OXWASP PROBABILITY AND APPROXIMATION MODULE MICRO-PROJECT: GROWTH RATES FOR POPULATIONS IN RANDOM ENVIRONMENTS

Population ecologists study the development of age-structured (or stage-structured) populations using *Leslie matrices*. Suppose the population is being studied in discrete time intervals (that we will call *years* here), and each individual is in one of a discrete set of classes $\{0, 1, \ldots, N\}$. Class 0 is understood to be the "juvenile" class into which individuals are born. Each year, a fraction λ_{ji} of the individuals in class i move into class j, for $1 \leq j \leq N$, and each individual in class i produces an average of b_i offspring in class 0. We assume the population is very large, so that these "fractions" may be considered to be exact and deterministic. The fraction of individuals from class i who die in a given year is $\mu_i = 1 - \sum_{i=1}^{N} \lambda_{ji}$. In the case where the classes are age classes we of course have $\lambda_{ji} = 0$ except when $j = i + 1$, and $\lambda_{i+1,i}$ is the survival rate of individuals aged i.

We define the Leslie matrix L to be an $(N + 1) \times (N + 1)$ matrix with entries — numbering the rows and columns $0, \ldots, N$ — λ_{ji} for $1 \leq j \leq N$ and $b_0, \ldots, b_N$ in row N. (Note that the rows and columns for transitions are reversed relative to the way we write Markov-chain transitions.) Then if we start with a population with v_i (of some units) in class i at the start, the population after t generations will be $L^t \mathbf{v}$.

In many situations researchers want to model the environment as random, with different demographic rates from year to year: matrix L_i in year i. Suppose the L_t are i.i.d. choices from some distribution on nonnegative $(N+1)\times(N+1)$ matrices, such that the product is eventually positive. (So there can't be any row or column that is always all 0.) Then the population after t generations will be

$$L_t L_{t-1} \cdots L_1 \mathbf{v}.$$

The average population growth rate will now be the top Lyapunov exponent, whose existence was first proved by Furstenberg and Kesten [1], and which follows from the subadditive ergodic theorem. There is no simple formula for this stochastic growth rate, but it may be estimated by simulation. Describe and program an algorithm for estimating the Lyapunov exponent, together with an estimate for the error. You may start by considering the sequence of normalised age distributions

$$w_t = \frac{L_t L_{t-1} \cdots L_1 \mathbf{v}}{\|L_t L_{t-1} \cdots L_1 \mathbf{v}\|}, \tag{1}$$

where $\|\mathbf{u}\| = \sum_{i=0}^{N} u_i$ is the total population. These form a Markov chain on the simplex

$$\mathcal{X} := \left\{(x_0, \ldots, x_N) \,:\, x_i \geq 0,\, \sum x_i = 1\right\}.$$

You may assume (or prove) that this converges to a stationary distribution μ on $\mathcal{X}$. Show that the top Lyapunov exponent is the expected value of $\log \|L_1\mathbf{w}\|$ where $\mathbf{w}$ is a random choice from the distribution μ. Approximate samples from μ for a Monte Carlo estimate may be obtained by multiplying together a finite number of random matrices.

Sampling error Use the CLT for the Markov chain w_t. How can you estimate the variance?

Bias The samples aren't from μ, but from an approximation to μ. The product $L_t \cdots L_1$ shrinks the simplex. Using the same ideas as in CFTP, you can show that your sample w_t differs from a "true" sample from μ by no more than the diameter of $L_t \cdots L_1\mathcal{X}$. It may be useful to think about distances between vectors in the Hilbert projective metric, that defines the distance between two vectors $\mathbf{v}$ and $\mathbf{w}$ to be

$$\rho(\mathbf{v}, \mathbf{w}) = \max_{0 \leq i,j \leq N} \log \frac{v_i w_j}{v_j w_i}.$$

Possible extensions:

(1) For $N = 1$ or 2 you may try to make plots of the stationary distribution on $\mathcal{X}$. How would you do this? What sort of distribution is it? Try to form some hypotheses about how the distribution is related to the choice of matrices and the probabilities on each matrix. In particular, compare the case when the matrices are chosen from some finite set to a continuous distribution of matrices.

(2) Suppose the population is not so large, so that stochasticity in the transitions and birth numbers cannot be neglected. Now there is a new phenomenon: Random extinction. How does the long-term growth rate affect the extinction probability? What tradeoffs in environmental factors will increase or decrease the extinction probability? Suggest ways to analyse this theoretically and/or through simulations? Some ideas may be found in [2].

References

[1] H. Furstenberg and H. Kesten. Products of random matrices. *The Annals of Mathematical Statistics*, 31(2):457–69, June 1960.

[2] Russell Lande. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *The American Naturalist*, 142(6):911–927, 1993.

[3] David Steinsaltz, Shripad Tuljapurkar, and Carol Horvitz. Derivatives of the stochastic growth rate. *Theoretical Population Biology*, 80(1):1–15, 2011.