Growth Rates for Populations in Random Environments

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Abstract

We study discrete-time population models in random environments by making use of stochastic Leslie matrices and Markov chains. We study the long-term growth rate given by the top Lyapunov exponent as well as the stationary distribution of the population across the age classes. We then discuss the systematic and sampling errors arising from the estimation of such growth rate and suggest a way to bound them.

1 Introduction

The study of structured populations is of great interest in ecology, biology and population dynamics. The population of a certain species is often divided into K age classes or stages and studied through a discrete time model. Leslie matrices are a popular way to represent and model the dynamics of these populations and can be used for instance to study design intervention strategies for declining populations. Migration is not incorporated in the model and usually only the female sex is considered. We will work with stochastic Leslie matrices so our L will be different at each time. At a given time $0 \leq t \leq T$, L_t is a $K+1$ square matrix which determines the transitions between the age classes. $N_t \in R^{K+1}$ is the population vector at time t. We define $f_k \geq 0$ as the fecundity at age k, that is, the number of female offspring for each mother in class k. We also define $0 \leq p_k \leq 1$ as the probability that an individual survives from class k to class $k+1$. Then, at each time step,

$$N_{t+1} = L_t N_t.$$

In matrix form, we can write this as

$$\begin{pmatrix} n_0^{(t+1)} \\ n_1^{(t+1)} \\ n_2^{(t+1)} \\ \vdots \\ n_K^{(t+1)} \end{pmatrix} = \begin{pmatrix} f_0^{(t)} & f_1^{(t)} & f_2^{(t)} & \dots & f_K^{(t)} \\ p_0^{(t)} & 0 & 0 & \dots & 0 \\ 0 & p_1^{(t)} & 0 & \dots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & p_{K-1}^{(t)} & 0 \end{pmatrix} \begin{pmatrix} n_0^{(t)} \\ n_1^{(t)} \\ n_2^{(t)} \\ \vdots \\ n_K^{(t)} \end{pmatrix}.$$

2 Background and methods

We start with an initial population distribution vector v, so at the first time step, $N_1 = L_1 N_0 = L_1 v$. Then, $N_t = L_t L_{t-1} \dots L_1 v$. This model is very similar to a discrete-time Markov chain taking the stochastic row vector as a column vector and working with the transpose of L as the stochastic matrix. The Markov property is satisfied since the probability of moving to the next state depends only on the present state. However, the sum of the rows (columns of L), given by $f_k^{(t)} + p_k^{(t)}$ does not necessarily sum to one. Suppose that the L_t are independent and identically distributed random matrices of some non-negative distribution such that the product of matrices is eventually positive, so there cannot be a row or column of zeros. We first consider a finite set $\mathcal{M}$ of size M and a discrete distribution d on $\mathcal{M}$. We define $w_t = N_t / \|N_t\|$ to be the normalised population distribution vector using the L^1-norm $\|u\| = \sum_{i=0}^{K} |u(i)|$. Let $\mathcal{X} = \{(x(0), \dots, x(K)); x(i) \geq 0, \sum_{i=0}^{K} x(i) = 1\}$ be the simplex where the w_t live. We also define the growth rate at time t to be the value a_t such that $\|N_t\| = e^{a_t} \|N_{t-1}\|$. We will show that w_t is a time-inhomogeneous Markov chain on $\mathcal{X}$ that converges in distribution to π and that the growth rate a_t converges to the stochastic growth rate a given by the top Lyapunov exponent.

2.1 Important result

Define $Y_t = L_t L_{t-1} \dots L_1$ and let $L_0, \dots, L_{t+1} \sim p$ i.i.d. We will first prove an important result, namely, that for any $u, u' \in U$,

$$\left| \log \frac{\|L_{t+1} Y_t u\|}{\|Y_t u\|} - \log \frac{\|L_{t+1} Y_t u'\|}{\|Y_t u'\|} \right| \leq k_2 r^t.$$

We use the L^1 norm defined as $\|x\| = \sum_{i=0}^{K} |x(i)|$. Let $\mathcal{S} = \{(x(0)\ ,\dots,\ x(K));\ x(i) > 0,\ \sum_{i=0}^{K} x(i) = 1\}$. We use the Hilbert projective metric, which is a metric on $\mathcal{S}$:

$$\rho(x, y) = \log \max_{0 \leq i \leq K} x(i)/y(i) + \log \max_{0 \leq i \leq K} y(i)/x(i).$$

