Lecture 4 - Density-independent stochastic growth

Announcement:

Bring laptops next class

Today's concepts:

Environmental vs. Demographic stochasticity

Expectation vs. Variance (uncertainty)

Geometric vs. Arithmetic expectation

All previous equations have been deterministic

... if we start with same N(0) and r we get exactly the same answer.

Add stochasticity: "Adding stochastic shell to deterministic core of our model"

Stochastic (from the Greek for aim or guess) = random with respect to considered variables A stochastic process is one whose subsequent state is determined by a random element.

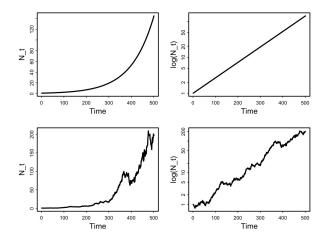
$$N_T = N_0 e^{(r \pm noise)T} = N_0 (\lambda \pm noise)^T$$

E.g., 4 years of stochastic growth

$$N_0 = 1$$

 $\lambda_1 = 2$ $N_1 = N_0 \lambda_1 = 1 \cdot 2 = 2$
 $\lambda_2 = 1$ $N_2 = N_1 \lambda_2 = 2 \cdot 1 = 2$
 $\lambda_3 = 3$ $N_3 = N_2 \lambda_3 = 2 \cdot 3 = 6$
 $\lambda_4 = 2$ $N_4 = N_0 \lambda_1 \lambda_2 \lambda_3 \lambda_4 = 12$

Run in R...



Want to characterize two things: Show on plot of $log(N_t)$ vs. t.

Expectations (mean) of
$$\lambda$$
 ($\bar{\lambda}$) and of N_T (\bar{N}_T)
Variance of λ (σ^2_{λ}) and of N_T ($\sigma^2_{N_T}$)

$$\bar{N}_T = E[N_T] = \frac{1}{T} \sum_{t=0}^{T} N_t = \frac{1+2+2+6+12}{5} = 4.6$$

$$\sigma_{N_T}^2 = Var[N_T] = \sum_{t=0}^{T} (N_t - \bar{N}_T)^2$$

$$= (1-4.6)^2 + (2-4.6)^2 + (2-4.6)^2 + (6-4.6)^2 + (12-4.6)^2 = 83.2$$

Note that $\sigma = \text{standard deviation}$

and that
$$CV$$
 (coefficient of variation) = $\frac{\sigma_N^2}{N}$

Environmental Stochasticity - temporal variation in population's per capita growth rate Importance of distinguishing between geometric vs. arithmetic mean...

Example: Dynamics of two populations with same initial size:

$$N(3) = N_0 \lambda_1 \lambda_2 \lambda_3$$

Population A: $N_A(3) = N_0 \cdot 2 \cdot 1 \cdot 3 = 6 \cdot N_0$ Population B: $N_B(3) = N_0 \cdot 2 \cdot 2 \cdot 2 = 8 \cdot N_0$

$$\bar{\lambda} = \sum_{t}^{T} \frac{\lambda_t}{T}$$

On natural (arithmetic) scale, $\bar{\lambda}_A = \bar{\lambda}_B = 2$.

So why does population B grow more?

Appropriate measure is the geometric mean (remember popn growth is a multiplicative process): (No standard symbol for geometric mean)

geometric mean
$$\lambda = \left(\prod_t^T \lambda_t\right)^{\frac{1}{T}} = \sqrt[T]{\prod_t^T \lambda_t}$$

Geometric mean of
$$\lambda_A=\sqrt[3]{\lambda_1\cdot\lambda_2\cdot\lambda_3}=\sqrt[3]{2\cdot1\cdot3}=1.817...$$

So in fact $N_A(3)=N_0\cdot1.817\cdot1.817\cdot1.817=6\cdot N_0$

Will show that: Natural log of geometric mean λ = arithmetic mean of natural log of the λ 's

$$\ln\left(\left(\prod_{t=1}^{T} \lambda_t\right)^{1/T}\right) = \frac{1}{T} \cdot \ln(\lambda_1 \cdot \lambda_2 \dots \lambda_T)$$

Since...
$$\ln(ab) = \ln(a) + \ln(b)$$

$$= \frac{1}{T} (\ln(\lambda_1) + \ln(\lambda_2) + \dots + \ln(\lambda_T))$$

$$= \frac{1}{T} \cdot T \cdot \overline{\ln(\lambda)}$$

$$= \overline{\ln(\lambda)}$$

Thus, could also calculate as:

Geometric mean
$$\lambda = e^{\ln(\lambda)}$$

An alternative approximation (provided in Case, pg. 35):

Geometric mean
$$\lambda = e^{\overline{\ln(\lambda)}} \approx e^{\ln(\bar{\lambda}) - \frac{\sigma_{\lambda}^2}{2\bar{\lambda}^2}}$$

(Note effects of σ_{λ} and of $\bar{\lambda}$.)

