Stat 534 Fall 2019

**Homework # 4**, Population models,

Due: 5pm Monday, 2 December 2019, to my office (2121 Snedecor) or mailbox (in 1121 Snedecor)

Reminders: Choose **2 of the 3** problems. You are not expected to do all three. Also problem 3 has 2 parts. If you choose to do this problem, do both parts.

I will be around and working over break so if you have any questions, just ask.

1. This problem looks at the demography of a tropical understory shrub. The transition matrix in shrub0.csv gives the average fecundity and annual transition probabilities for plants in densely shaded understory conditions. Plants are classified into 8 stages. Stage 1 is a seed. Stage 2 is a seedling. Stages 3 through 8 are increasingly-large size plants.

   Using the transition matrix given in shrub0.csv:

   (a) What is the asymptotic growth rate, $\lambda$?

   (b) and stable stage distribution?

   (c) If you ignore seeds, what is the stable stage distribution of the remaining 7 stages?

   (d) If you were able to increase any single matrix element to 110% of its current value, increasing which element will increase $\lambda$ the most? How large is that increase?

   (e) Like many understory plants, the demography of this shrub depends on canopy cover. The data in shrub25.csv are the fecundity and transition probabilities for patches with approximately 25% open canopy. The asymptotic growth rate for this transition matrix is much larger. The LTRE computations decompose the net change in $\lambda$ into contributions from each transition matrix element. Which element of the transition matrix contributes the most (positively or negatively) to the change in $\lambda$? Second and third largest?

   (f) The LTRE computation relies on a linear approximation to the change in $\lambda$. If that linear approximation is exact, the sum of the LTRE contributions (summed over all matrix elements) will equal the difference in population growth rates. Compare the sum to the actual difference. How close are the two?

   The last few questions make a point about constructing demographic transition matrices.

   (f) Based on the transition matrix as given to you, if a plant flowers in 2010, in what year do "its" seedlings (stage 2) arrive? I.e., how many years elapse between a plant flowering and the appearance of a seedling (stage 2)? Briefly explain your answer.

   (g) An alternative view of the biology is that:
   1) seeds that do not germinate immediately die (or are eaten).
   2) so seedlings are produced within a year after a plant flowers.
   Rewrite the transition matrix to better reflect this biology.
   Hint: The rewritten transition matrix will be 7x7.

(h) What are the asymptotic growth rate and stable stage distribution for the rewritten transition matrix?

(i) Does the stable stage distribution from question 1h match the 'non-seed' stage distribution from question 1c? Is it roughly similar? What does this (and potentially the difference in population growth rates) tell you about constructing transition matrices?

2. The biologists studying the tropical shrub in problem 1 have transition matrices for different amounts of canopy openness. We will use four of them: densely shaded (< 5% open, ca 25% open, ca 45% open, and ca 65% open). These are the 8x8 matrices that include seeds. Hurricanes are the major disturbance event that opens up the canopy. The four demographic matrices are in allshrubRev.csv. The env and open variables indicate the different matrices. Env is 1 through 4; open is the canopy openness. 1 is densely shaded, 4 is 65% open.

   We will use environmental transition matrices to describe the probability of a hurricane and subsequent regrowth of the canopy. Remember that 4 probabilities in column 1 of the environmental matrix give the probabilities that a population currently in environment 1 will be in environments 1, 2, 3 or 4 the next year. The environmental transition matrix in hurricane.csv describes a world where hurricanes occur only to densely shaded sites, with probability 0.05. The canopy regrows at 20% per year without any randomness, so every environment 4 site moves to environment 3 the next year, every 3 moves to 2 and every 2 moves to 1. Ask if you don't see how the description matches the matrix.

   The code in markov.r shows you how to read the collection of population transition matrices, reshape that into an array, and use the rand.env() function.

   (a) Estimate the mean and variance of the stochastic log lambda using hurricane.csv. Is the population growing or shrinking, on average?

   (b) Does the variance of stochastic log lambda reported by the code describe the precision of the estimated mean (i.e. a squared standard error) or the year-year variability (i.e. a squared standard deviation)?
   Hint: Look at the code to see how the variance is computed.

