unstructed-stochasticity

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1 Module 1: Unstructured Population Models

1.1 Section 3: Population dynamics and stochasticity

1.1.1 Deterministic vs. stochastic factors

- **Deterministic factors** are predictable, such as predation, competition, etc.
- **Stochastic factors** are unpredictable

1.1.2 Basic forms of stochasticity and definitions

1.1.2.1 Demographic stochasticity **Demographic stochasticity** refers to chance events of individual mortality and reproduction (inevitable deviation in mean birth and death rates) (Lande *et al.*, 2003).

- Only significant in small populations
- *Example* 1: Flipping a coin 10,000 times, one will get approximately 5,000 times heads; flipping the same coin 100 times, there could be some deviations from the expected 50:50; flipping the same coin 10 times, it is not suprising that one only gets 2 heads. The probability of getting head is approaching 0.5 as the number of trials increases.

```
# toss a coin
toss10 <- sample(c(0,1), size = 10, prob = c(0.5,0.5), replace = TRUE)
toss100 <- sample(c(0,1), size = 100, prob = c(0.5,0.5), replace = TRUE)
toss10k <- sample(c(0,1), size = 10000, prob = c(0.5,0.5), replace = TRUE)
results <- data.frame(c(sum(toss10), 10-sum(toss10)),
                      c(sum(toss100), 100-sum(toss100)),
                      c(sum(toss10k), 10000-sum(toss10k)))
colnames(results) <- c("10 tosses", "100 tosses", "10,000 tosses")
rownames(results) <- c("heads", "tails")
results
```

```
##       10 tosses 100 tosses 10,000 tosses
## heads         7         54          5061
## tails         3         46          4939
```

- *Example 2*: The expected sex ratio for a newborn is 50:50. When there 3 new births, we cannot have 50% males and 50% females. Unbalanced sex ratio will influence future birth rate, especially in a small population. Similarly, a death rate of 0.2 does not mean after a year an animal is 0.8 alive–it either survives or dies. When the population size is large, we may use the product of the total populatiom and a mean birth/death rate to estimate the number of births/deaths. However, such estimation is not accurate when the population size is small.

1.1.2.2 Environmental stochasticity

Environmental stochasticity often refers to temporal fluctuations in the probability of mortality and reproduction (unpredictable catastrophes) (Lande *et al.*, 2003)

- Often driven directly or indirectly by weather
- *Example*: Climate factors have a strong influence on the ecology of red deer on Rum (Albon *et al.*, 1987). Real-world data between 1971 and 1991 has shown that the changes in red deer population size correlates strongly with annual rainfall (Benton *et al.*, 1995).

Figure 1: Red deer (Cervus elaphus) young stage (Wikimedia Commons, credit: Charles J. Sharp)

1.1.2.3 Sampling error

Sampling error (or sampling variance) is the measurement error in estimates of population size or density. Some researchers categorized it as a basic form of stochasticity (Lande *et al.*, 2003), while some distinguished it from deterministic and stochastic factors (Mills, 2007).

1.1.3 Implications of variation in population growth

- An obvious outcome is that future population size outcomes become more uncertain and more variable.
- A less intuitive outcome is that the likelihood of any particular population size at time t in the future becomes more skewed (most populations being relatively small, with a tiny fraction being huge). We will discuss it soon.

1.1.4 Stochastic effects to population growth rates

1.1.4.1 Arithmetic mean vs. geometric mean

- Let λ_A and λ_G denote the arithmetic and geometric mean, respectively,

$$\lambda_A = \frac{1}{k}\sum_{i=1}^{k}\lambda_i,$$

$$\lambda_G = \left(\prod_{i=1}^{k}\lambda_i\right)^{\frac{1}{k}}.$$

- *Example*: Consider $N_t = \lambda_t N_{t-1}$, where N_t is the population at time t, and during each time interval $(t-1, t)$ the growth rate is λ_t. Assume $\lambda_t = 1.55$ or $\lambda_t = 0.55$ with the same probability. Assuming that the population grows at a constant arithmetic mean rate $\lambda_A = (1.55 + 0.55)/2 = 1.05$, the population at $t = 16$ is

