

Projection matrix calibration under reproductive uncertainty: the maximization of λ_1 and the merit of indication

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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. In a kind of experiment design, the transition rates can be calculated directly from the data for two successive time moments, while the stage-specific fertility rates still remain uncertain, being only constrained to a linear-type equality with known coefficients. Simple additional assumptions could technically eliminate the uncertainty, but they contravene the biology of a species in which the diversity of ontogenetic pathways and reproductive efforts is considered to be the major mechanism of adaptation. Given the data and expert constraints, I assume instead that the adaptation distributes the uncertain fertility rates in such a way that maximizes λ_1 , the population growth potential to be evaluated. Matrix calibration thus reduces to a nonlinear constraint maximization problem, and 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, which turns out linear with regard to the fertility rates. 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, colonizing forest clear-cut areas.

Keywords: Constraint maximization · Dominant eigenvalue · Double-structured population · Life cycle graph · Net reproductive rate · Polyvariant ontogeny · Projection matrix

1. Introduction

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

$$\mathbf{x}(t+1) = \mathbf{L} \mathbf{x}(t), t = 0, 1, 2, \dots, \quad (1)$$

the dominant eigenvalue (or the *Perron root*), λ_1 , of the *projection* matrix \mathbf{L} is well-known to serve as the analogue to the scalar population growth rate for the n -dimensional case. In the general case, the *stage* is understood as a discrete *status* of individuals and matrix \mathbf{L} consists of *survival* and *fertility rates*, which are *status-specific*.

The dominance of λ_1 ensues from the Perron–Frobenius theorem for nonnegative matrices provided that the matrix is indecomposable and primitive. These conditions for a square matrix have equivalents in its *associated directed graph* (Svirezhev, Logofet, 1978; Horn, Johnson, 1990; Logofet, 1993), which coincides, in the case of projection matrices, with the *life cycle graph* (Caswell, 1989, 2001), or the *LCG* (Logofet, Belova, 2008). Matrix being *indecomposable* (or *irreducible* in some texts) is equivalent to the LCG being strongly connected (Harary et al., 1965; Horn, Johnson, 1990), and primitivity ensues, for instance, from the LCG having at least one self-loop (Svirezhev, Logofet, 1978; Caswell, 1989, 2001; Logofet, 1993).

While the classical *Leslie* matrix for an age-structured population does not meet the latter condition as its principal diagonal contains exclusively zeros (unless the youngest age class produces offspring), the original *Lefkovich* matrix for a stage-structured population (Lefkovich, 1965; Caswell, 1989, 2001) always appears to be primitive due to its nonzero diagonal elements. For more complicated LCGs and more versatile patterns of the *projection* matrix \mathbf{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, Logofet, 1978; Voyevodin, Kuznetsov, 1984; Logofet, 1993; Caswell, 2001; Logofet, 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 appear only for quite specific allocation of the reproductive stages in the life cycle.

So, there is no obstacle in theory to define a measure of how a population is adapted to its environment as its growth potential expressed as $\lambda_1(\mathbf{L})$ where matrix \mathbf{L} collects the vital rates evaluated in that specific environment. In practice, however, this concept encounters both the general problems of model parameter estimation and specifically high sensitivity of $\lambda_1(\mathbf{L})$ to variations in fertility rates (Caswell, 1989, 2001; Li, Schneider, 2002; Logofet, 2008). But 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 cites as “identified individuals”, there are plants “in a quadrat” where “each individual is observed at each time” (*ibidem*), and it is 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, 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 or genetic analysis, 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 L deserved no special attention in a number of plant case studies (Pfister, 1998; Ehrlén, 2000; Ehrlén, Lehtilä, 2002; Ramula, Lehtilä, 2005) – perhaps, because it was provided by computer routines. Yet it remained unclear how the uncertainties were overcome in those routines.

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 investigation.

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, Yicang, 1994; Cushing, 1998; Caswell, 2001). The fundamental property of $R_0(L)$ consists in its *indication* ability: $R_0(L)$ always lies on the same side of 1 as does $\lambda_1(L)$, thus indicating

population growth or decline simultaneously with λ_1 . The advantage of $R_0(\mathbf{L})$ appears due to its linearity with regard to fertility rates, in contrast to $\lambda_1(\mathbf{L})$, for a wide class of matrix patterns. To solve the linear maximization problem (under the same constraints as for $\lambda_1(\mathbf{L})$) 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 potential benefits of indication are discussed in general terms.

2. General Form of Matrix Population Models: λ_1 and R_0 Revisited

Since Leslie (1945) and Lefkovich (1965), there appeared a vast variety in the *patterns* that the *projection matrix* \mathbf{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, Schneider, 2002), matrix \mathbf{L} can be represented as

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

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

$$0 < \sum_{i=1}^n \tau_{ij} \leq 1, \quad j = 1, \dots, n; \quad (3)$$

the nonnegative nonzero matrix $\mathbf{F} = [f_{ij}]$ has no more restrictions in the most general case. However, for the sake of technical simplicity, I consider the case where \mathbf{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, Johnson, 1990), so that the Perron–Frobenius theorem for nonnegative matrices guarantees the existence (and the unitary algebraic multiplicity) of $\lambda_1(\mathbf{L}) > 0$ (*ibidem*). However, if \mathbf{L} is decomposable, its maximal indecomposable submatrix \mathbf{L}' should then be considered instead that corresponds to the *reproductive core* of the LCG (Logofet et al., 2006).

