Growth Rates for Populations in Random Environments

OxWaSP Module 2: Probability and Approximation

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Overview

1 Introduction

2 Estimation of the growth rate and errors

3 Lyapunov exponents and the Multiplicative Ergodic Theorem

The Leslie model

Elements

- K age classes
- Fecundity $f_k \geq 0$
- Survival between classes $0 \leq p_k \leq 1$
- $N_{t+1} = L_t N_t$
- Growth rate a_t given by $\|N_t\| = e^{a_t}\|N_{t-1}\| \implies a_t = \log \frac{\|N_t\|}{\|N_{t-1}\|}$

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

Background

- L_t i.i.d
- Normalised population distribution $w_t = \frac{N_t}{\|N_t\|} = \frac{L_t L_{t-1} \dots L_1 v}{\|L_t L_{t-1} \dots L_1 v\|}$
- $\{w_t : t > 0\}$ forms a (continuous state space) Markov chain on the simplex S
- Stationary distribution π stable under the transformation $(u, L) \to (Lu/\|Lu\|, L')$
- The growth rate $a_t = \log \frac{\|N_t\|}{\|N_{t-1}\|}$ converges to the stochastic growth rate given by the top Lyapunov exponent

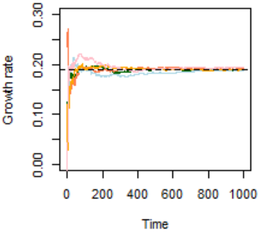
$$a = \lim_{t\to\infty} \frac{1}{t} \log \frac{\sum_{i=0}^{K} N_t(i)}{\sum_{i=0}^{K} N_0(i)} = \lim_{t\to\infty} \frac{1}{t} \log \frac{\|L_t L_{t-1} \dots L_1 v\|}{\|v\|} = \mathrm{E}[\log \|Lu\|]$$

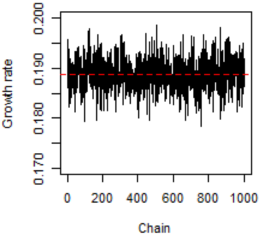
Estimation of the growth rate and errors

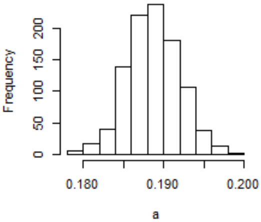
- The Monte-Carlo estimate with J samples is given by

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

- Systematic error $\left|\mathbb{E}\left[\log \frac{\|L_{t+1}L_t\dots L_1U\|}{\|L_t\dots L_1U\|}\right]-\mathbb{E}\left[\log \frac{\|L_{t+1}L_t\dots L_1v\|}{\|L_t\dots L_1v\|}\right]\right|$
- Sampling error $\left|\frac{1}{J}\sum_{j=1}^{J}\left(\log \frac{\|L_T^{(j)}\dots L_1^{(j)}v\|}{\|L_{T-1}^{(j)}\dots L_1^{(j)}v\|}\right)-\mathrm{E}\left[\log\|Lu\|\right]\right|$







Lyapunov exponents and the Multiplicative Ergodic Theorem

Asymptotic behavior of random product of matrices :

$$P_n(\omega) = L_n(\omega)\dots L_2(\omega)L_1(\omega) \quad \text{where } L_t \in \{M_1, \dots M_k\}$$

Example

2 fixed matrices A and B and a coin

$$P_n = ABBBAABA\dots$$

Lyapunov exponents and the Multiplicative Ergodic Theorem

Generalization of the eigen-decomposition of $L \in \mathcal{S}_k(\mathbf{R})$:

$$L = S^{-1} DS \quad \text{where } D = diag(\lambda_1, \ldots, \lambda_k)$$

Then for $v = \sum_{i=1}^{k} a_i v_i$, in the limit $n \to \infty$,

$$L^n v \approx \lambda_1^n a_1 v_1$$

Multiplicative ergodic theorem

$L_1, L_2, \ldots$ stationary sequence of random matrices in $\mathbf{R}^{k \times k}$. There exists k Lyapunov exponents $\lambda_k \geq \cdots \geq \lambda_1$ and a random subdivision of $\mathbf{R}^k$ such that for $v \in \mathbf{R}^k$ (random) :

$$L_n \ldots L_2 L_1 v \quad \approx \quad e^{\lambda_{\mathbf{k}} \cdot n} \times c \times V_\infty$$

