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RANDOM EVOLUTION IN POPULATION DYNAMICS

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We present a perturbative formalism to deal with linear random *positive* maps. We generalize the biological concept of the population growth rate when a Leslie matrix has random elements (i.e. characterizing the macroscopic disorder in the vital parameters). The dominant eigenvalue of which defines the asymptotic dynamics of the mean-value population vector state, is presented as the effective growth rate of a random Leslie model. The problem was reduced to the calculation of the smallest positive root $\tilde{z}_1$ of the secular polynomial appearing in the general expression for the mean-value Green function $\langle \mathbf{G}(z) \rangle$. This nontrivial polynomial can be obtained order by order in terms of a diagrammatic technique built with Terwiel's cumulants, which have carefully been identified in the present work. By understanding how this smallest positive root $\tilde{z}_1 = 1/\tilde{\lambda}_1$ depends on the model of disorder, one can link the asymptotic population dynamics with the statistical properties of the errors (mutations) in the vital parameters. This eigenvalue has the meaning of an *effective* Perron–Frobenious eigenvalue for a random positive matrix. Analytical (exact and perturbative calculations) results are presented for several models of disorder.

Keywords: Random linear maps; Leslie matrices; population dynamics; Perron–Frobenius; effective Lyapunov exponent.

1. Asymptotic Analysis of Leslie's Dynamics

1.1. *General remarks on age-structured populations*

Projection matrix is an increasingly popular tool for modeling population dynamics. Since the pioneering work of Leslie [1945] to tackle ecology problems, population projection matrices have been applied to a wide array of demographic problems (vegetative propagation, predator–prey interaction, competition, etc., for a review see [van Groenendael *et al.*, 1988]). Time fluctuating combinations of projection matrices have been used to simulate the time variability of the environment. These studies have shown the dramatic effects of the stochastic variations on the asymptotic properties of projection matrices, as well as the need to modify the concepts of population growth rate [Cohen, 1979], and the accuracy in predicting the fate of a population in a stochastic environment [Tuljapurkar, 1982].

In the work of Leslie, the specific structure of the projection matrices $\mathbf{M}$ is based on age intervals of the same duration as the time step in the model [Leslie, 1945]. Then the age-specific fecundity (fertility parameters) f_j were placed in the first row, and age-specific survival probabilities p_j on the subdiagonal, and zeros elsewhere. However, when the demographic properties of individuals class (subgroups) are not closely related to age, alternative classifications are needed. The categories into which individuals are classified should be defined in such a way that transitions between categories are as unambiguous as possible [van Groenendael *et al.*, 1988]. Thus uncertainty in the vital parameters play a fundamental role in the description of the system and the problem that we have to face is to learn how to handle a matrix random model [Cohen, 1986; Caswell, 1978, 1983]. For example, the sampling error in estimating the vital rates is an important ingredient to be considered in order to improve the population dynamics description of marine mammals [Brault *et al.*, 1993; Cáceres *et al.*, 2008].

1.2. *Green function and Tauberian asymptotic approach*

In this section we will present the analysis of the stability of population dynamics. Here, we use a Tauberian theorem to study the stability in the Leslie model because it is suitable when disorder is present.

Consider a $m \times m$ Leslie matrix where all its elements are *sure* quantities (in general, we know that $f_j \geq 0$, and $p_j \in (0, 1]$ because these last ones are probabilities)

$$\mathbf{M} = \begin{pmatrix} f_1 & f_2 & f_3 & \cdots & \cdots & f_m \\ p_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & p_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & p_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & 0 & p_{m-1} & \cdots \end{pmatrix}. \quad (1)$$

Due to the positive structure of this matrix, it is possible to apply the Perron–Frobenius theorem and realize (if it is nonreducible) the existence of a nondegenerated positive eigenvalue λ_1 fulfilling $\lambda_1 \geq |\lambda_j|$ for all $j = 2, 3, 4, \ldots$. This particular eigenvalue, λ_1, is associated with a positive eigenvector Ψ_1 (the stable population). Thus, it is simple to prove that the stability of the population dynamics is controlled asymptotically by the behavior λ_1^n. If $\lambda_1 < 1$ the stable population declines at a constant rate λ_1. In a time-continuous representation we can define a Lyapunov exponent as $r = \ln \lambda_1$. On the other hand, if $\lambda_1 > 1$ the stable population Ψ_1 grows at a constant rate λ_1. For the ordered case, Perron–Frobenius analysis is powerful to calculate the asymptotic behavior of the vector state [Arnold *et al.*, 1994]. Here, we are going to introduce an alternative approach in order to study the long time behavior $n \gg 1$ of the population vector state. Our approach will be a useful technique to calculate the asymptotic behavior of the mean population vector in the case when the Leslie matrix has random elements, this will be shown in the next section.

Consider the linear matrix dynamics (difference equations) written in the form:

$$X_{n+1} = \mathbf{M} \cdot X_n, \quad (2)$$

where X_n is a state vector of dimension m characterizing the population at the time step n. Each component j of the population vector, $X_n(j)$, represents the number of individuals in each recognized category j. The linear map (2) can be solved by using a generating function technique. We define the generating function $G(z)$ associated to the state vector X_n by

$$G(z) = \sum_{n=0}^{\infty} z^n X_n, \quad (3)$$

multiplying (2) by z^n and summing over all n we get

$$\sum_{n=0}^{\infty} z^n X_{n+1} = \frac{1}{z} \sum_{n=1}^{\infty} z^n X_n = \frac{1}{z}(G(z) - X_0)$$

$$= \mathbf{M} \cdot \sum_{n=0}^{\infty} z^n X_n = \mathbf{M} \cdot G(z).$$

From this equation we can solve $G(z)$ and get the following expression for the generating function (vector $G(z)$)

$$G(z) - z\mathbf{M} \cdot G(z) = X_0. \quad (4)$$

Introducing the $(m \times m)$ identity matrix $\mathbf{1}$ we can define an associated Green function matrix to Eq. (2) of the form

$$\mathbf{G}(z) = [\mathbf{1} - z\mathbf{M}]^{-1}. \quad (5)$$

It is now clear that the Green function $\mathbf{G}(z)$ is a matrix of dimension $(m \times m)$, and the dynamics information of the recurrence relation (2) is contained in the poles of the $\mathbf{G}(z)$. In the nonrandom case these poles are completely equivalent to the eigenvalues of the matrix $\mathbf{M}$. The solution of (2) can be obtained by using the z-inversion technique. Nevertheless, what is more important here is the asymptotic value of X_n for large n, this behavior can be obtained from a Tauberian theorem for power series [Hardy, 1949].