When \mathbf{L} is *primitive*, i.e. when $\lambda_1(\mathbf{L}) > |\lambda_j(\mathbf{L})|$, $j = 2, \dots, n$, the asymptotic behaviour is well known:

$$\mathbf{x}(t) \cong c(\mathbf{x}(0)) \lambda_1^t \mathbf{x}^* \text{ as } t \rightarrow \infty, \quad (4)$$

¹ Standard for mathematics, the applications feature particular patterns of matrices \mathbf{T} and \mathbf{F} .

where $\mathbf{x}^* > \mathbf{0}$ is the positive eigenvector corresponding to λ_1 and constant $c(\mathbf{x}(0)) > 0$ depends on the initial population vector. Therefore,

$$\mathbf{x}(t) \rightarrow \begin{cases} \infty & \text{if } \lambda_1 > 1, \\ 0 & \text{if } \lambda_1 < 1, \\ c\mathbf{x}^* & \text{if } \lambda_1 = 1. \end{cases} \quad (5)$$

Given a matrix \mathbf{L} , this property of principal importance can also be verified by means of the *net reproductive rate* R_0 (Cushing, Yicang, 1994), a positive scalar function of the vital rates,

$$R_0(\mathbf{T} + \mathbf{F}) = \rho(\mathbf{F}(\mathbf{I} - \mathbf{T})^{-1}), \quad (6)$$

where \mathbf{I} is the identity matrix $n \times n$ and $\rho(\dots)$ denotes the spectral radius of the argument matrix (Caswell, 2001; Li, Schneider, 2002). Formula (6) is valid when matrix $(\mathbf{I} - \mathbf{T})$ is not singular, which is practically not restrictive.

The equivalence relations

$$\lambda_1(\mathbf{L}) \begin{cases} > \\ < \\ = \end{cases} 1 \Leftrightarrow R_0(\mathbf{L}) \begin{cases} > \\ < \\ = \end{cases} 1 \quad (7)$$

express the fundamental property of R_0 (Cushing, Yicang, 1994; Cushing, 1998). It appears to be of practical importance when $R_0(\mathbf{L})$ is expressed in explicit form, such as

$$R_0(\mathbf{L}) = \sum_{i=1}^n f_{1i} \prod_{j=1}^i \frac{\tau_{j,j-1}}{1 - \tau_{jj}} \quad (\tau_{10} = 1), \quad (8)$$

for any *Lefkovich*-type matrix \mathbf{L} , i.e., when \mathbf{T} is of a 2-diagonal pattern, while \mathbf{F} being of the single row pattern (Cushing, 2011).

It follows from (8) that $R_0(\mathbf{L})$ is linear with regard to fertility rates. It follows from (6) that $R_0(\mathbf{L})$ is also linear when \mathbf{T} is of general pattern:

$$R_0(\mathbf{L}) = \sum_{j=1}^n f_{1j} \operatorname{cof}_{1j}(\mathbf{I} - \mathbf{T}) / \det(\mathbf{I} - \mathbf{T}), \quad (9)$$

where $\operatorname{cof}_{1j}(\dots)$ denotes the *cofactor* of element $(1, j)$ in the argument matrix (Horn and Johnson, 1990). The single-row pattern of \mathbf{F} preserves in the product $\mathbf{F}(\mathbf{I} - \mathbf{T})^{-1}$ too, hence the product element $(1, 1)$, the right-hand side of (9), represents both the unique nonzero eigenvalue and the spectral radius of the product.

In Sections 4–5, we will see how the linearity of $R_0(\mathbf{L})$ facilitates maximizing λ_1 in practice.

3. Calibration of Matrix F as the Maximization of λ_1

Let the matrix T of $L = T + F$ be known numerically (from ‘identified individuals’ data), so that the calibration of L reduces to that of F . For the matrix F , in which nonzero entries concentrate in the first row and begin with status $p \geq 1$, the first-component equation of system (1) reduces to

$$x_1(1) - \tau_{11} x_1(0) = f_{1p} x_p(0) + \dots + f_{1n} x_n(0), \quad (10)$$

which is the *recruitment equation*. The unknowns are fertility rates $f_p, \dots, f_n \geq 0$ (subscript 1 being omitted) with known (observed) coefficients $x_j(0)$ and a known left-hand side. The upper bounds for the fertility rates are also assumed known,

$$f_j \leq f_{j\max}, \quad j = p, \dots, n, \quad (11)$$

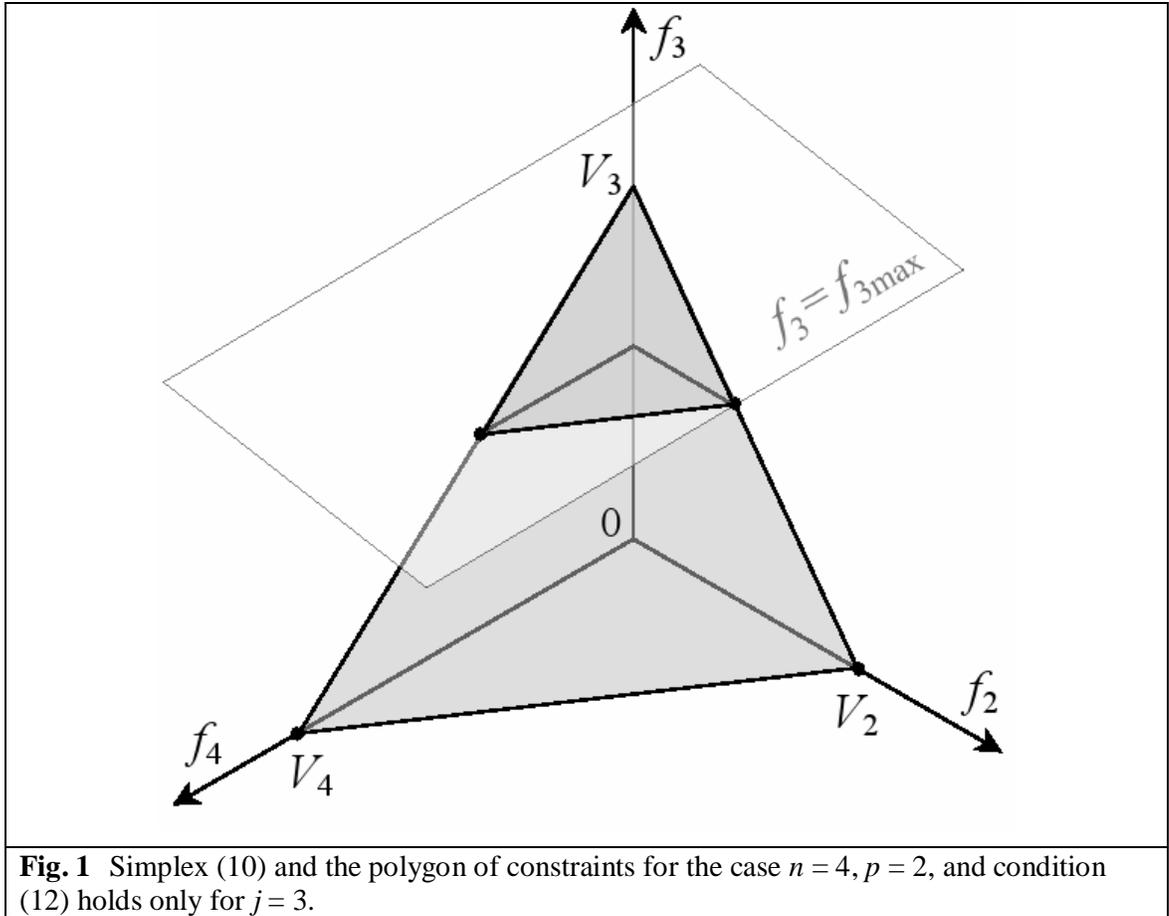
as *feasibility constraints*. If these constraints are loose enough to be already implied by Eq.(10), then the subset \mathcal{B} of all feasible solutions to the calibration problem is an $(n-p)$ D simplex in the $(n-p+1)$ D cone of potentially nonzero fertility rates. But if some of the constraints (11) appear to be constraining indeed, i.e., if we have

