming more complex too.

Motivated by *C. canescens* example, I address the calibration problem for a general-type matrix population model and formulate an extremal principle to eliminate the uncertainty in fertility rates. The calibration thereafter reduces to a constraint nonlinear maximization problem, the advance depending on the existence of a unique global solution to that problem. The corresponding theorem is proved that establishes sufficient conditions for the solution to be unique.

In practice, however, checking the theorem conditions for a given matrix and data may face technical obstacles, while irrespective maximization by means of a computer routine leaves it uncertain whether a local maximum returned by the routine provides for the global one too, the issue requiring further nontrivial study.

I propose an axillary, heuristic, way to tackle the problem that makes use of a positive scalar function, R_0, of matrix elements well-known as the *net reproductive rate* (Cushing and Yicang, 1994; Cushing, 1998; Caswell, 2001). The fundamental property of $R_0(\boldsymbol{L})$ consists in its *indication* ability: $R_0(\boldsymbol{L})$ always lies on the same side of 1 as does $\lambda_1(\boldsymbol{L})$, thus indicating population growth or decline simultaneously with λ_1. The advantage of $R_0(\boldsymbol{L})$ appears due to its linearity with regard to fertility rates, in contrast to $\lambda_1(\boldsymbol{L})$, for a wide class of matrix patterns. To solve the linear maximization 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 prior to calculation, although these two solutions do not necessarily coincide. The solutions to both maximization problems are illustrated with the *C. canescens* model and data, after which the indication is discussed as a heuristic tool to tackle a complicated problem.

2. General form of matrix population models: $\boldsymbol{\lambda_1}$ and $\boldsymbol{R_0}$ revisited

Since Leslie (1945) and Lefkovitch (1965) times, there appeared a vast variety in the *patterns* that the *projection matrix* **L** of Eq. (1) may have in the allocation of its nonzero elements called *vital rates* (Caswell, 1989, 2001). In a *standard matrix model*[1] (Li and Schneider, 2002), matrix $\boldsymbol{L}$ can be represented as

$$\boldsymbol{L} = \boldsymbol{T} + \boldsymbol{F}, \tag{2}$$

where nonnegative nonzero matrix $\boldsymbol{T} = [\tau_{ij}]$ is *substochastic* in columns, i.e.,

$$0 < \sum_{i=1}^{n} \tau_{ij} \le 1, \quad j = 1, \ldots, n, \tag{3}$$

while nonnegative nonzero matrix $\boldsymbol{F} = [f_{ij}]$ has no more restrictions in the most general case. However, for the sake of technical simplicity, I consider the case where $\boldsymbol{F}$ has only one nonzero row, and let it be the first row without loss of generality. It means that population recruitment appears only in the first status group. I will discuss later how this *single-row* restriction can be attenuated.

In what follows, matrix (2) is also assumed to be *indecomposable* (or *irreducible* in some texts, e.g., Horn and Johnson, 1990), so that the Perron–Frobenius theorem for nonnegative matrices guarantees the existence (and the unitary algebraic multiplicity) of $\lambda_1(\boldsymbol{L}) > 0$ (Horn and Johnson, 1990). However, if $\boldsymbol{L}$ is decomposable, its maximal indecomposable submatrix $\boldsymbol{L}'$ should then be

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[1] Standard for mathematics, the applications feature particular patterns of matrices $\boldsymbol{T}$ and $\boldsymbol{F}$.