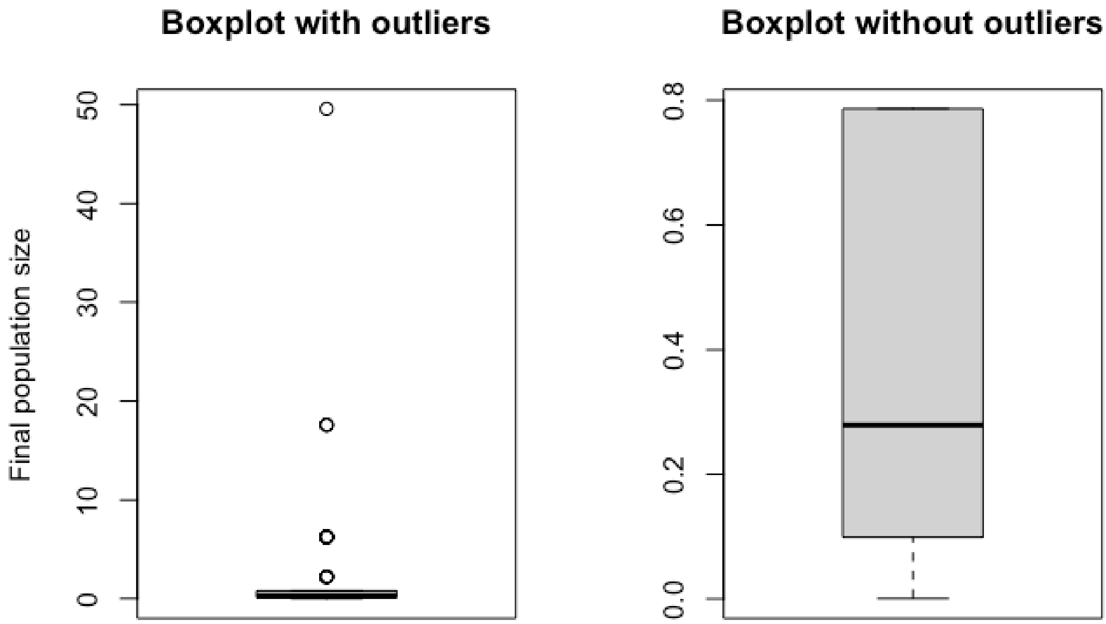
$$N_{16} = 1.05^{16} N_0 = 2.18 N_0.$$

  Instead, if we assume that the growth rate alternated between 1.55 and 0.55, the population at $t = 16$ becomes

$$N_{16} = 1.55^8 \times 0.55^8 N_0 = [(1.55 \times 0.55)^{1/2}]^{16} N_0 = 0.28 N_0,$$

  which indicates that the variation in population growth leads to a likely decline for the population, even though the (arithmetic) average growth rate is larger than 1 (Mills, 2007). Here, the geometric mean growth rate is $\lambda_G = (1.55 \times 0.55)^{1/2} \approx 0.9233$.

```r
N0 <- 1
lambda <- matrix(rbinom(1600, 1, 0.5), ncol = 16)
lambda[lambda==1] <- 1.55
lambda[lambda==0] <- 0.55
# lambda is a 100-by-16 matrix
# each row represents a possible population change in 16 years
outcome <- N0*apply(lambda, 1, prod)
par(mfrow=c(1,2))
boxplot(outcome, main = "Boxplot with outliers",
        ylab = "Final population size")
boxplot(outcome, outline = FALSE, main = "Boxplot without outliers")
```



- *Conversion between λ and r*: Recall that $r = \ln \lambda$, so

$$\ln(\lambda_1 \lambda_2 \cdots \lambda_k) = \ln \lambda_1 + \ln \lambda_2 + \cdots + \ln \lambda_k = r_1 + r_2 + \cdots + r_k,$$

which gives

$$\ln(\lambda_1 \lambda_2 \cdots \lambda_k)^{1/k} = \frac{1}{k} \ln(\lambda_1 \lambda_2 \cdots \lambda_k) = \frac{1}{k}(r_1 + r_2 + \cdots + r_k),$$

and thus

$$\ln \lambda_G = r_A.$$

- *Variation around λ*: Increasing the variance of the growth rates (σ_λ^2) makes the geometric mean growth rate less than the arithmetic mean. Let $\lambda_t = \lambda_A + \epsilon_t$, where ϵ_t is the deviation of λ_t from the arithmetic mean λ_A with zero mean. Using Taylor expansion, one could obtain

$$\begin{aligned}\ln \lambda_t &= \ln \lambda_A + \ln(1 + \epsilon_t/\lambda_A) \\ &= \ln \lambda_A + \epsilon_t/\lambda_A - (\epsilon_t/\lambda_A)^2/2 + O(\epsilon_t^3).\end{aligned}$$

Hence, taking the expectation of both sides gives

$$r_A = E(\ln \lambda_t) \cong \ln \lambda_A - \frac{E[(\lambda_t - \lambda_A)^2]}{2\lambda_A^2} = \ln \lambda_A - \frac{\sigma_\lambda^2}{2\lambda_A^2},$$

which further gives

$$\lambda_G \cong \exp\left(\ln \lambda_A - \frac{\sigma_\lambda^2}{2\lambda_A^2}\right).$$

1.1.4.2 Temporal autocorrelation

- Above examples assume that r_t does not depend on previous growth rates, nor will it influence subsequent growth rates. The autocorrelation describes the relationship between r_t and $r_{t+\tau}$, its value at a time lag τ. One way to incorporate teporal autocorrelation is to:

  $$r_{t+\tau} = r_A + \rho(r_t - r_A) + \epsilon_{t+\tau},$$

  where ρ is the coefficient of lag-τ autocorrelation, and $\epsilon_t \sim N(0, \sigma_\epsilon^2)$ is white noise with zero mean and constant variance. An example would be the case $\tau = 1$ (lag-1 autocorrelation), where $r_{t+1} = r_A + \rho(r_t - r_A) + \epsilon_{t+1}$. When $\rho = 0$, $r_{t+1} = r_A + \epsilon_{t+1}$ and there is no temporal autocorrelation.