$$f_{j\max} < (x_1(1) - \tau_{11} x_1(0))/x_j(0), \quad j \in \{p, p+1, \dots, n\}, \quad (12)$$

for some j , then the hyperplane $f_j = f_{j\max}$ cuts the vertex V_j off the simplex, turning the simplex to a polyhedral² (a polygon in a particular case, Fig. 1). The polyhedral has a combinatorial number of vertices as a function of whether inequality (12) does or does not hold for each particular $j = p, p+1, \dots, n$. Still \mathcal{B} contains a continual number of feasible calibration solutions for f_p, \dots, f_n unless the upper-bound constraints (11) are too small, contradicting the equality constraint (10).

A technically simplest way to make a solution of Eq. (10) certain is to assume that all the positive fertility rates, $\{f_j, f_k, \dots, f_m\} \subseteq \{f_p, f_{p+1}, \dots, f_n\}$, are equal. The solution is then arithmetically obvious and unique when compatible with the constraints. Akçakaya et al. (1999) suggested particular cases as educational exercises: a single $f_p = f > 0$ or the uniformly equal fertility rates $f_p = \dots = f_n = f > 0$ resolve the uncertainty. This resolution however contravenes the *polyvariant ontogeny*, which suggests variable reproductive efforts along different pathways in the LCG (Zhukova, Komarov, 1990; Ulanova et al., 2001, 2002).

² I use *polyhedral* in order to have the terminology consistent for any $m = n - p + 1$ ($2 \leq m \leq n$) in the m D Euclidean geometry.



In a species with polyvariant ontogeny, the diversity of reproductive pathways contributes to the adaptation mechanism mentioned above, while the observations confine the actual reproductive contributions by various status groups to a single recruitment equation (10) for several unknown fertility rates (f_p, \dots, f_n) with known coefficients. Then, a continuum of feasible solutions would respectively generate the continuum of λ_1 estimates, and since we treat λ_1 as a growth potential of the population in certain conditions, it is logical to relate the potential with the maximal possible value of λ_1 under those conditions. Outside the model, it would look like the adaptation provides for a distribution of reproductive efforts among the various ontogenetic pathways that maximizes the population growth potential. The best-adapted status-specific fertility rates should therefore maximize $\lambda_1(f_p, \dots, f_n)$ and meet the constraints. The calibration problem thus reduces to the maximization:

$$\lambda_1(f_p^*, \dots, f_n^*) = \max_{\mathbb{B}} \{ \lambda_1(f_p, \dots, f_n) \} \quad (13)$$

under constraints (10)–(11).

Whether this principle eliminates the uncertainty or just reduces it to a set of feasible solutions for the problem $\{(10), (11), (13)\}$ depends on whether or not the set is nonempty and singular, i.e., whether an existence-and-uniqueness theorem holds true for this problem.

Theorem 1. *Let $\mathbf{L} = \mathbf{T} + \mathbf{F}$ be a standard indecomposable projection matrix (2), let its transition part \mathbf{T} be column-substochastic and fixed, leaving the fertility part \mathbf{F} variable in its first-row nonnegative entries f_p, \dots, f_n , and let the constraints (10)–(11) define a polyhedral \mathbb{B} with faces $\mathbb{G}_1, \dots, \mathbb{G}_h$ constituting altogether $\partial\mathbb{B}$, the boundary of \mathbb{B} . Suppose also that*

$$\mathbf{P} \mathbf{grad} \lambda_1(\mathbf{f}) \neq \mathbf{0} \quad \forall \mathbf{f} = (f_p, \dots, f_n) \in \mathbb{B}, \quad (14)$$

where \mathbf{P} denotes the operator projecting the orthant \mathbb{R}_+^{n-p+1} on the hyperplane (10). Moreover, if $d = n - p \geq 2$, let the gradient be non-zero:

$$\mathbf{P}_k \dots \mathbf{grad} \lambda_1(\mathbf{f}) \neq \mathbf{0} \quad \forall \mathbf{f} = (f_p, \dots, f_n) \in \partial \dots \partial \mathbb{G}_k, k = 1, \dots, h, \quad (14')$$

when projected on any of the faces of dimensions $(d - 1)$ to 1. Then the maximization problem (13) under constraints (10)–(11) has a unique solution, the solution being reached at a vertex of the constraint polyhedral \mathbb{B} .

The proof is given in Appendix A.

The ‘solution at a vertex of the polyhedral’ looks similar to the well-known result of linear programming (LP) theory (Johnson, Smythe, 1966; Korn, Korn, 1968), though matrix eigenvalues are generally not linear functions of the matrix entries. Eigenvalues satisfy the (first-order) homogeneity but not additivity (Horn, Johnson, 1990), hence not linearity. Nevertheless, checking the value of $\lambda_1(\mathbf{V}_j)$ at each of the finite number of vertices \mathbf{V}_j must eventually reveal the maximum of $\lambda_1(\mathbf{V})$.