If the matrix $\mathbf{M}$ is irreducible, the matrix $\mathbf{G}(z)$ will have a simple pole of the form $(z_1 - z)$, and each element of the Green function $\mathbf{G}(z)$ will have, in the limit $z \to z_1$, the dominant diverging form: $\mathbf{G}(z) \sim (z_1 - z)^{-1}$, then applying Tauberian's theorem we get asymptotically for large n that (see

Appendix A, Eq. (A.2))

$$X_n \sim \left(\frac{1}{z_1}\right)^n = \lambda_1^n, \tag{6}$$

where z_1 is the smallest positive pole of $\mathbf{G}(z)$. This is the expected result in the ordered case. For the disordered case, the average of the Green function $\langle \mathbf{G}(z) \rangle$ characterizes the asymptotic behavior of the *mean-value* vector state $\langle X_n \rangle$. The new dominant pole $\tilde{z}_1$ (the smallest positive one, which of course is not the average of z_1) characterizes the *effective* rate at which the population grows in a random Leslie model.

2. Average of the Green Function

Consider a Leslie matrix as in (1) but with random elements. Noting that all the elements of $\mathbf{M}$ must be positives, we adopt the following notation:

$$f_j \to f_j - \alpha_j \quad \text{with } (f_j - \alpha_j) \geq 0 \tag{7}$$

$$p_j \to p_j - \beta_j \quad \text{with } 1 \geq (p_j - \beta_j) > 0, \tag{8}$$

where the quantities α_j, β_j represent the random elements in a general Leslie dynamics. In principle, we are going to work out the problem for *arbitrary* random variables $\{\alpha_j, \beta_j\}$, with the only restriction that the support of these random variables must fulfill conditions (7) and (8) for each sample of the disorder (the use or not of the statistical independence assumption of the set $\{\alpha_j, \beta_j\}$ will be analyzed in future contributions). Therefore, in what follows we do not need to emphasize any *specific* distribution for these random variables. Using the definition (7) and (8) we can rewrite vital parameters in the form

$$f_j - \alpha_j = f_j - \langle \alpha_j \rangle + \langle \alpha_j \rangle - \alpha_j \equiv f_j^* + \xi_j \tag{9}$$

$$p_j - \beta_j = p_j - \langle \beta_j \rangle + \langle \beta_j \rangle - \beta_j \equiv p_j^* + \eta_j, \tag{10}$$

where $\langle \alpha_j \rangle$ and $\langle \beta_j \rangle$ are mean values, thus it is clear that f_j^* and p_j^* are sure *positive* numbers, and $\{\xi_j \equiv \langle \alpha_j \rangle - \alpha_j; \eta_j = \langle \beta_j \rangle - p_j\}$ are random numbers with *mean-value zero*. Using these facts we can write the random equation for the Green function (5) as:

$$\frac{1}{z}(\mathbf{G}(z) - \mathbf{1}) = (\mathbf{H} + \mathbf{B}) \cdot \mathbf{G}(z), \tag{11}$$

where we have defined $\mathbf{H} + \mathbf{B} \equiv \mathbf{M}$. Here $\mathbf{H}$ is a sure Leslie matrix and $\mathbf{B}$ a random matrix (not necessarily with positive elements) but with the particular structure:

$$\mathbf{B} = \begin{pmatrix} \xi_1 & \xi_2 & \xi_3 & \cdots & \cdots & \xi_m \\ \eta_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & \eta_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & \eta_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & 0 & \eta_{m-1} & \cdots \end{pmatrix}. \tag{12}$$

Note that by construction $\langle \mathbf{B} \rangle = 0$, and $\mathbf{H}$ is a sure Leslie matrix with shifted elements given by:

$$f_j^* = f_j - \langle \alpha_j \rangle, \qquad p_j^* = p_j - \langle \beta_j \rangle. \tag{13}$$

In order to calculate the average of the Green function $\langle \mathbf{G}(z) \rangle$ we need to find its evolution equation, this can be done by using a projector operator technique, see for example [Hernandez *et al.*, 1990a; Hernandez *et al.*, 1990b; Cáceres *et al.*, 1997; Cáceres, 2003, 2004]. The average of $\mathbf{G}(z)$, i.e. averaging over the random variables $\{\xi_j, \eta_j\}$, can formally be carried out by introducing the projector operator $\mathcal{P}$ that averages over the disorder, and its complementary projector $\mathcal{Q} \equiv (1 - \mathcal{P})$, i.e.

$$\langle \mathbf{G}(z) \rangle = \mathcal{P}\mathbf{G}(z), \quad \mathbf{G}(z) = \mathcal{P}\mathbf{G}(z) + \mathcal{Q}\mathbf{G}(z).$$

Using this projector technique a closed *exact* evolution equation can be obtained. Applying the operator $\mathcal{P}$ to Eq. (11) we obtain

$$\frac{1}{z}[\mathcal{P}\mathbf{G}(z) - \mathbf{1}] = \mathbf{H}\mathcal{P}\mathbf{G}(z) + \mathcal{P}\mathbf{B}\mathcal{P}\mathbf{G}(z) + \mathcal{P}\mathbf{B}\mathcal{Q}\mathbf{G}(z). \tag{14}$$

Also, applying the operator $\mathcal{Q}$ to Eq. (11) we obtain

$$\frac{1}{z}\mathcal{Q}\mathbf{G}(z) = \mathbf{H}\mathcal{Q}\mathbf{G}(z) + \mathcal{Q}\mathbf{B}\mathcal{P}\mathbf{G}(z) + \mathcal{Q}\mathbf{B}\mathcal{Q}\mathbf{G}(z). \tag{15}$$

A formal solution of Eq. (15) can be obtained using the *nondisordered* Green matrix:

$$\mathbf{G}^0 \equiv \left[\frac{1}{z}\mathbf{1} - \mathbf{H}\right]^{-1}. \tag{16}$$