1.1.5 Estimating population growth rates

1.1.5.1 Process error Process error results from variation in true population size due to biotic or abiotic processes (Ahrestani *et al.*, 2013).

- Environmental and demographic stochasticity are examples of process errors
- When only process error exists, the population at each time t, N_t, is known and accurate. The growth rate λ_t is a random variable. For example, a geometric model with only process error can be described as

  $$N_{t+1} = \lambda_t N_t,$$
  $$\lambda_t \sim N(\bar{\lambda}, \sigma_p^2),$$

  where λ_t follows a normal distribution with mean $\bar{\lambda}$ and variance σ_p^2.
- Since the population at each time t, N_t, is known and accurate, we can calculate the estimated growth rate using geometric mean

  $$\hat{\lambda} = \left(\prod_{i=1}^{t} \frac{N_i}{N_{i-1}}\right)^{\frac{1}{t}},$$

  or equivalently,

  $$\hat{r} = \frac{1}{t}\sum_{i=1}^{t} \ln \frac{N_i}{N_{i-1}}.$$

- We can see that the estimated growth rate is only related to the initial and the final population size, as all the terms between them can be cancelled out. In other words,

  $$\hat{\lambda} = \left(\frac{N_t}{N_0}\right)^{\frac{1}{t}}$$

  and

  $$\hat{r} = \frac{\ln N_t - \ln N_0}{t}.$$

1.1.5.2 Observation error Observation error results from variation in the methodology used to obtain the population size (Ahrestani *et al.*, 2013).

- Examples of observation error include difficulty in counting animals, which might due to lack of technical expertise, insufficient funding, etc.
- When only observation error exists, the growth rate is accurate. A possible geometric model with only observation error can be described as

  $$\ln N_t = \ln N_0 + rt + \eta_t,$$
  $$\eta_t \sim N(0, \sigma_o^2),$$

where η_t follows a normal distribution with mean 0 and variance σ_o^2. Here we ignore the subscript of r as we assume the growth rate is some constant. We could also convert the above equation to

$$N_{t+1} = \lambda^t N_t e^{\eta_t},$$

where $e^{\eta_t} > 0$ so that the population is always non-negative.

- The equation $\ln N_t = \ln N_0 + rt + \eta_t$ is in the form of a linear model in which $\ln N_t$ is the response variable and t is the predictor variable. Using simple linear regression, the slope of the fitted function is the estimated r. Moreover, the y-intercept is the estimated $\ln N_0$.

1.1.6 Paper discussion

Shoemaker, L. G., Sullivan, L. L., Donohue, I., Cabral, J. S., Williams, R. J., Mayfield, M. M., Chase, J. M., Chu, C., Stanley Harpole, W., Huth, A., HilleRisLambers, J., James, A. R. M., Kraft, N. J. B., May, F., Muthukrishnan, R., Satterlee, S., Taubert, F., Wang, X., Wiegand, T., Yang, Q., and Abbott, K. C. (2020) Integrating the underlying structure of stochasticity into community ecology. *Ecology*, 101(2):e02922.

1.1.6.1 Snapshot of the study

- Studies tend to focus on single forms of stochasticity, while this paper provides a more holistic view on how stochasticity mediates community dynamics, with a focus on population persistence and community alpha diversity
- The authors incorporate a stochastic version of the Beverton-Holt model (Beverton and Holt, 1957)

$$N_{t+1} = RN_t \frac{1}{1 + \alpha N_t}$$

from a single species to diverse communities of 20 species. For each species, demographic and environmental stochasticity are considered as follows:

$$N_{t+1} \sim \text{Poisson}\left(RN_t \frac{1}{1 + \alpha N_t} + N_t \zeta \sigma_t\right).$$

- Models yield different predictions for alpha diversity dynamics depending on whether demographic, environmental, or both forms of stochasticity is/are included. Underlying distributions of predicted outcomes differ greatly in both their mean and variance, despite little difference appeared in observations
- When carrying capacity increases, the mean time to extinction increases exponentially as the effect of demographic stochasticity decreases. High probability of extinction is predicted for small populations
- The authors compared white (no autocorrelation) and red (positive autocorrelation) noises. Increasing the autocorrelation of environmental stochasticity increases the correlation of population dynamics.
- The authors also extend the insights about stochasticity in diverse communities to metacommunities and diversity-stability relationships, which is beyond the scope of this chapter.
- One sentence to conclude–"Stochasticity is more than simple uncertainty, but has profound and predictable effects on community that are critical for understanding how diversity is maintained."

1.1.7 References

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Benton, T. G., Grant, A. and Clutton-Brock, T. H. (1995) Does environmental stochasticity matter? Analysis of red deer life-histories on Rum, *Evolutionary Ecology*, **9**:559–574.

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Case, T. (2000) *An Illustrated Guide to Theoretical Ecology*, Oxford University Press.

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Mills, L. S. (2007) *Conservation of Wildlife Populations: Demography, Genetics, and Management*, Wiley-Blackwell Publishing.