4. *Calamagrostis* Example: Age-Stage-Structured Population

C. canescens LCG (Fig. 2) summarizes both general knowledge on the course of ontogeny in perennial grasses (Zhukova, Ermakova, 1985) and specific observations on how the *status* of individual plants, in the terms of their chronological *ages* and ontogenetic *stages*, may change through years after a forest habitat has been clear-cut (Ulanova, Demidova, 2001). The stages are defined by morphological characteristics; there also exists a technique to determine the age of individual plants in the field (*ibidem*). Fig. 2 shows the possible pathways of individual development from the virginal stage (**v**), through the generative (**g**) one, to the post-reproductive, subsenile (**ss**) and senile (**s**), stages for a one-year time step. Since the initial stages cease within one season, they are combined with the 1-y.o. virginal stage in this LCG.

The age-stage status changes in a number of apparently different ways, and this *polyvariant ontogeny* is considered to be the major mechanism of population adaptation to the environment (Zhukova, Komarov, 1990; Ulanova et al., 2002).

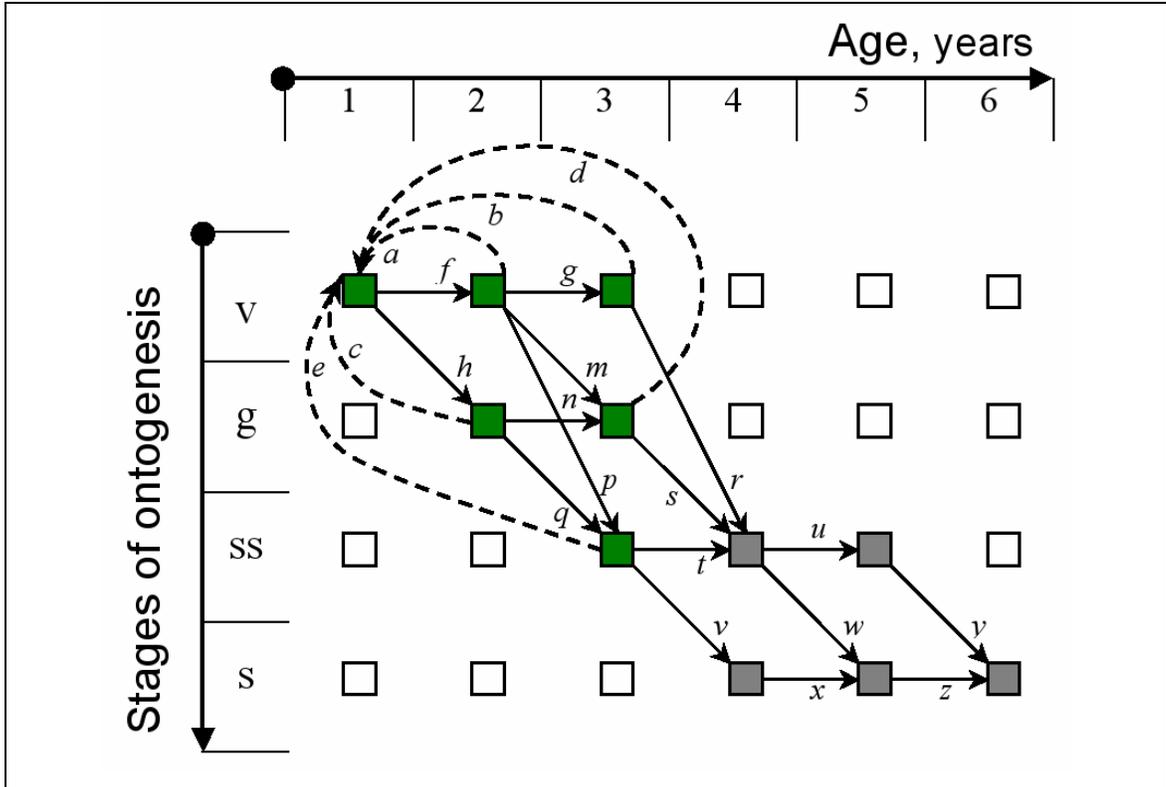


Fig. 2 The woodreed (*C. canescens*) LCG (life cycle graph) accounting for stages of ontogeny and chronological age for the vegetative mode of reproduction. The stages are: **v** virginal, **g** generative, **ss** subsenile, **s** senile; the shorter initial, *plantule* and *immature*, stages are incorporated into the 1-year virginal one. Empty boxes designate the age-stage states not observed in the field study, green boxes indicate the states participating in reproduction; solid arrows represent aging and ontogenetic transitions in one year, dashed arrows correspond to reproduction; Latin letters associated with arrows denote the age-stage-specific rates (adapted from Ulanova et al., 2002).

A matrix model was developed (Logofet, 2002; Ulanova et al., 2002) that describes the age-stage-structured population dynamics in the terms of 11D vector

$$\mathbf{x}(t) = [v^1, v^2, v^3, g^2, g^3, ss^3, ss^4, ss^5, s^4, s^5, s^6]^T, \quad (15)$$

where the superscript denotes age in years and the components represent the absolute numbers of individuals on a sample plot in the year t . Following the LCG of Fig. 2, the projection matrix takes on the form (Logofet, 2002)

$$\mathbf{A} = \begin{bmatrix} \mathbf{L} & \mathbf{0} \\ \mathbf{N} & \mathbf{P} \end{bmatrix}, \quad (15)$$

with submatrix L :

$$L = \begin{bmatrix} 0 & a & b & c & d & e \\ f & 0 & & & & \\ 0 & g & 0 & & & \\ h & 0 & 0 & 0 & & \\ 0 & m & 0 & n & 0 & \\ 0 & p & 0 & q & 0 & 0 \end{bmatrix}, \quad (16)$$

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

$$P = \begin{bmatrix} 0 & & & & \\ u & 0 & & & \\ 0 & 0 & 0 & & \\ w & 0 & x & 0 & \\ 0 & y & 0 & z & 0 \end{bmatrix}, \quad (17)$$

corresponding to transitions among the post-reproductive groups.