Distribution of the random vector V_∞

- $V_\infty \sim \mu$ and μ is the stationary distribution of the Markov chain $\{w_t\}$
- No general explicit expression !
- Numerical approximation : distribution of $\{w_t\}$ after some "burn-in" time B

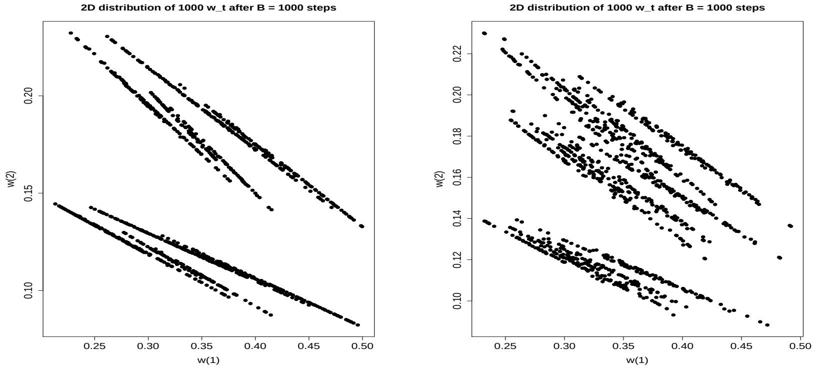


FIGURE – 1000 values of the Markov chain after B = 1000 time steps with 2 matrices (left) and 3 matrices (right)

Link with top eigen-vectors ?

With $N = 2$ matrices

- v_1 top eigen-vector of L_1
  $\{L_1^t\}_t$ is a possible sequence $\rightarrow$ v_1 belongs to μ
- idem for L_2

But also for any finite product of n matrices :

$$L_{i_1} L_{i_2} \dots L_{i_n}$$

Plots of the stationary distribution

Where are some top eigenvectors ?

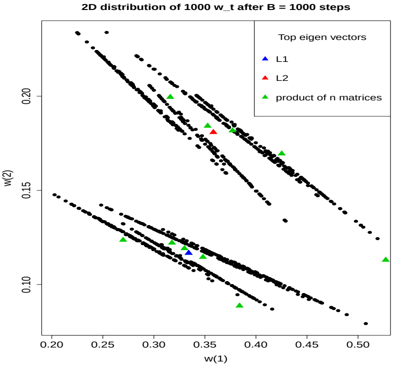


FIGURE – 1000 values of the Markov chain after B = 1000 time steps with 2 matrices

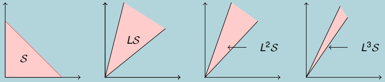
Extension : Pollicott's approximation of *a*

Hilbert Projective Metric and Contraction

$$\rho(u, v) = \max_{0 \le i,j \le N} \log \frac{u_i v_j}{u_j v_i}$$

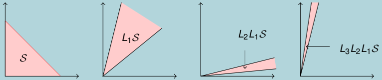
$$\rho(\lambda u, \lambda v) = \rho(u, v) \quad \forall \lambda$$

Same Leslie matrix



Contraction in one direction

Different Leslie matrices

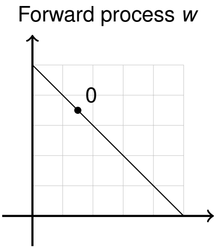


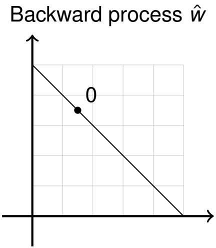
Contraction in a random direction $\rightarrow$ study the backward process