One can show that for any L^p-norm, $\|x - y\| \leq \exp[\rho(x, y)] - 1$. Thus, convergence in the projective metric implies convergence in standard norms. The Birkhoff contraction coefficient for non-negative matrices is given by

$$\tau_B(L) = \sup_{u \neq v \in \mathcal{S}} \frac{\rho(Lu, Lv)}{\rho(u, v)} = \frac{1 - \Phi(L)^{1/2}}{1 + \Phi(L)^{1/2}} < 1,$$

where $\Phi(L) = \min_{i,j,k,l} \frac{L_{ik} L_{jl}}{L_{jk} L_{il}}$ if $L > 0$ and 0 otherwise. We now define r as $\max_{L_T, \dots, L_1} \tau_B(L_T \dots L_1)^{1/T}$ for any T. Then, for any t,

$$\tau_B(L_t \dots L_1) \leq k_1 r^t,$$

where $k_1 = r^{1/T - 1}$. Define $\mathcal{U} \in \mathcal{S}$ as a compact subset with stability properties. Using the previous metric, we call $\Delta = \sup_{u,u' \in U} \rho(u, u')$ the diameter of $\mathcal{U}$, which is finite since $\mathcal{U}$ is compact. For $u, u' \in U$, it follows that there is a constant $k_2 = k_1 \Delta$ such that

$$\rho(L_t \dots L_1 u, L_t \dots L_1 u') \leq k_1 r^t \rho(u, u') \leq k_2 r^t.$$

Therefore,

$$\left| \log \frac{\|L_{t+1} L_t \dots L_1 u\|}{\|L_t \dots L_1 u\|} - \log \frac{\|L_{t+1} L_t \dots L_1 u'\|}{\|L_t \dots L_1 u'\|} \right| \leq k_2 r^t.$$

2.2 Time reversal and convergence of the Markov chain

We will show that the Markov chain of the normalised population distribution $w_t = \frac{N_t}{\|N_t\|} = \frac{L_t L_{t-1} \dots L_1 v}{\|L_t L_{t-1} \dots L_1 v\|}$ converges to a stationary distribution π which is stable under the transformation $(u, L) \to (Lu/\|Lu\|, L')$ where L and L' are i.i.d. For any s, we have a Markov chain $w_s, w_{s+1}, w_{s+2} \dots$, and the reverse $w_s, w_{s-1}, w_{s-2} \dots$ is also a Markov chain. For a population vector $v \in \mathcal{U}$ and for $s > t$, let

$$U_{s,t} = \frac{L_s L_{s-1} \dots L_t v}{\|L_s L_{s-1} \dots L_t v\|}.$$

From the earlier result, it follows that for any $t_1, t_2 \geq T$, $\rho(U_{s,-t_1}, U_{s,-t_2}) \leq k_2 r^{T+s}$, so $(U_{s,-t})_{t=0}^{\infty}$ is Cauchy, hence convergent as we have a complete space. Furthermore, for any t, $U_{0,-t}$ has the same distribution as $U_{t,0}$. Therefore, w_t converges in distribution to the stationary distribution π.

2.3 The top Lyapunov exponent and the Furstenberg-Kesen Theorem

The growth rate converges to a limit a, called the stochastic growth rate and given by the top Lyapunov exponent:

$$a = \lim_{t \to \infty} \frac{1}{t} \log \frac{\sum_{i=0}^{K} N_t(i)}{\sum_{i=0}^{K} N_0(i)} = \lim_{t \to \infty} \frac{1}{t} \log \frac{\|L_t L_{t-1} \dots L_1 v\|}{\|v\|},$$

which we can approximate by the simulated expectation of E[log $\|Lu\|$], where (u, L) is selected from π. This follows from Kingman's sub-additive ergodic theorem and Furstenberg-Kesen theorem which we can apply if we show that the Markov chain is uniquely ergodic (both ergodic and has a unique stationary distribution). Suppose $u \sim \pi$ and $u^* \sim \mu$. Let $X_T = \dfrac{L_T \dots L_1 u}{\|L_T \dots L_1 u\|}$ and $X_T^* = \dfrac{L_T \dots L_1 u^*}{\|L_T \dots L_1 u^*\|}$. Then, $\rho(X_T, X_T^*) \to 0$ as $T \to \infty$, which implies $\mu_T \to \pi$ and $\mu = \pi$, so π is uniquely ergodic.

2.4 Estimation of the growth rate a

To estimate the growth rate a, we need to sample from the invariant distribution π and compute an estimator of the expectation $\mathrm{E}[\log \|Lu\|]$. We run the Markov chain for T time steps:

$$a_T = \mathrm{E}\left[\log \frac{\|L_T \dots L_1 v\|}{\|L_{T-1} \dots L_1 v\|}\right].$$

The Monte-Carlo estimate with J samples is given by:

$$\widehat{a}_T \approx \frac{1}{J} \sum_{j=1}^{J} \left(\log \frac{\|L_T^{(j)} \dots L_1^{(j)} v\|}{\|L_{T-1}^{(j)} \dots L_1^{(j)} v\|} \right).$$

This gives two kind of errors for the estimation of a: the systematic error, as we are not sampling exactly from π, and the sampling error, due to the Monte-Carlo estimate.