The spectrum of matrix (3) combines the spectra of its diagonal blocks L and P , with nontrivial eigenvalues belonging to L and being neutral with regard to block N (Geramita, Pullman, 1984; Logofet, 1993). The digraph associated with matrix L coincides with the reproductive core of the *Calamagrostis* LCG: the maximal subgraph in Fig. 2 spanning the green nodes. The digraph of L is strongly connected, and it contains cycles of length 2 or 3 only, with $\text{g.c.d.}\{2, 3\} = 1$. Hereafter, matrix L is indecomposable and primitive according to the known graph criteria (Horn, Johnson, 1990; Voyevodin, Kuznetsov, 1984). Therefore, $\lambda_1(L)$ and its positive eigenvector serve as the major characteristics to evaluate the growth potential and the population steady-state structure.

The data available to calibrate matrix L was typical for the “identified individuals” (Caswell, 2001), yet with unknown parents (see page 3 above). Correspondingly, matrix T was calculated from the data for two successive time moments, $t = 0, 1$ (Logofet, 2008, table 2):

$$T = \begin{bmatrix} 0 & & & & & \\ \frac{238}{418} & 0 & & & & \\ 0 & \frac{23}{233} & 0 & & & \\ \frac{66}{418} & 0 & 0 & 0 & & \\ 0 & \frac{4}{233} & 0 & \frac{4}{79} & 0 & \\ 0 & \frac{5}{233} & 0 & \frac{7}{79} & 0 & 0 \end{bmatrix}, \quad (18)$$

representing a particular case of (3); the recruitment equation (10) was reduced to

Table 1 Status-specific fertility rates calibrated on the same *C. canescens* data with or without maximization of λ_1 and R_0 (adapted from Logofet, 2008)

Version of constraints	Age-stage-specific fertility rates					Dominant eigenvalue $\lambda_1(a, b, c, d, e)$	Net reproductive rate $R_0(a, b, c, d, e)$
	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	<i>e</i>		
Sole nonzero rate <i>a</i> (without maximization)	408/233	0	0	0	0	0.9985	0.9970
Sole nonzero rate <i>c</i> (without maximization)	0	0	408/79	0	0	0.9030	0.8155
Equal rates (without maximization)	408/339	408/339	408/339	408/339	408/339	0.9981	0.9959
No upper-bound constraints in maximization	0	0	0	408/4	0	1.2192	1.8125
Upper-bound-constraint maximization (UBCM)	354/233	2	0	2	2	1.0294	1.0654
UBCM, with eliminating zero rate <i>c</i>	353/233	2	1/79	2	2	1.0292	1.0650
UBC and ($b > d > e$) maximization	357/233	2	1/79	7/4	13/8	1.0274	1.0605
UBC and ($a < b < d < e$) maximization	358/233	26/15	1/79	7/4	2	1.0262	1.0578

$$233a + 15b + 79c + 4d + 8e = 408 \quad (19)$$

(*ibidem*, Eq.(22)). To illustrate the method, the upper-bound constraints (11) are assumed to be uniform (Ulanova, personal communication) as an *ad hoc* approximation:

$$a, b, c, d, e \leq 2. \quad (20)$$

The diversity of feasible calibrations regardless of the adaptation principle is so wide that it contains solutions both with $\lambda_1 > 1$ and $\lambda_1 < 1$ (Table 1).

Constraints (19)–(20) define a polyhedral \mathcal{B} on the 4D hyperplane (19) in \mathbf{R}_+^5 . It has 16 vertices as far as conditions (12) reduce to $2 < 408/x_j(0)$, $j=2, \dots, 6$, which is only true for $x_1(0) = 233$, hence the number of vertices equals that of 2^4 combinations in the values of $b, c, d, e \in \{0, 2\}$. If Theorem 1 holds true, it reduces maximization problem (13) to a finite enumeration:

$$\lambda_1(\mathbf{f}^*) = \max\{\lambda_1(\mathbf{V}_j), j = 1, \dots, 16\}, \quad (21)$$

where $\mathbf{f} = (a, b, c, d, e) \geq 0$ and \mathbf{V}_j denotes a vertex. The enumeration reveals

$$\mathbf{f}^* = \mathbf{V}^* = (354/233, 2, c = 0, 2, 2). \quad (22)$$

On the other hand, *fmincon*³, a computer routine (MathWorks, 2012a), also returns $\mathbf{V}^* = (354/233, 2, c = 0, 2, 2)$ as a local solution, complying with Theorem 1 (Table 1, line UBCM). The global character of the solution ensues from its invariance to changes in the starting point as an input argument of the routine. It could be verified afterwards by comparing the value of $\lambda_1(\mathbf{V}^*)$ to those at another vertices.

As regards the linear function $R_0(a, b, c, d, e)$, it follows from (9) and (18) that

$$R_0(a, b, c, d, e) = (2190433a + 216223b + 607431c + 68360d + 100828e)/3847063 \approx \quad (23)$$

$$\approx 0.5694a + 0.0562b + 0.1579c + 0.0178d + 0.0262e.$$

The maximum of $R_0(a, b, c, d, e)$ over the polyhedral (19)–(20) is found by the simplex method, a standard technique to solve LP-problems, implemented in computer routines, e.g., *linprog* in Matlab (MathWorks, 2012b). The method reveals the maximizing solution to be unique and attained at the same vertex \mathbf{V}^* (Table 1). Although this coincidence is not general (Cushing, 2011), the uniqueness of the LP solution is at least of heuristic value, indicating the absence of singularities in the polyhedral \mathcal{B} relative to matrix \mathbf{L} that might provide for the multiplicity in maximizing solutions.

³ For the equivalent minimization of $-\lambda_1(\mathbf{f})$.

In the next Section, I speculate more on the role the maximization of R_0 plays in that of λ_1 .