Applying $\mathbf{G}^0(z)$ to Eq. (15) and using the definition given in Eq. (16), results in

$$\mathcal{Q}\mathbf{G}(z) = \mathbf{G}^0[\mathcal{Q}\mathbf{B}\mathcal{P}\mathbf{G}(z) + \mathcal{Q}\mathbf{B}\mathcal{Q}\mathbf{G}(z)]. \tag{17}$$

This equation can be solved iteratively for $\mathcal{Q}\mathbf{G}(z)$,

$$\mathcal{Q}\mathbf{G}(z) = \sum_{k=1}^{\infty}[\mathbf{G}^0\mathcal{Q}\mathbf{B}]^k\mathcal{P}\mathbf{G}(z). \tag{18}$$

Placing this formal solution in Eq. (14) we find a close *exact* equation for the function $\mathcal{P}\mathbf{G}(z)$,

$$\frac{\mathcal{P}\mathbf{G}(z)-\mathbf{1}}{z} = \mathbf{H}\mathcal{P}\mathbf{G}(z) + \mathcal{P}\mathbf{B}\mathcal{P}\mathbf{G}(z) + \mathcal{P}\mathbf{B}\sum_{k=1}^{\infty}[\mathbf{G}^0\mathcal{Q}\mathbf{B}]^k\mathcal{P}\mathbf{G}(z). \quad (19)$$

This equation can be rewritten in a more friendly way

$$\langle\mathbf{G}(z)\rangle = \left[\mathbf{1} - z\left(\mathbf{H} + \left\langle\sum_{k=0}^{\infty}[\mathbf{B}\mathbf{G}^0\mathcal{Q}]^k\mathbf{B}\right\rangle\right)\right]^{-1}. \quad (20)$$

Here, we can see the nontrivial structure that the average Green function obtained as a consequence of its evolution in time.

We remark that even in the case when the random Leslie matrix $\mathbf{M}$ is of dimension m, the number of z-poles in $\langle\mathbf{G}(z)\rangle$ will depend on the number of nonnull contributions from the series expansion appearing in (20). From this solution we can easily demonstrate that the "naive" approximation: $\langle\mathbf{G}(z)\rangle \simeq [\mathbf{1} - z\mathbf{H}]^{-1}$ corresponds to neglecting all "cumulant contributions" with $k \geq 1$. Each cumulant represents a particular *structure of correlation* that we need to evaluate carefully.

Remark. The important task is to calculate the different k-contributions from the object ($\langle\mathbf{B}\rangle = 0$)

$$\left\langle\sum_{k=0}^{\infty}[\mathbf{B}\mathbf{G}^0\mathcal{Q}]^k\mathbf{B}\right\rangle, \quad (21)$$

as a function of z for a given model of disorder. In fact, we will prove that the operator (21) can be studied in terms of statistical objects called Terwiel's *cumulants*, that will be defined later [Terwiel, 1974; Hernandez *et al.*, 1990a; Cáceres, 2003], see Appendix B. In particular, if the intensity of the random variables $\{\xi_j, \eta_j\}$ can be considered as a small parameter, we can analyze the behavior of the dominant pole of the averaged Green function (20), order-by-order to any contribution that comes from a different k in Eq. (21). By virtue of the Tauberian theorem, the long-time behavior of $\langle\mathbf{G}(z)\rangle$ will be dominated by the smallest strictly positive root $\tilde{z}_1$ of

$$\det\left|\mathbf{1} - z\left(\mathbf{H} + \left\langle\sum_{k=0}^{\infty}[\mathbf{B}\mathbf{G}^0\mathcal{Q}]^k\mathbf{B}\right\rangle\right)\right| = 0. \quad (22)$$

Remark. We conclude that the stability of the *mean-value* population vector state shall be characterized as

$$\lim_{n\to\infty}\langle X_n\rangle \sim \left(\frac{1}{\tilde{z}_1}\right)^n = (\tilde{\lambda}_1)^n. \quad (23)$$

This formula generalizes (6) in the case when the dynamics are characterized by a random Leslie matrix. Note that if the pole $\tilde{z}_1$ were degenerated we can still apply the Tauberian theorem and, of course, a different asymptotic behavior ($n \gg 1$) to obtain the mean-value population vector state. In Appendix C, we present an example of stability analysis for a particular random survival model in a general $m \times m$ Leslie matrix.

3. An Exact 2×2 Soluble Case

Consider a 2×2 Leslie matrix where the fertility of the subclass 2 has a random element of the form $f_2 - \alpha_2$, then following the previous sections we see that the problem is completely characterized by defining the matrices:

$$\mathbf{G}^0 = \left[\frac{1}{z}\mathbf{1} - \mathbf{H}\right]^{-1}, \quad \mathbf{H} = \begin{pmatrix} f_1 & f_2^* \\ p_1 & 0 \end{pmatrix}, \quad \mathbf{B} = \begin{pmatrix} 0 & \xi_2 \\ 0 & 0 \end{pmatrix}, \quad (24)$$

where $\xi_2 = \langle\alpha_2\rangle - \alpha_2$, $f_2^* = f_2 - \langle\alpha_2\rangle$. From (24) we can calculate the Terwiel operator (21). We get for every k

$$\langle[\mathbf{B}\mathbf{G}^0\mathcal{Q}]^k\mathbf{B}\rangle = \begin{pmatrix} 0 & g_{21}^k\langle[\xi_2\mathcal{Q}]^k\xi_2\rangle \\ 0 & 0 \end{pmatrix},$$

here, as before, g_{jl} are the matrix elements of the ordered Green function $\mathbf{G}^0$. Summing all k contributions we obtain

$$\left\langle\sum_{k=0}^{\infty}[\mathbf{B}\mathbf{G}^0\mathcal{Q}]^k\mathbf{B}\right\rangle = \begin{pmatrix} 0 & \sum_{k=0}^{\infty} g_{21}^k\langle[\xi_2\mathcal{Q}]^k\xi_2\rangle \\ 0 & 0 \end{pmatrix}. \quad (25)$$

Then, we have proved that for this 2×2 case and for any statistics of the random variables ξ_2, we only have to calculate the statistical object

$$\langle[\xi_2\mathcal{Q}]^k\xi_2\rangle, \quad k = 1, 2, 3, \ldots, \quad (26)$$

these are in fact Terwiel's cumulants, see Appendix B.