3 Error bounds

3.1 Systematic error

Let $v \in \mathcal{U}$, $U \sim \pi(.,L)$ and $a = E\left[\log \frac{\|L_{t+1} Y_t U\|}{\|Y_t U\|}\right]$, which we approximate by $E\left[\log \frac{\|L_{t+1} Y_t v\|}{\|Y_t v\|}\right]$.
The bias or the expectation of the systematic error is then:

$$\begin{aligned}
\mathrm{Error}_{\mathrm{sys}} &= \left| E\left[\log \frac{\|L_{t+1} Y_t U\|}{\|Y_t U\|}\right] - E\left[\log \frac{\|L_{t+1} Y_t v\|}{\|Y_t v\|}\right] \right| \\
&\leq E\left[\left|\log \frac{\|L_{t+1} Y_t U\|}{\|Y_t U\|} - \log \frac{\|L_{t+1} Y_t v\|}{\|Y_t v\|}\right|\right] \\
&\leq E\left[\sup_{u,u' \in \mathcal{U}} \left|\log \frac{\|L_{t+1} Y_t u\|}{\|Y_t u\|} - \log \frac{\|L_{t+1} Y_t u'\|}{\|Y_t u'\|}\right|\right] \\
&\leq k_2 r^T.
\end{aligned}$$

3.2 Sampling error

We define the sampling error as $\mathrm{Error}_{\mathrm{samp}} = \left| \frac{1}{J} \sum_{j=1}^{J} \left(\log \frac{\|L_T^{(j)} \dots L_1^{(j)} v\|}{\|L_{T-1}^{(j)} \dots L_1^{(j)} v\|} \right) - \mathrm{E}\left[\log \|Lu\|\right] \right|$.
We can apply the Hoeffding's inequality since the random variables are independent and bounded. The Hoeffding's inequality states that for $X_1 \dots X_J$ i.i.d. random variables with $\alpha \leq X_j \leq \beta$ and for any $z > 0$,

$$P\left(\left| \frac{1}{J} \sum X_j - E[X] \right| > z \right) \leq 2\exp\left(-2J\epsilon^2\right),$$

where $\epsilon = z/(\beta - \alpha)$. For a fixed confidence level p, $z = (\beta - \alpha)\sqrt{\frac{-1}{2J}\log(p/2)}$. Let $\mathrm{X}_j = \log \frac{\|L_T \dots L_1 v\|}{\|L_{T-1} \dots L_1 v\|}$, $\alpha = \log \frac{\inf_{u \in \mathcal{U}} \min_{L \in \mathcal{M}} \|Lu\|}{\inf_{u \in \mathcal{U}} \|u\|}$, $\beta = \log \frac{\sup_{u \in \mathcal{U}} \max_{L \in \mathcal{M}} \|Lu\|}{\inf_{u \in \mathcal{U}} \|u\|}$ and $\epsilon = \left(\frac{-\log(p/2)}{2J}\right)^{1/2}$ in the expression above. Then,

$$\begin{aligned}
P\left(\mathrm{Error}_{\mathrm{samp}} > z\right) &= P\left(\left| \frac{1}{J} \sum_{j=1}^{J} \left(\log \frac{\|L_T^{(j)} \dots L_1^{(j)} v\|}{\|L_{T-1}^{(j)} \dots L_1^{(j)} v\|} \right) - \mathrm{E}\left[\log \|Lu\|\right] \right| > z \right) \\
&\leq 2\exp\left(-2J\epsilon^2\right) \\
&= 2\exp\left[-2J\left(\frac{-\log(p/2)}{2J}\right)\right] \\
&= 2\exp\log(p/2) \\
&= p.
\end{aligned}$$

Hence, at confidence level p and with J estimates,

$$\begin{aligned} \text{Error}_{\text{samp}} &\leq (\beta - \alpha)\sqrt{\frac{-1}{2J}\log(p/2)} \\ &= \left(\log \frac{\sup_{u\in\mathcal{U}} \max_{L\in\mathcal{M}} \|Lu\|}{\inf_{u\in\mathcal{U}} \min_{L\in\mathcal{M}} \|Lu\|}\right)\left(\frac{-\log(p/2)}{2J}\right)^{1/2}. \end{aligned}$$