5. Uniqueness Theorem and the Heuristic Role of Indication

The uniqueness Theorem 1 of Section 3 gives certain guidelines to solving the nonlinear maximization problem in practical cases, but not an immediate solution. Given a particular matrix L with known transition rates and unknown fertility ones, it may not be easy to verify the Theorem terms. On the other hand, the number of vertices in polyhedral \mathcal{B} may be large enough already for $(n-p) \geq 4$ (16 in the *Calamagrostis* example above) to turn screening all of them into a boring occupation. The computer might help, but even specialized computer routines, such as *fmincon* in MATLAB (MathWorks, 2012a), do not guarantee that the local solution they return for a given initial approximation provides for the global solution, too.

Reducing the nonlinear constrain maximization problem to finite enumeration is of practical help even when we cannot verify strictly the Theorem terms. Speaking generally, the terms should rather be met than broken in practical cases as far as the violation of (14) or (14') means the gradient vector being orthogonal to the hyperplane (10) or some of the polyhedral faces, i.e., an equality-type relationship holds among model parameters to be estimated. However, the equality would no longer be true after a tiniest change in the estimates, e.g., due to measurement errors.

A special *ad hoc* example (Appendix B) presents an artificial construction that provides for non-uniqueness in the maximization solutions. Polyhedral \mathcal{B} represents a triangle, and both the maximal λ_1 and the maximal R_0 turn out constant along a whole edge of the triangle. This observation signifies both the irrelevance of Theorem 1 for this case (its term (14') fails respectively on that edge) and conformity to the LP theory: if a solution is attained at several vertices, then it is also attained at any point of the convex hull spanning all those vertices (Johnson, Smythe, 1966; Korn, Korn, 1968).

When solving numerically the λ_1 maximization problem, we can only get a hint of non-uniqueness as the computer routine output depends on the starting point (Appendix B). Although the LP routine is not specifically designed to cope with non-unique solutions, the starting-point dependence of the output does also reveal non-uniqueness in the maximal R_0 , thus indicating a potential failure of Theorem 1 prior to its application. More advanced simplex method routines might automatically detect this situation and return the proper convex hull in explicit form. Testing the value of λ_1 through the hull (a polyhedral face or edge in particular cases) could then confirm or disprove non-uniqueness.

6. Discussion

The dominant $\lambda_1(\mathbf{L})$ shows the rate at which the population vector $\mathbf{x}(t)$ increases along its asymptotic direction (given by the corresponding positive eigenvector, expression (4), Section 2), i.e., after a great enough number of time steps under the constancy of matrix \mathbf{L} . However, the asymptotic growth rate is related, in a unique algebraic way, to the matrix entries, whose numeric values are actually determined by those particular transitions and reproductions that have occurred between the moments of observation, say $t = 0$ and $t = 1$. This is why λ_1 , in spite of its asymptotic role, does determine the growth potential the population possessed in a given environment at the given time moment $t = 1$.

For a longer time series, the least-square model fitting (Jørgensen, 1986; Jørgensen, Bendoricchio, 2001) is known to give the best approximation to model parameters. However, the situations where linear matrix models can fit real data are few. *Calamagrostis* is fit by linear models only for a few years after forest disturbance, when the woodreed grows extensively and colonizes the open area (Ulanova et al., 2002). After five years, intra- and inter-species competitions begin to retard the growth and to stabilize the dynamics (Ulanova et al., 2008), so that nonlinear population models are mandatory in this case.

In contrast, identified individuals allow us to calculate the vital rates directly, from the data of only two successive moments. The third time step may result in different rates, hence a different value of $\lambda_1(\mathbf{L})$, and the difference can be attributed to a variation in the environment during that short interval of time.

However, when the parents of identified individuals are unknown, the state-specific fertility rates involve uncertainty (called *reproductive uncertainty*), which leaves a space for speculations, artificial assumptions, or arbitrariness in the calibration problem, thus questioning the reliability of $\lambda_1(\mathbf{L})$ estimation. The remedies suggested in ecological software products to eliminate the reproductive uncertainty are often inappropriate for the task (Logofet, 2008, Section 7), producing respectively incorrect results with $\lambda_1 < 1$ (such as those in Table 1). Another solution, which seemed biologically reasonable, namely, assuming that the relative fertility rates are proportional to the observed “state-specific numbers of renewal buds on rhizomes” (Logofet, 2008, p. 222), did eliminate the uncertainty, but resulted in $\lambda_1 < 1$, too (*ibidem*, Table 1), contravening the fact the population was growing.

The adaptation principle proposed in Section 3 looks a sound alternative that is more universal. Even if we don’t believe that natural selection has resulted in such a perfect adaptation mechanism that maximizes λ_1 , the maximizing assumption still provides for a single

general approach to comparison studies under reproductive uncertainty. It does generate a solution to the calibration problem that is unique when the λ_1 maximization problem meets the conditions of Theorem 1. The conditions are not too restrictive, yet the verification in practical cases may be cumbersome. The R_0 maximization yields the same result in the *C. canescens* case, though a counterexample can also be offered where the solutions are different for the linear and nonlinear problems; Cushing (2011) commented on general reasons for this discrepancy. Nevertheless, the linear R_0 maximization, with its ever-ready solution, is of heuristic value for the nonlinear problem (Section 5).

The unique solution, such as solution (22) under constraints (19)–(20), just achieves the upper-bound values in several components. Given as an *ad hoc* expert estimation in the *C. canescens* case considered here, the upper bounds may certainly be age-stage-specific, rather than uniform, which deserves a deeper consideration but does not affect the method proposed.

The adaptation principle can also provide for testing additional hypotheses concerning a hierarchy among fertility rates (11) or their contributions to (i.e., the summands of) the recruitment equation (10). The hierarchy means some inequality to hold true among the rates or contributions, and it just adds more constraints to the original constraint maximization problem (13). The solution would then verify whether the hypotheses be compatible with the data and with the idea of population growth, i.e., with the condition $\lambda_1(\mathbf{L}) > 1$. In the *Calamagrostis* example, the hypotheses of $b > d > e$ or $a < b < d < e$ are both compatible with population growth, yet the former provides for a greater λ_1 (Table 1, bottom lines).