3.1. *Binary disorder in the fertility*

In order to continue the analysis of our example (24), suppose now that the random variable α_2 can only take two discrete values $\pm\Delta$, i.e.

$$\alpha_2 = \begin{cases} \Delta & \text{with probability } c \\ -\Delta & \text{with probability } (1-c) \end{cases}. \tag{27}$$

In order to assure that the random fertility $f_2 - \alpha_2$ is a positive quantity for each sample of the disorder, we have to assume that $0 \le \Delta \le f_2$. From (27) it is simple to see that (for $q = 1, 2, 3, \ldots$)

$$\langle \alpha_2^{2q+1} \rangle = \Delta^{2q+1}(2c-1); \quad \langle \alpha_2^{2q} \rangle = \Delta^{2q}. \tag{28}$$

It is also possible to prove that Terwiel's cumulants of the random variable $\xi_2 = \langle \alpha_2 \rangle - \alpha_2$ are (for $k = 1, 2, 3, \ldots$)

$$\langle [\xi_2 \mathcal{Q}]^k \xi_2 \rangle = \Delta^{k+1} c(1-c)(2c-1)^{k-1} 2^{k+1}. \tag{29}$$

From this result, we get the important conclusion that for a *symmetric* binary random perturbation (i.e. with $c = 1/2$) all Terwiel's cumulants vanish for $k \ge 2$. Then in the symmetric case, the only non-null Terwiel's cumulant appearing in (26) will be $\langle \xi_2 \mathcal{Q} \xi_2 \rangle = \Delta^2$. In order to remark the difference between Terwiel's cumulant with the *simple* cumulants, we write here the formula for the usual cumulants corresponding to the random variable ξ_2; using (27) for the symmetric case, i.e. $\xi_2 = \alpha_2$ (when $c = 1/2$) we get [Cáceres, 2003]

$$\langle\langle \xi_2^{2q} \rangle\rangle = \frac{-2^{2q-1}(2^{2q}-1)B_q}{i^{2q} q} \Delta^{2q}, \qquad q = 1, 2, 3, \ldots,$$

where B_q are the Bernoulli numbers: $\{B_q\} = \{1/6, 1/30, 1/42, \ldots\}$. This result shows, for the symmetric binary case, the simplicity of Terwiel's cumulants against the usual ones.

3.2. *The symmetric binary case*

From all these previous facts we see that for this 2×2 case we can write the *exact solution* of the averaged Green function. From model (24) with a *symmetric* binary random variable, using the general expression (20) and noting that $f_2^* = f_2$ we get

$$\begin{aligned} \langle \mathbf{G}(z) \rangle &= \left[\mathbf{1} - z \left(\mathbf{H} + \left\langle \sum_{k=0}^{\infty} [\mathbf{B}\mathbf{G}^0 \mathcal{Q}]^k \mathbf{B} \right\rangle \right) \right]^{-1} \\ &= \left[\mathbf{1} - z \begin{pmatrix} f_1 & f_2 + g_{21}\Delta^2 \\ p_1 & 0 \end{pmatrix} \right]^{-1}, \end{aligned} \tag{30}$$

here

$$g_{21} = \frac{p_1 z^2}{1 - f_1 z - p_1 f_2 z^2} = \frac{p_1}{\left(\frac{1}{z} - \lambda_1\right)\left(\frac{1}{z} - \lambda_2\right)},$$

where $\lambda_{1,2}$ are the eigenvalues of the sure matrix $\mathbf{H}$, in the case when $c = 1/2$, these eigenvalues coincide with the 2×2 nonrandom Leslie matrix $\mathbf{M}$, see (11) and (24), i.e.

$$\lambda_{1,2} = \frac{1}{2}\left(f_1 \pm \sqrt{f_1^2 + 4p_1 f_2} \right). \tag{31}$$

In order to find the dominant pole of $\langle \mathbf{G}(z) \rangle$, we study (30) introducing the notation $z = 1/\lambda$, then we solve the roots of

$$(\lambda^2 - \lambda f_1 - f_2 p_1) = \frac{(p_1 \Delta)^2}{(\lambda^2 - \lambda f_1 - f_2 p_1)}.$$

This equation implies fourth roots (we adopt $0 \le \Delta \le f_2$ to assure the positivity of the Perron–Frobenius eigenvector Ψ_1 for each sample of the disorder), then

$$\tilde{\lambda}_{1,2} = \frac{1}{2}\left(f_1 \pm \sqrt{f_1^2 + 4p_1(f_2 + \Delta)} \right)$$
$$\tilde{\lambda}_{3,4} = \frac{1}{2}\left(f_1 \pm \sqrt{f_1^2 + 4p_1(f_2 - \Delta)} \right).$$

It is now clear that the largest positive one is

$$\tilde{\lambda}_1 = \frac{1}{2}\left[f_1 + \sqrt{f_1^2 + 4p_1(f_2 + \Delta)} \right]. \tag{32}$$

As we mentioned before this *effective* eigenvalue is different from the average of λ_1.

Remark. The *effective* finite growth rate of the disordered Leslie model (24) with a symmetric binary random perturbation α_2 is characterized by $\tilde{\lambda}_1$. This exact result shows, by using the Tauberian theorem, that the average of the population grows faster than in the ordered case (without a random element in the fertility f_2), i.e.

$$\lim_{n\to\infty}\langle X_n\rangle \sim \left(\frac{1}{\tilde{z}_1}\right)^n = (\tilde{\lambda}_1)^n = \left(\frac{1}{2}\left[f_1 + \sqrt{f_1^2 + 4p_1(f_2+\Delta)}\right]\right)^n, \tag{33}$$

where Δ^2 is the dispersion of α_2 (see (28)). An equivalent analysis can also be carried out by putting a random element in the survival parameter p_1.