4 Simulations

The following plots correspond to simulations with continuous random matrices where the population parameters for fecundity and survival are uniformly distributed. We choose $K = 3$ age classes and $T = 1000$ time steps with 5 possible starting values. The population size was chosen to be 100 and the number of Markov chains used for estimating the growth rate was $J = 1000$. We let $f_0 = 0, f_1 = 1.5 + \delta, f_2 = 0.9 + \delta, p_0 = \min(1, 0.8 + \delta)$ and $p_1 = \min(1, 0.5 + \delta)$, where $\delta \sim \text{Uni}(-0.3, 0.3)$. The growth rate converges to the value 0.189 and the population distribution converges to (0.520, 0.342, 0.138). Similar simulations were produced for a finite set of matrices.

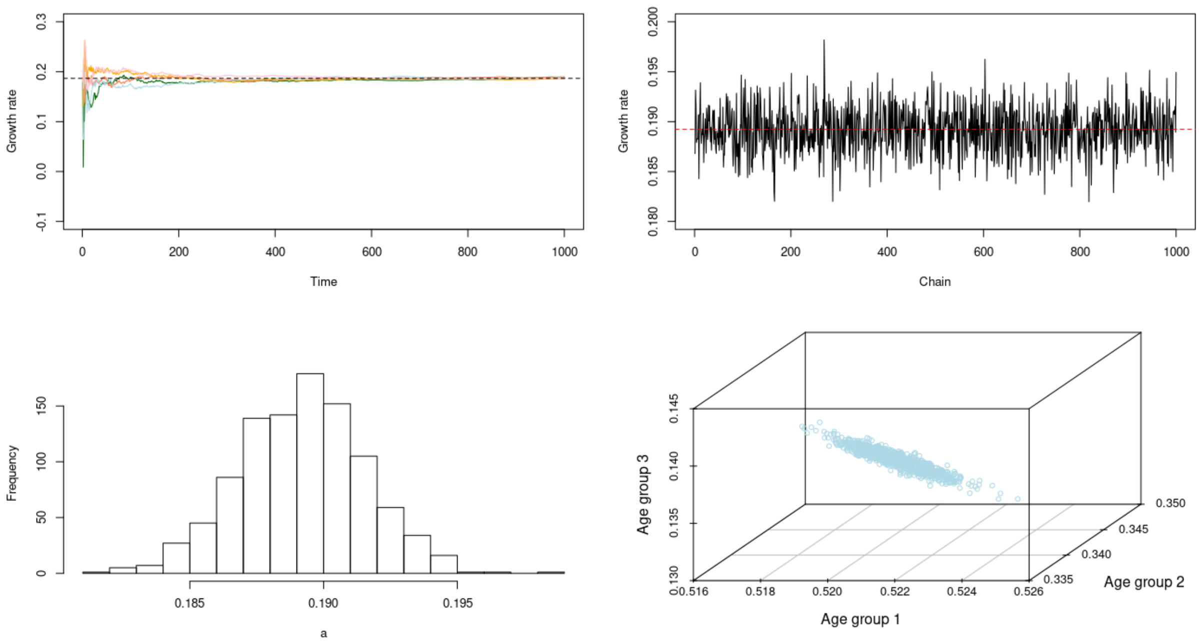

Figure 1: Convergence of the growth rate and stationary distribution ($K = 3, J = 1000, T = 1000$).

References

[1] M. A. Berger, "Central limit theorem for products of random matrices," *Transactions of the American Mathematical Society*, vol. 285, no. 2, pp. 777–803, 1984.

[2] M. O. Cáceres and I. Cáceres-Saez, "Random leslie matrices in population dynamics," *Journal of mathematical biology*, vol. 63, no. 3, pp. 519–556, 2011.

[3] H. Furstenberg and H. Kesten, "Products of random matrices," *The Annals of Mathematical Statistics*, vol. 31, no. 2, pp. 457–469, 1960.

[4] V. Kargin *et al.*, "Products of random matrices: Dimension and growth in norm," *The Annals of Applied Probability*, vol. 20, no. 3, pp. 890–906, 2010.

[5] R. Lande, "Risks of population extinction from demographic and environmental stochasticity and random catastrophes," *The American Naturalist*, vol. 142, no. 6, pp. 911–927, 1993.

[6] N. A. Slade and H. Levenson, "Estimating population growth rates from stochastic leslie matrices," *Theoretical Population Biology*, vol. 22, no. 3, pp. 299–308, 1982.

[7] D. Steinsaltz, S. Tuljapurkar, and C. Horvitz, "Derivatives of the stochastic growth rate," *Theoretical population biology*, vol. 80, no. 1, pp. 1–15, 2011.