The adaptation principle and Theorem 1 provide the basis for the general methodological approach to the calibration of matrix $\mathbf{L} = \mathbf{T} + \mathbf{F}$, where arbitrariness in the technical aspects of the former approaches gives way to the expert opinion of the upper bounds for the fertility rates, the constraints (11). The approach is general, indeed, since matrix \mathbf{T} (3) is general, while the single-row restriction of matrix \mathbf{F} is not essential for the proof of Theorem 1. A double-row matrix would just result in two recruitment equations instead of a single one (10), the equations comprising now two nonintersecting sets of unknown fertility rates. Therefore, the former maximization problem would theoretically split into two problems, each over its own polyhedral, \mathbb{B}_i ($i = 1, 2$) with $v(\mathbb{B}_i)$ vertices, treating the complementary set of unknowns as parameters. In practice, this would mean checking the values of $\lambda_1(\mathbf{L})$ at each of the product number of vertices, $v(\mathbb{B}_1)v(\mathbb{B}_2)$.

The single-row restriction of \mathbf{F} is rather essential for the indicator $R_0(\mathbf{L})$ being linear with regard to fertility rates: a double-row \mathbf{F} would imply, in the calculation of $R_0(\mathbf{L})$ by formula (6),

an eigenvalue of a 2×2 submatrix, which might no longer be linear. For example, the matrices T and F from Camino-Beck and Lewis (2007, Eq.(B.1), p. 1353) take on the form

$$\mathbf{T} = \begin{bmatrix} \tau_{11} & 0 & 0 & 0 \\ \tau_{21} & 0 & 0 & 0 \\ 0 & \tau_{32} & 0 & 0 \\ 0 & \tau_{42} & \tau_{43} & 0 \end{bmatrix}, \quad \mathbf{F} = \begin{bmatrix} 0 & f_{12} & f_{13} & f_{14} \\ 0 & f_{22} & f_{23} & f_{24} \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix} \quad (24)$$

in the notation of the present paper, and of $R_0(\mathbf{T} + \mathbf{F})$ was proved to be still linear with regard to f_{ij} (*ibidem*, Eq.(B.3)). The linearity is however lost when an additional entry, such as $\tau_{31} > 0$ or $\tau_{41} > 0$, appears into matrix T .

Losing the linearity of $R_0(\mathbf{L})$ means hereafter losing the merit of indication for the λ_1 maximization problem. Meanwhile, a double-(or a few-)row pattern occurs in F when the population recruitment appears in two (or more) stages of the life cycle (Werner, Caswell, 1977; Caswell, 2001, Example 4.1; Camino-Beck, Lewis, 2008; Pathikonda et al., 2009). In these circumstances, another indicator might be useful, namely, the *potential growth indicator* (Klochkova, 2004; Logofet, Belova, 2008), which, in contrast to $R_0(\mathbf{L})$, has rather algebraic than biological meaning.

7. Conclusion

When identified individuals in a structured population lack data on the stage their parents belong to, this uncertainty admits a variety of solutions to the calibration problem for the projection matrix in matrix population models. The Perron root λ_1 – a quantitative measure of how well the population is adapted to a given environment – varies respectively too much to serve as a measure. Given the data of only two successive time moments and a set of expert constraints, the extremal adaptation principle provides a unique solution, the one which maximizes the value of λ_1 on a polyhedral defined by the constraints in the positive cone of unknown, state-specific fertility rates. The uniqueness has been proved for a general class of projection matrices and for a set of constraints typical for ‘unknown parents’: the solution to the constraint nonlinear maximization of λ_1 is attained at a vertex of the polyhedral. When the fertility matrix has a single-row pattern, indicator R_0 , the net reproductive rate, is linear with regard to fertility rates, and the conjugated maximization of R_0 represents a standard LP-problem. Its standard solution is of heuristic value for the technical aspects of the nonlinear maximization. Obtained in this way, λ_1 yields an objective measure of adaptation – a growth potential inherent in the population in a given place at a given time.

Appendix A: Proof of Theorem 1.

In this proof, I omit subscript 1 to simplify the notation λ_1 of the dominant eigenvalue.

Polyhedral \mathbb{B} is a compact, hence the continuous function $\lambda(f_p, \dots, f_n)$ attains its maximum value on it (Sundaram, 1996) at a point $\mathbf{f}^* = (f_p^*, \dots, f_n^*) \in \mathbb{B}$, which proves the existence part of the Theorem.

To prove the rest by contradiction, assume that $\mathbf{f}^* \in \text{Int } \mathbb{B}$. By condition (14) we have

$$\mathbf{P} \text{ grad } \lambda(\mathbf{f}^*) \neq \mathbf{0}, \quad (\text{A1})$$

and respectively nonzero will be the increment of $\lambda(\mathbf{f}^*)$ for any change, $\Delta \mathbf{f}$, in the direction (A1) on the hyperplane (10), small enough to stay within \mathbb{B} : $\mathbf{f}^* + \Delta \mathbf{f} \in \mathbb{B}$. If the increment of $\lambda(\mathbf{f}^*)$ is positive, then we get a point in \mathbb{B} where $\lambda(\mathbf{f}^* + \Delta \mathbf{f}) > \lambda(\mathbf{f}^*)$. If the increment is negative, then consider a change in the opposite direction, $-\Delta \mathbf{f}$, still retaining the point within \mathbb{B} : $\mathbf{f}^* - \Delta \mathbf{f} \in \mathbb{B}$. Since the constraint (10) is linear w.r.t. f_p, \dots, f_n and $\lambda(f_p, \dots, f_n)$ is a monotone increasing function w.r.t. each of its arguments (Gantmacher, 1967, Theorem 6, p. 372), the increment of $\lambda(\mathbf{f}^*)$ should be positive in the direction of $-\Delta \mathbf{f}$, and we get a point in \mathbb{B} where $\lambda(\mathbf{f}^* - \Delta \mathbf{f}) > \lambda(\mathbf{f}^*)$. The both results contradict the extremality of \mathbf{f}^* , hence point \mathbf{f}^* can not be interior in \mathbb{B} .