Now, we show another exact result for the *effective* finite growth rate, but in the case of having a *symmetric* random perturbation α_1 in the fertility parameter $f_1 \to f_1 - \alpha_1$. As in (24) the problem is now defined by considering

$$\mathbf{G}^0 = \left[\frac{1}{z}\mathbf{1} - \mathbf{H}\right]^{-1}, \quad \mathbf{H} = \begin{pmatrix} f_1 & f_2 \\ p_1 & 0 \end{pmatrix}, \quad \mathbf{B} = \begin{pmatrix} \xi_1 & 0 \\ 0 & 0 \end{pmatrix}, \tag{34}$$

where $\xi_1 = -\alpha_1$, $f_1^* = f_1$ adopting a symmetric binary random variable for α_1. The exact averaged Green function now looks like

$$\langle \mathbf{G}(z)\rangle = \left[\mathbf{1} - z\left(\mathbf{H} + \left\langle \sum_{k=0}^{\infty}[\mathbf{B}\mathbf{G}^0\mathcal{Q}]^k\mathbf{B}\right\rangle\right)\right]^{-1} = \left[\mathbf{1} - z\begin{pmatrix} f_1 + g_{11}\Delta^2 & f_2 \\ p_1 & 0 \end{pmatrix}\right]^{-1}, \tag{35}$$

where $g_{11} = ((p_1/z)/(((1/z)-\lambda_1)((1/z)-\lambda_2)))$, and as before $\lambda_{1,2}$ are the eigenvalues of the sure matrix $\mathbf{H}$, see Eq. (31). From the poles of Eq. (35) we immediately get that the dominant (smallest positive) pole $\tilde{z}_1 = 1/\tilde{\lambda}_1$ is (adopting $0 \le \Delta \le f_1$) characterized by the largest positive eigenvalue

$$\tilde{\lambda}_1 = \frac{1}{2}\left[f_1 + \Delta + \sqrt{(f_1+\Delta)^2 + 4p_1 f_2}\right]. \tag{36}$$

This exact result shows that from the model (34), the average of the population grows faster than in the ordered case. In this case, the population vector state grows as

$$\lim_{n\to\infty}\langle X_n\rangle \sim \left(\frac{1}{\tilde{z}_1}\right)^n = (\tilde{\lambda}_1)^n = \left(\frac{1}{2}\left[f_1 + \Delta + \sqrt{(f_1+\Delta)^2 + 4p_1 f_2}\right]\right)^n. \tag{37}$$

It is important to mention that the convexity of the effective growth rate $\tilde{\lambda}_1$ (36) as a function of the random intensity Δ, is different when compared with the previous case (32). Nevertheless, in both cases the effective eigenvalue $\tilde{\lambda}_1$ is larger than in the nonrandom case $\lambda_1 = (1/2)(f_1 + \sqrt{f_1^2 + 4p_1 f_2})$. In order to quantify this comment we can take the derivative of $\tilde{\lambda}_1$ with respect to the strength Δ and evaluate $d\tilde{\lambda}_1/d\Delta$ at $\Delta = 0$. In this form, we can measure the variation of the effective eigenvalue to a small random perturbation and prove that if the perturbation is symmetric the effective eigenvalue $\tilde{\lambda}_1$ is always larger than in the nonrandom case.

For a symmetric binary random perturbation in the fertility f_2, i.e. from (32) we get

$$\tilde{\lambda}_1 \simeq \lambda_1 + \frac{p_1}{\sqrt{f_1^2 + 4p_1 f_2}}\Delta. \tag{38}$$

But for a symmetric binary random perturbation in the fertility f_1, i.e. from (36) we get

$$\tilde{\lambda}_1 \simeq \lambda_1 + \frac{1}{2}\left(1 + \frac{f_1}{\sqrt{f_1^2 + 4p_1 f_2}}\right)\Delta. \tag{39}$$

These simple but interesting results can be of great use in modeling biological population growth, for example, using fixed (mean values) Leslie vital parameters, we see that $\lambda_1 < 1$. Nevertheless, considering *symmetric* fluctuations (sampling error in estimating the vital rates) we could get $\tilde{\lambda}_1$ larger than 1, and in this way predict an increasing population.

One last remark concerning our 2×2 model: suppose now that random elements appear in both fertilities f_1, f_2, or simultaneously in the three Leslie vital parameters f_1, f_2, p_1. Then, it is possible to see that even if we would have used *the statistically independent assumption* for the set $\{\xi_1, \xi_2, \eta_1\}$ the Terwiel operator

$$\left\langle \sum_{k=0}^{\infty}[\mathbf{B}\mathbf{G}^0\mathcal{Q}]^k\mathbf{B}\right\rangle, \tag{40}$$

would not cut in the second Terwiel's cumulant! This is due to the occurrence of a higher order nontrivial Terwiel's structure between the different random variables. For example, in the presence of random elements in both fertilities f_1, f_2, it is possible to see that apart from the simplest second order contribution: $\langle \mathbf{B}\mathbf{G}^0\mathcal{Q}\mathbf{B}\rangle$, higher order statistical contributions come from non-null Terwiel's cumulants like:

$$\langle \xi_1 \mathcal{Q} \xi_2 \mathcal{Q} \xi_1 \mathcal{Q} \xi_2 \rangle; \quad \langle \xi_1 \mathcal{Q} \xi_2 \mathcal{Q} \xi_2 \mathcal{Q} \xi_1 \rangle;$$

$$\langle \xi_1 \mathcal{Q} \xi_2 \mathcal{Q} \xi_2 \mathcal{Q} \xi_2 \mathcal{Q} \xi_2 \mathcal{Q} \xi_1 \rangle; \quad \langle \xi_1 \mathcal{Q} \xi_2 \mathcal{Q} \xi_1 \mathcal{Q} \xi_2 \mathcal{Q} \xi_1 \mathcal{Q} \xi_2 \rangle,$$

etc.

These cumulants lead to the occurrence of a nontrivial structure in the calculation of the dominant pole of the mean-value Green function.