   (c) The environment matrix in hurricane.csv only allows hurricanes to occur to densely shaded sites. You know that hurricanes can affect any site. After a hurricane, the site is always in state 4. Rewrite the environmental transition matrix so that hurricanes can occur to any site. The hurricane probability is still 5% per year. Report your environmental transition matrix and estimate the mean and variance of the stochastic log lambda for this scenario.

   (d) Now, let's reduce the frequency of hurricanes. Now the probability of a hurricane is 1% in any year, and that can affect any type of site. Report your environmental transition matrix and estimate the mean and variance of the stochastic log lambda for this scenario.

   (e) Now let's speed up canopy regrowth. Return the hurricane frequency to 5%. The year after a hurricane, a state 4 site has a 45% probability of being a state 2 site (25% open), a 50% probability of being a state 1 site, and a 5% probability of being hit by a second hurricane. Report your environmental transition matrix and estimate the mean and variance of the stochastic log lambda for this scenario.

3. Two unrelated analytical issues; answer them both.

(a) Sensitivity to changes in multiple vital rates.

Here is a typical transition matrix for a short-lived plant that propagates only by seed. The stages are non-flowering individual, small flowering individual, and flowering individual:

$$\begin{array}{rrr} 0.2 & 2 & 30 \\ 0.05 & 0.3 & 0 \\ 0 & 0.12 & 0.7 \end{array}$$

This stage-based model can be reparameterized in terms of growth and survival. For example, the two survival-related transitions for small flowering individuals, $a_{22}$ and $a_{32}$ can be parameterized as "survive, don't grow" $= s_2(1-g_2)$ and "survive and grow to next stage" $= s_2g_2$. That gives the following parameterization:

$$\begin{array}{lll} s_1(1-g_1) & f_2 & f_3 \\ s_1g_1 & s_2(1-g_2) & 0 \\ 0 & s_2g_2 & s_3 \end{array} \tag{1}$$

where $s_i$ is a stage-specific survival probability and $g_i$ is a stage-specific conditional probability that a surviving plant will grow into the next stage. For many species, the sensitivity of $\lambda$ to changes in $s_i$ or $g_i$ may be more important than the sensitivities for matrix elements ($s_{ij} = \partial\lambda/\partial a_{ij}$). The sensitivities to $s_i$ or $g_i$ can be computed from the $s_{ij}$.

i. What is the expression for $\frac{\partial\lambda}{\partial s_1}$, i.e., the sensitivity with respect to $s_1$?

ii. What is the expression for the elasticity with respect to $s_1$, i.e., $\frac{\partial \log\lambda}{\partial \log s_1}$?

(b) In class, we introduced environmental (year-year) variability into population growth models using the simple discrete time unstructured model. This problem clears up some of the jumbled presentation in lecture. For this problem, we will assume that the year-specific population growth rates are normally distributed with mean $\mu$ and variance $\sigma^2$. The model is:

$$\begin{aligned} \log N_t &= \log N_{t-1} + \log R_{t-1} \\ R_t &\sim N(\mu, \sigma^2) \;\; \forall t \\ N_0 &= \text{known constant} \end{aligned}$$

with all $R_t$ independent of each other. It may help to know the following facts about log normal distributions. When $Y \sim \text{logN}(\mu,\ \sigma^2)$, $\log Y \sim N(\mu,\ \sigma^2)$:

$$\begin{aligned} \text{E } Y &= \exp\left(\mu + \sigma^2/2\right) \\ \text{Var } Y &= \exp\left(2\mu + 2\sigma^2\right) - \exp\left(2\mu + \sigma^2\right) \\ \text{cv } Y &= \sqrt{\text{Var } Y}/\text{E } Y = \sqrt{\exp(\sigma^2) - 1} \end{aligned}$$

i. Derive the distribution of $\log N_t$ in terms of $t$, $\mu$, $\sigma^2$, and $N_0$.

ii. What is the expected population size at time $t$, i.e. E $N_t$?

iii. If you plot $\log \text{E } N_t$ against $t$, what is the slope of that line?

iv. Now derive the distribution of mean population growth: $(\log N_t - \log N_0)/t$?

v. Question 3(b)iii derived what I called the growth of the mean population while question 3(b)iv derived the mean population growth. In lecture, I said that the growth of the mean population (question **??**) was $\geq$ the mean population growth (question 3(b)iv). When the annual log growth rates follow a normal distribution, how much larger is the mean population growth (3(b)iii)?