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Alpine resort or battle for survival: A didactic story about short-lived perennials and their matrix models

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Motivation and Aim: Population structures of two short-lived perennial species, *Androsace albana* and *Eritrichium caucasicum*, have been monitored, in terms of ontogenetic stages, annually on permanent plots in the alpine belt of the North-West Caucasus during 13 years (2009–2021). Data from each pair of successive years (t, $t+1$) provided for the accurate calibration of $\boldsymbol{L}(t)$, the annual population projection matrix (PPM), with its dominant eigenvalue λ_1 considered as the asymptotic growth rate. If $\lambda_1 < 1$, then the population declines, otherwise it grows exponentially. This advantage of the matrix formalism turns into a serious problem as different PPMs have different λ_1s corresponding to respectively different, sometimes controversial, forecasts of population viability. The challenge was therefore to invent a technique summarizing the whole period of monitoring. The technique was actually invented about 30 years ago within the paradigm of the *stochastic growth rate* (λ_S) of a population in the random environment [1]. The problem is however an artificial nature of the randomness model adopted in the current literature on λ_S, such as the *i.i.d.* (independent, identically distributed) environments [2]. The aim is therefore to find an alternative method of viability forecast summarizing the whole period of monitoring.
Methods and Algorithms: The alternative method relies on the original concept of pattern-multiplicative average for nonnegative matrices [3]. If $\boldsymbol{x}(t)$ denotes the vector of population structure and $\boldsymbol{L}(t)$ is the annual PPM, then 12 annual projections in the form of
$\boldsymbol{x}(t+1) = \boldsymbol{L}(t)\,\boldsymbol{x}(t)$, $t = 2009, \ldots, 2020$,
provide for the following projection from $\boldsymbol{x}(2009)$ to $\boldsymbol{x}(2021)$:
$\boldsymbol{x}(2021) = \boldsymbol{L}(2020)\,\boldsymbol{L}(2019) \ldots \boldsymbol{L}(2009)\,\boldsymbol{x}(2009)$.
The logic behind the concept of *pattern-multiplicative average* suggests that the average matrix $\boldsymbol{G}$ ought to do exactly the same projection, whereby we have
$$\boldsymbol{G}^{12} = \boldsymbol{L}(2020)\,\boldsymbol{L}(2019) \ldots \boldsymbol{L}(2009), \qquad (*)$$
and $\boldsymbol{G}$ has the same zero/nonzero pattern as the annual PPMs. Consider this matrix equation as a system of scalar algebraic equations for the unknown elements of $\boldsymbol{G}$. Since the pattern of $\boldsymbol{G}$ is nontrivial (it corresponds to the life cycle graph of organisms), the number of unknowns is substantially greater than the number of scalar equations in the system behind (*), i.e., the system is *overdetermined*. Therefore, there is no exact solution to (*), and we have to content with an approximate one. The algorithm reduces to solving the corresponding nonlinear constraint minimization problem for the approximation error, the constraints being determined by the set of annual PPMs. An eternal obstacle we encounter along this way is the local vs. global character of the

solution. What MATLAB® proposes to break through this obstacle is called GlobalSearch [4] and suggests certain adjustment of the local routine.

Results: The dominant eigenvalue of the pattern-multiplicative average matrix $\boldsymbol{G}$ for *A. albana* has turned out equal $\lambda_1(\boldsymbol{G}) = 0.83580$, which is markedly less than that of the arithmetic mean of the annual PPMs [3]. Because of reproductive uncertainty in the data of *E. caucasicum*, we have $\lambda_1(\boldsymbol{G}) \in [0.945004, 0.959403]$, whereas the arithmetic mean interval goes beyond $\lambda_1(\boldsymbol{G}) = 1$ by its right bound, thus leaving the viability forecast uncertain [3].

Conclusion: The pattern-multiplicative average has revealed that the local population of each species actually fights a battle for survival in the long term rather than rests in the alpine resort. This conclusion is consonant with those obtained by a traditional method within the paradigm of stochastic growth rate (λ_S), albeit with realistic models of randomness correlated to variations in local weather indexes [5, 6]. Minor quantitative differences between $\lambda_1(\boldsymbol{G})$ and λ_S can be attributed to the approximation error inherent in solving the averaging problem.

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