Remark. Note that even in the case when the random variables ξ_1, ξ_2 are *statistically independent* these cumulants do not cancel. Terwiel's cumulants can easily be evaluated using diagrams, but we will leave this discussion for a future contribution, see Appendix B for details. In order to calculate the averaged Green function we have to introduce a criterion to cut the Terwiel cumulant series. A possible way is to invoke an expansion in the intensity of the random perturbation. For example, if Δ is a small parameter, it is clear that higher Terwiel's cumulants are of lower order, then we can approximate (40) up to some $\mathcal{O}(\Delta^q)$ in order to calculate the mean-value Green function. From this approximated (truncated) function $\langle \mathbf{G}(z) \rangle$ we can estimate the *effective* finite growth rate of the mean-value population vector state. An example in that direction will be shown in future contributions considering the presence of uniformly distributed random variables perturbing all the vital rates.

4. Conclusions

The main concern of this paper is to relate the characteristics of disorder (sampling error in estimating the vital rates) appearing in a Leslie matrix $\mathbf{M}$ with the dynamics of the population. The focus was on the effects that fluctuations have on the dominant eigenvalue $\tilde{\lambda}_1$ (the largest positive one) associated to the mean-value Green function of the random matrix problem. A general approach, to get this effective eigenvalue, was described. We calculate the dynamics of the mean-value population vector state under the assumption that the random variables, appearing in the Leslie matrix, are described with arbitrary distributions. The problem was reduced to the calculation of the smallest positive root $\tilde{z}_1$ of the secular polynomial appearing in the general expression for the mean-value Green function $\langle \mathbf{G}(z) \rangle$. This nontrivial polynomial can be obtained order by order in terms of a diagrammatic technique built with Terwiel's cumulants, which have carefully been identified in the present work. By understanding how this smallest positive root $\tilde{z}_1 = 1/\tilde{\lambda}_1$ depends on the model of disorder one can link the asymptotic population dynamics with the statistical properties of the errors in the vital parameters. Particular examples were presented using binary random variables affecting the survival parameters in Leslie matrices of dimensions 2×2. It was shown that the *effective* growth rate $\tilde{\lambda}_1$ has a nontrivial response to the perturbation. In particular, it was proved that if the random variables are *symmetric*, the effective positive eigenvalue is enlarged with respect to the mean-value growth rate. On the other hand, it is possible to prove that even when fluctuations (due to the presence of random variables) always reduce the vital parameters of the model, the *effective* eigenvalue is always larger than the naive approximation associated to the mean-value of the Leslie matrix $\langle \mathbf{M} \rangle = \mathbf{H}$. This result teaches us that fluctuations increase the final *effective* growth rate. In the present paper, we have worked out an *exact* 2×2 model with *symmetric* fluctuations, but an equivalent analysis can also be done for nonsymmetric disorder. Here, we would like to remark:

(a) By using a Green function technique we have studied the time evolution of the mean-value population vector $\langle X_n \rangle$ (this is the so-called z-transform technique).
(b) The long-time asymptotic limit ($n \gg 1$) of the mean-value population vector is $\langle X_n \rangle \sim (\tilde{\lambda}_1)^n$ (we prove this fact using the Tauberian theorem).
(c) The effective eigenvalue $\tilde{\lambda}_1$ can be calculated, order-by-order, by solving the smallest positive root ($\tilde{z}_1 = 1/\tilde{\lambda}_1$) of the secular polynomial (22), which is written in terms of all the correlations coming from $\mathbf{B}$.
(d) Our approach is independent of the statistics chosen for the random variables that may appear in $\mathbf{B}$.
(e) If the dimension of the Leslie matrix is small, there is hope that an analytical approximation can be found (see our examples in dimension 2×2). For large dimension analysis our method is constructive, i.e. the calculation of the root $\tilde{z}_1$ can be done numerically and the error can be computed from the neglected terms in Eq. (21).
(f) The present perturbation theory can be applied to any random Leslie's matrix of arbitrary dimension with or without the statistical independent assumption.

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Appendix A The Tauberian Approach

The Tauberian theorem is as follows [Hardy, 1949]. Let $U(y)$ be defined by

$$U(y) = \sum_{n=0}^{\infty} a_n \exp(-ny), \tag{A.1}$$

where $a_n > 0$. Let $U(y)$ have the asymptotic form, as $y \to 0, U(y) \sim \varphi(y^{-1}) = y^{-\gamma} L(y^{-1})$, where $L(x)$ is a slowly varying function, and $x^{\gamma} L(x)$ is a positive increasing function of x for sufficiently large x. Then as $n \to \infty$

$$a_0 + a_1 + a_2 + \cdots + a_n \sim \frac{\varphi(n)}{\Gamma(\gamma+1)},$$

where $\Gamma(\gamma+1)$ is the gamma function. If a_n are monotonic and $\varphi(x)$ is differentiable, it follows that

$$a_n \sim \left. \frac{\dfrac{d\varphi(x)}{dx}}{\Gamma(\gamma+1)} \right|_{x=n}.$$

This is the important result that we use to study the asymptotic behavior of X_n for large n.

In order to apply the Tauberian theorem to our problem, we introduce the change of variable $z \to z_1 e^{-y}$, where $z_1 = 1/\lambda_1$, then from the generating function (3) of Sec. 1 we get

$$G(z = z_1 e^{-y}) = \sum_{n=0}^{\infty} \exp(-yn) z_1^n X_n.$$

Thus, we can derive from (A.1) that $a_n = z_1^n X_n$. On the other hand, if the Leslie matrix $\mathbf{M}$ is irreducible, the matrix $\mathbf{G}(z)$ (Sec. 1, Eq. (5)) will have a simple pole of the form $(z_1 - z)$, thus the Green function

$\mathbf{G}(z)$ will have in the limit $z \to z_1$ the dominant diverging form

$$\mathbf{G}(z) \to \frac{1}{(z_1 - z)}\mathcal{G},$$

where the $m \times m$ matrix $\mathcal{G}$ remains finite in the limit $z \to z_1$. Using $U(y) = G(z = z_1 e^{-y}) \sim (z_1 - z_1 e^{-y})^{-1}$, and in the limit of $y \to 0$ we get $U(y) \sim \varphi(y^{-1}) \sim y^{-\gamma}/z_1$, where $\gamma = 1, L(x) = 1$. For $n \to \infty$, and using the Tauberian theorem we obtain asymptotically that $a_n \sim \varphi'(n)/\Gamma(2) \sim 1$. Going back to the old variable we obtain in the limit $n \gg 1$

$$X_n \sim \left(\frac{1}{z_1}\right)^n = \lambda_1^n, \tag{A.2}$$

which is the asymptotic behavior of the vector state in the ordered case.