Time Reversal

The sequence considered

$$L_1 L_2 L_2 L_1 v$$



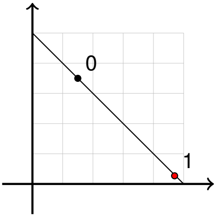


Time Reversal

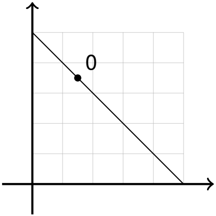
The sequence considered

$$L_1 L_2 L_2 {\color{red}L_1 v}$$

Forward process w



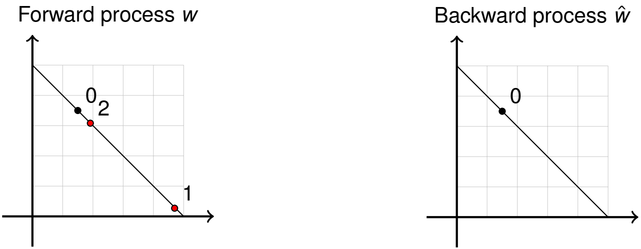
Backward process $\hat{w}$



Time Reversal

The sequence considered

$$L_1 L_2 \color{red}{L_2 L_1 v}$$

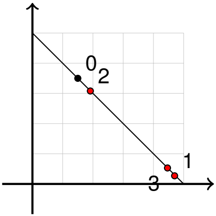


Time Reversal

The sequence considered

$$L_1 \, L_2 L_2 L_1 \, v$$

Forward process w



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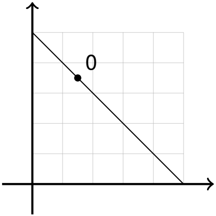

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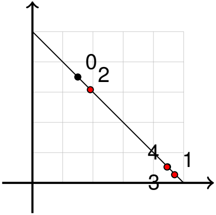

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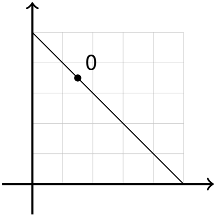

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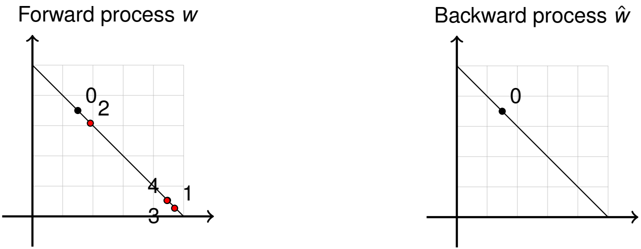

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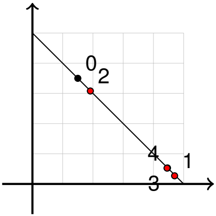

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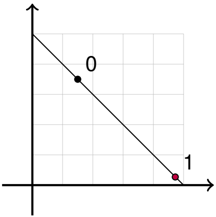

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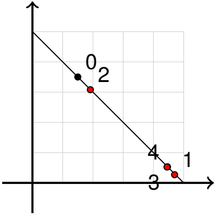

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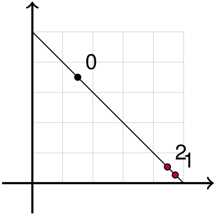

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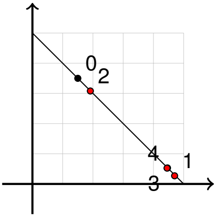

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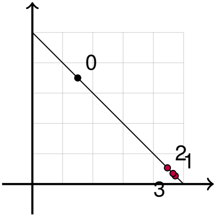

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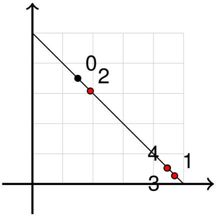