The boundary of polyhedral \mathbb{B} consists of the faces $\mathcal{G}_1, \dots, \mathcal{G}_h$, which are $(n - p - 1)$ -dimensional, and assume, as before, that $\mathbf{f}^* \in \text{Int } \mathcal{G}_1 \subset \partial \mathbb{B}$ (as the faces are numbered arbitrary, let the first one be exactly the face with \mathbf{f}^*). By condition (14'), we have

$$\mathbf{P}' \text{ grad } \lambda(\mathbf{f}^*) \neq \mathbf{0}, \quad (\text{A2})$$

where \mathbf{P}' is the operator projecting on \mathcal{G}_1 , and, repeating the previous arguments, we come to the conclusion that point \mathbf{f}^* cannot be interior in face \mathcal{G}_1 .

Thus, $\mathbf{f}^* \in \partial \mathcal{G}_1 \subset \partial \mathbb{B}$, where $\dim \partial \mathcal{G}_1 < n - p - 1$. Repeating the same arguments with the boundary dimension being reduced the proper number of times, we get $\mathbf{f}^* \in \partial \dots \partial \mathcal{G}_1 \subset \partial \mathbb{B}$, where $\dim \partial \dots \partial \mathcal{G}_1 = 0$, i.e., \mathbf{f}^* is a vertex of \mathbb{B} . The Theorem is proved. ■

Appendix B: Ad Hoc Case of Calamagrostis

Matrix (16) exemplifies how specific the relationships among transition rates (i.e., eventually within the data) should be to produce a non-uniqueness case in the solution of the maximization problem for nonzero fertility rates constrained to a 2D simplex.

If it were a priori known that $a = b = 0$ in matrix (16), while the data component were $x_4(0) = 64$, then the recruitment equation (19) would reduce to $64c + 4d + 8e = 408$, or

$$16c + d + 2e = 102, \quad (\text{B1})$$

implying somewhat higher fertility rates for vegetative expansion. Let the entries of matrix L have the following numeric values:

$$L_{\text{ah}} = \begin{bmatrix} 0 & 0 & 0 & c & d & e \\ f & 0 & & & & \\ 0 & g & 0 & \mathbf{0} & & \\ h & 0 & 0 & 0 & & \\ 0 & m & 0 & n & 0 & \\ 0 & p & 0 & q & 0 & 0 \end{bmatrix} = \begin{bmatrix} 0 & 0 & 0 & c & d & e \\ 16/17 & 0 & & & & \\ 0 & 1/9 & 0 & \mathbf{0} & & \\ 8/17 & 0 & 0 & 0 & & \\ 0 & 1/18 & 0 & 1/18 & 0 & \\ 0 & 1/9 & 0 & 1/9 & 0 & 0 \end{bmatrix}, \quad (\text{B3})$$

with parameters c , d , and e satisfying Eq. (B1). Then the dominant eigenvalue of L_{ah}

$$\lambda_1(c, d, e) = ((4d + 8e)/51)^{1/3} = 2, \quad \forall (c, d, e) \in \{c = 0, d + 2e = 102\}, \quad (\text{B4})$$

i.e., $\lambda_1(c, d, e)$ equals identically 2 along the edge (B4) of triangle (B1), and this is the maximal value of $\lambda_1(c, d, e)$ over the triangle. Correspondingly, Theorem 1 fails in this case as its term (14') is violated with respect to the "face" (B4).

For matrix (B3), the indicator (9) reduces to

$$R_0(c, d, e) = (6c + d + 2e)(4/51), \quad (\text{B5})$$

whose maximum over the triangle (B1) equals identically 8 everywhere on its edge (B4), too.

Tables B1 and B2 present the outputs of some standard computer routines in this special case.

Table B1 Outputs of Matlab function *fmincon* as solutions to the $\lambda_1(c, d, e)$ maximization problem with constraint (B1) for various initial values of nonnegative c, d, e

Algorithm used	Starting point	Output: solution for c, d, e	Maximum of $\lambda_1(c, d, e)$
<i>Active set</i> ¹	10, 10, 10	Local minimum found ² : 0, 24.40, 38.80	2
<i>Active set</i>	6, 2, 2	Local minimum found: 0, 21.20, 40.40	2
<i>Active set</i>	5, 2, 10	Local minimum found: 0, 18.00, 42.00	2
<i>Active set</i>	4, 20, 9	Local minimum found: 0, 32.80, 34.60	2
<i>Active set</i>	4, 38, 0	Local minimum found: 0, 50.80, 25.60	2
<i>Active set</i>	2, 20, 40	Local minimum found: 0, 20.40, 40.80	2
<i>Active set</i>	2, 40, 30	Local minimum found: 0, 40.40, 30.80	2
<i>Active set</i>	0, 42, 30	Local minimum found: 0, 42, 30	2
<i>Active set</i>	0, 102, 0	Local minimum found: 0, 102, 0	2
<i>Active set</i>	0, 0, 51	Local minimum found: 0, 0, 51	2

¹ The alternative, *Interior point*, algorithm returns the same results in all these examples.

² ‘Local minimum found that satisfies the constraints’.

Table B2 Outputs of Matlab function *linprog* as solutions to the $R_0(c, d, e)$ maximization problem with constraint (B1) for nonnegative c, d, e

Algorithm used	Starting point ³	Output: solution for c, d, e	Maximum of $R(c, d, e)$
<i>Interior point</i>	n.a.	LINPROG converged to a solution: 0, 36.414, 32.793	8
<i>Active set</i>	2, 40, 30	LINPROG converged to a solution: 0, 40.4, 30.8	8
<i>Active set</i>	51/8, 0, 0	LINPROG converged to a solution: 0, 20.4, 40.8	8
<i>Active set</i>	0, 102, 0	LINPROG converged to a solution: 0, 102, 0	8
<i>Active set</i>	0, 52, 25	LINPROG converged to a solution: 0, 20.4, 40.8	8
<i>Active set</i>	0, 0, 51	LINPROG converged to a solution: 0, 0, 51	8
<i>Simplex</i>	n.a.	LINPROG converged to a solution: 0, 0, 51	8

³ This option is only available with the active-set algorithm. The interior-point and simplex algorithms ignore any non-empty starting point.

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