Remark. The Tauberian approach teaches us that if we want to tackle the random case we should first calculate the average of the Green function $\langle \mathbf{G}(z) \rangle$, then from its poles we can infer which is the asymptotic behavior of the average of the vector state $\langle X_n \rangle$. The smallest positive pole $\tilde{z}_1 = 1/\tilde{\lambda}_1$ characterizes the rate at which the population grows in a random Leslie model.

Appendix B
Terwiel's Cumulants

The calculations of Terwiel's cumulants are not so complex [Terwiel, 1974]. Here we recall some general properties of these cumulants. Consider the *general* situation when we have a set of random variables $\{\xi_j\}$, then a Terwiel cumulant of order q can be written in terms of the moments of the variables $\{\xi_j\}$ by using the following formula

$$\begin{aligned}&\langle \xi_1 \mathcal{Q} \xi_2 \mathcal{Q} \xi_3 \mathcal{Q} \cdots \xi_{q-1} \mathcal{Q} \xi_q \rangle \\ &\quad = \sum_{r=0}^{q-1} (-1)^r \sum_{1 \le l_1 \le \cdots \le l_r \le q} \langle \xi_1 \cdots \xi_{l_1} \rangle \langle \xi_{l_1+1} \cdots \xi_{l_2} \rangle \\ &\quad \times \cdots \langle \xi_{l_r+1} \cdots \xi_q \rangle,\end{aligned} \tag{A.3}$$

where as before $\mathcal{Q}$ is the projection operator $(1 - \mathcal{P})$. Explicit examples of this formula are:

$$\begin{aligned}\langle \xi_1 \mathcal{Q} \xi_2 \rangle &= \langle \xi_1 \xi_2 \rangle - \langle \xi_1 \rangle \langle \xi_2 \rangle \\ \langle \xi_1 \mathcal{Q} \xi_2 \mathcal{Q} \xi_3 \rangle &= \langle \xi_1 \xi_2 \xi_3 \rangle - \langle \xi_1 \rangle \langle \xi_2 \xi_3 \rangle - \langle \xi_1 \xi_2 \rangle \langle \xi_3 \rangle \\ &\quad + \langle \xi_1 \rangle \langle \xi_2 \rangle \langle \xi_3 \rangle \\ \langle \xi_1 \mathcal{Q} \xi_2 \mathcal{Q} \xi_3 \mathcal{Q} \xi_4 \rangle &= \langle \xi_1 \xi_2 \xi_3 \xi_4 \rangle - \langle \xi_1 \rangle \langle \xi_2 \xi_3 \xi_4 \rangle \\ &\quad - \langle \xi_1 \xi_2 \rangle \langle \xi_3 \xi_4 \rangle - \langle \xi_1 \xi_2 \xi_3 \rangle \langle \xi_4 \rangle \\ &\quad + \langle \xi_1 \rangle \langle \xi_2 \rangle \langle \xi_3 \xi_4 \rangle + \langle \xi_1 \xi_2 \rangle \langle \xi_3 \rangle \langle \xi_4 \rangle \\ &\quad + \langle \xi_1 \rangle \langle \xi_2 \xi_3 \rangle \langle \xi_4 \rangle \\ &\quad - \langle \xi_1 \rangle \langle \xi_2 \rangle \langle \xi_3 \rangle \langle \xi_4 \rangle.\end{aligned} \tag{A.4}$$

In the particular case when the random variables $\{\xi_j\}$ have zero mean-value, Terwiel's cumulants simplify notably, for example:

$$\begin{aligned}\langle \xi_1 \mathcal{Q} \xi_2 \rangle &= \langle \xi_1 \xi_2 \rangle \\ \langle \xi_1 \mathcal{Q} \xi_2 \mathcal{Q} \xi_3 \rangle &= \langle \xi_1 \xi_2 \xi_3 \rangle \\ \langle \xi_1 \mathcal{Q} \xi_2 \mathcal{Q} \xi_3 \mathcal{Q} \xi_4 \rangle &= \langle \xi_1 \xi_2 \xi_3 \xi_4 \rangle - \langle \xi_1 \xi_2 \rangle \langle \xi_3 \xi_4 \rangle \\ \langle \xi_1 \mathcal{Q} \xi_2 \mathcal{Q} \xi_3 \mathcal{Q} \xi_4 \mathcal{Q} \xi_5 \rangle &= \langle \xi_1 \xi_2 \xi_3 \xi_4 \xi_5 \rangle \\ &\quad - \langle \xi_1 \xi_2 \rangle \langle \xi_3 \xi_4 \xi_5 \rangle \\ &\quad - \langle \xi_1 \xi_2 \xi_3 \rangle \langle \xi_4 \xi_5 \rangle \\ \langle \xi_1 \mathcal{Q} \xi_2 \mathcal{Q} \xi_3 \mathcal{Q} \xi_4 \mathcal{Q} \xi_5 \mathcal{Q} \xi_6 \rangle &= \langle \xi_1 \xi_2 \xi_3 \xi_4 \xi_5 \xi_6 \rangle \\ &\quad - \langle \xi_1 \xi_2 \rangle \langle \xi_3 \xi_4 \xi_5 \xi_6 \rangle \\ &\quad - \langle \xi_1 \xi_2 \xi_3 \rangle \langle \xi_4 \xi_5 \xi_6 \rangle \\ &\quad - \langle \xi_1 \xi_2 \xi_3 \xi_4 \rangle \langle \xi_5 \xi_6 \rangle \\ &\quad + \langle \xi_1 \xi_2 \rangle \langle \xi_3 \xi_4 \rangle \langle \xi_5 \xi_6 \rangle.\end{aligned} \tag{A.5}$$

These formulae are general for any kind of random distribution.