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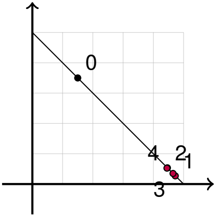

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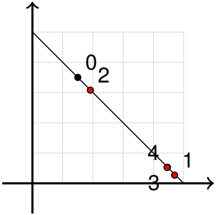
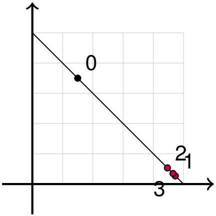


Backward process $\hat{w}$



$\forall q, p > m$

$$\rho\left(\hat{w}_q, \hat{w}_p\right) = \rho\left(\frac{L_{i_1}\cdots L_{i_q} v}{\|L_{i_1}\cdots L_{i_q} v\|}, \frac{L_{i_1}\cdots L_{i_p} v}{\|L_{i_1}\cdots L_{i_p} v\|}\right) = \rho\left(L_{i_1}\cdots L_{i_m}\cdots L_{i_q} v, L_{i_1}\cdots L_{i_m}\cdots L_{i_p} v\right) \leq k r^m$$

Plots of the stationary distribution

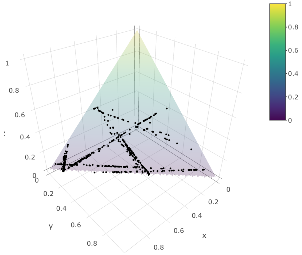


FIGURE – 1000 values of 1 Markov chain after 9000 time steps

$$L_1 = \begin{bmatrix} 0.5 & 0.4 & 0.1 \\ 0.8 & 0 & 0 \\ 0 & 0.4 & 0 \end{bmatrix} \qquad L_2 = \begin{bmatrix} 0 & 0 & 6 \\ 0.5 & 0 & 0 \\ 0 & 1/3 & 0 \end{bmatrix}$$

$$L_3 = \begin{bmatrix} 2 & 1 & 0.5 \\ 0.2 & 0 & 0 \\ 0 & 0.3 & 0 \end{bmatrix}$$

$$p = (0.2, 0.7, 0.1)$$

$$\begin{cases} \lambda_1 \approx 0.9 \\ \lambda_2 = 1 \\ \lambda_3 \approx 2.1 \end{cases}$$

Annex I : Pollicott's approximation

Computation of the Lyapunov exponent using the top eigenvalue of a parametrized transfer operator acting on the function space of the function acting on $\mathcal{S}$:

$$(\mathcal{L}_t f)(x) = \sum_{i=1}^{M} p_i e^{t\mathbb{E}[log\|Ax\|]} f(\frac{L_i x}{\|L_i x\|})$$

where $t \in \mathbb{R}$ real parameter
$\mathcal{L}_t$ has a top eigenvalue $\lambda(t)$ and $\lambda'(0) = \lambda_k$

Annex I : Pollicott's approximation

It can also be expressed in another way using the determinant of the transfer operator $d^{(i)}(z,t) = det(\mathbb{I} - z\mathcal{L}_t) = 1 + \sum_{j=1}^{\infty} a_j^{(i)}(t) z^j$:

$$\lambda = \sum_{i=1}^{M} \frac{\frac{\partial d^{(i)}}{\partial t}(1,0)}{\frac{\partial d^{(i)}}{\partial z}(1,0)}$$

where the $a_j^{(i)}$ can be written explicitely in terms of top eigenvectors and eigenvalues of product of up to j matrices. Then a n-th approximation of λ_k is obtained by truncating the sums :

$$\lambda_n = \sum_{i=1}^{M} \frac{\sum_{j=1}^{n} a_j^{(i)\prime}(0)}{\sum_{j=1}^{n} j a_j^{(i)}(0)}$$

Better rate of convergence compared to the Monte-Carlo method :

$$|\lambda_n - \lambda| \sim O(e^{-n^{1+1/k}})$$