To end these remarks, note that Terwiel's cumulants preserve the order of the random variables $\{\xi_j\}$. There is another very important property of any Terwiel cumulant

$$\langle \xi_1 \mathcal{Q} \xi_2 \mathcal{Q} \cdots \mathcal{Q} \xi_k \mathcal{Q} \xi_{k+1} \cdots \mathcal{Q} \xi_m \rangle,$$

if it is possible to split it into two sets $\{\xi_1 \xi_2 \cdots \xi_k\}$ and $\{\xi_{k+1} \cdots \xi_m\}$ without altering the order of the $\xi's$ in such a way that the variables in one of the sets are *statistically independent* of those in the other set, the cumulant vanishes (this is, the *partition* property of Terwiel's cumulants). Terwiel's cumulants are different from the *simple* cumulants that naturally appear in a Taylor expansion of the logarithm of the characteristic function of a random variable [Cáceres, 2003].

Appendix C
Stability, Up to 2nd Order, in a Random Leslie Matrix Model

Here we apply the general formula:

$$\det \left| \mathbf{1} - z \left(\mathbf{H} + \left\langle \sum_{k=0}^{\infty} [\mathbf{B}\mathbf{G}^0 \mathcal{Q}]^k \mathbf{B} \right\rangle \right) \right| = 0, \quad \text{(A.6)}$$

to calculate the dominant pole $\tilde{z}_1$. Then, from the asymptotic behavior:

$$\lim_{n\to\infty} \langle X_n \rangle \sim \left(\frac{1}{\tilde{z}_1} \right)^n,$$

we can analyze the *mean-value* population stability in a concrete biological case. We chose here a particular model of disorder in an arbitrary $m \times m$ Leslie matrix. Following the notation given in Sec. 2, we define a random *survival* model. Then the matrix $\mathbf{B}$ will have the particular structure (with $\langle \eta_l \rangle = 0$):

$$\mathbf{B} = \begin{pmatrix} 0 & 0 & 0 & 0 & \cdots & 0 \\ \eta_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & \eta_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & \eta_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & 0 & \eta_{m-1} & \cdots \end{pmatrix}, \quad \text{(A.7)}$$

The random fertility model can also be worked in an analogous way. From this matrix $\mathbf{B}$, we consider now the cumulant structure given in Eq. (A.6); using $\langle \mathbf{B} \rangle = 0$ the first non-null contribution in (A.6) is of the form

$$\langle \mathbf{B}\mathbf{G}^0 \mathcal{Q} \mathbf{B} \rangle. \quad \text{(A.8)}$$

This cumulant is of $\mathcal{O}(\mathbf{B}^2)$ in the random perturbation and has the structure of a second Terwiel cumulant.

There are some special cases that can be solved in an exact way, but in general, we have to invoke a perturbation approach to keep only a few cumulants in order to arrive at some analytical calculation. In solid state physics, this technique is the starting point to introduce a self-consistent approximation to tackle the problem of transport in random media [Hernandez *et al.*, 1990a; Hernandez *et al.*, 1990b; Pury *et al.*, 2002]. A self-consistent approximation is a good technique to tackle enlarged Leslie's matrices with transition rates between spatial locations [Caswell, 1983], this will be the subject of a future work.

Using the definition of $\mathbf{G}^0 \equiv [(1/z)\mathbf{1} - \mathbf{H}]^{-1}$in terms of the sure $m \times m$ Leslie matrix $\mathbf{H}$ and using (A.7), we get up to $\mathcal{O}(\mathbf{B}^2)$, for example, for the elements $\{j, 2\}, j = 1, 2, 3, \ldots$

$$\langle \mathbf{B}\mathbf{G}^0 \mathcal{Q} \mathbf{B} \rangle_{j2} = \begin{pmatrix} 0 \\ \langle \eta_1 \mathcal{Q} \eta_2 \rangle g_{13} \\ \langle \eta_2 \mathcal{Q} \eta_2 \rangle g_{23} \\ \langle \eta_3 \mathcal{Q} \eta_2 \rangle g_{33} \\ \langle \eta_4 \mathcal{Q} \eta_2 \rangle g_{43} \\ \cdots \end{pmatrix}. \quad \text{(A.9)}$$

This expression is the exact contribution considering all the correlations up to second order. Here g_{jl} are the matrix elements of the ordered Green function $\mathbf{G}^0$, this formula can easily be handled in a computer. Thus, we see that our approach is not restricted to the assumption of statistically independent random perturbations.

A great analytical simplification arises if we consider that all the random variables are *statistically independent*, in this case and using that the set $\{\eta_j\}$ has mean-value zero, we get for the elements $\{j, 2\}, j = 1, 2, 3, \ldots$

$$\langle \mathbf{B}\mathbf{G}^0 \mathcal{Q} \mathbf{B} \rangle_{j2} = \begin{pmatrix} 0 \\ 0 \\ \langle \eta_2 \mathcal{Q} \eta_2 \rangle g_{23} \\ 0 \\ 0 \\ \cdots \end{pmatrix}. \quad \text{(A.10)}$$

In this case, it is now clear that up to $\mathcal{O}(\mathbf{B}^2)$ the only statistical objects that we need to calculate are:

$$\langle \eta_j \mathcal{Q} \eta_j \rangle, \quad j = 1, 2, \ldots, m-1.$$

These numbers depend on the statistical properties that we chose for the set of random variables $\{\eta_j\}$. In total analogy, if we want to study the perturbation up to $\mathcal{O}(\mathbf{B}^3)$, we have to calculate the Terwiel operator:

$$\langle \mathbf{B}\mathbf{G}^0 \mathcal{Q} \mathbf{B}\mathbf{G}^0 \mathcal{Q} \mathbf{B} \rangle.$$

This object looks much more complex, but if we use the statistical independence assumption, the corresponding expression can also be handled analytically.

Remark. Up to $\mathcal{O}(\mathbf{B}^2)$ in the random perturbation and by virtue of the Tauberian theorem, the long-time behavior of the averaged Green function will be dominated by the smallest positive root $\tilde{z}_1(= 1/\tilde{\lambda}_1)$ of

$$\det|\mathbf{1} - z(\mathbf{H} + \langle \mathbf{B}\mathbf{G}^0 \mathcal{Q} \mathbf{B} \rangle)| = 0. \qquad \text{(A.11)}$$

Following [Boyce, 1977] we consider $\tilde{\lambda}_1$ as the *effective* finite growth rate in a disordered Leslie's population model. So in a time-continuous representation, we can consider the number $r = \ln \tilde{\lambda}_1$ as the effective Lyapunov exponent.