Class R exercise - random vector draws - compare geometric and arithmetic means

- Effect of $\sigma = 0$, and increasing σ values:
 - Geometric mean will always be less than arithmetic mean

The more variation, the lower the geometric mean

• Effect of sample size, n:

Little effect, very low n might have more variation in depression amount

• Effect of $\bar{\lambda}$:

Raises and lowers, but not that at $\bar{\lambda} \approx 1$, geometric mean $\lambda < 1$ (declining population)!!

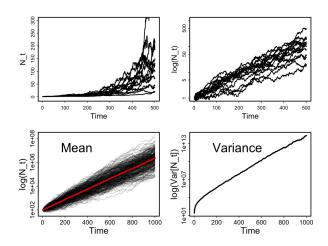
What does this mean for the dynamics of a given focal population?

Population change	Deterministic λ	Deterministic $\ln(\lambda)$	Environmental noise $\ln(\lambda \pm \text{noise}]$
No change	1	0	NA
Growth	> 1	> 0	$\ln(\bar{\lambda}) - \frac{\sigma_{\bar{\lambda}}^2}{2\bar{\lambda}^2} > 0$
Decline	< 1	< 0	$\ln(\bar{\lambda}) - \frac{\sigma_{\bar{\lambda}}^2}{2\bar{\lambda}^2} < 0$

What are the expected mean and variance of N_T for an "average" (typical) population? That is, we will now ask a different question...

 \Rightarrow What is the expected population size N_T over an ensemble of replicate populations? (The average of n replicate populations.)

Run in R...



Will show that

$$\bar{N}_T = N_0 \bar{\lambda}^T = N_0 e^{\bar{r}t}$$

And that...

when there is environmental variation only:

$$\sigma_{ln(N_T)}^2 = T \cdot \sigma_{ln(\lambda_t)}^2$$

when there is only demographic variation:

$$\sigma_{N_T}^2 = \begin{cases} 2N_0\bar{b}T & \text{if } \bar{b} = \bar{d} \\ \frac{\bar{b} + \bar{d}}{\bar{b} - \bar{d}}N_0e^{\bar{r}T}(e^{\bar{r}T} - 1) & \text{if } \bar{b} \neq \bar{d} \end{cases}$$

How to get $E[N_T]$?

Let λ be a random variable from a normal distribution.

Any given λ from this distribution is denoted by λ_t .

$$N_T = N_0 \prod_{t=1}^T \lambda_t = N_0 \cdot (\lambda_1 \lambda_2 \dots \lambda_T)$$

$$E[N_T] = N_0 \cdot E[\prod_{t=1}^T \lambda_t] \qquad \text{(since } N_0 \text{ is a constant)}$$

$$= N_0 \cdot \prod_{t=1}^T E[\lambda]$$

$$= N_0 \cdot E[\lambda]^T$$

$$= N_0 \cdot \bar{\lambda}^T$$

How to get variance?

Transform by taking the log..

$$\ln(N_T) = \ln(N_0) + \ln\left(\prod_{t=1}^T \lambda_t\right) = \ln(N_0) + \left[\sum_{t=1}^T \ln(\lambda_t)\right]$$

Now working on the arithmetic scale!

Allows us to apply Central Limit Theorem (pg. 41 of Case):

The sum of independent, identically distributed random variables x_i tends to asymptote to the normal density distribution, no matter the underlying distribution of x_i

Under a sufficiently large number of independent random variable draws:

$$\left[\sum_{i=1}^{n} x_i \right] = \mathcal{N}(n \cdot E[x_i], \ n \cdot Var[x_i])$$

$$= \mathcal{N}(n\bar{x}_i, n\sigma_{x_i}^2)$$

The mean of the sum equals the sum of all individual means The variance of the sum equals the sum of all individual variances

Inserting $ln(\lambda_t)$ for x_i , we thus have

$$\sum_{t=1}^{T} \ln(\lambda_t) = \mathcal{N}(T \cdot E[\ln(\lambda_t)], \ T \cdot Var[\ln(\lambda_t)])$$
$$= \mathcal{N}(T \cdot \overline{\ln(\lambda_t)}, \ T \cdot \sigma_{\ln(\lambda_t)}^2)$$

Therefore,

$$E[\ln(N_T)] = \ln(N_0) + T \cdot \overline{\ln(\lambda_t)}$$

and

$$\sigma_{\ln(N_T)}^2 = T \cdot \sigma_{\ln(\lambda_t)}^2$$

To translate expectation back to arithmetic scale:

$$N_T \sim log \mathcal{N}$$
 with median = $e^{\ln(N_0) + T \cdot \overline{\ln(\lambda)}}$

Take-home message:

When modeling $N_{t+1} = \lambda N_t$ with environmental noise in growth rate, error must be $log \mathcal{N}!$

In Problem Set #2 you should therefore use $N_{t+1} = N_t(\lambda \pm e^{\epsilon})$, where $\epsilon \sim \mathcal{N}(0, \sigma_{\epsilon}^2)$.

Summary

- The solution to $Var[N_T]$ is sensitive to assumed model-formulation!
- Dependent on how stochasticity is assumed to affect λ .
- If you assume $N_T = N_0(\lambda \pm \epsilon)^T$ with $\epsilon \sim \mathcal{N}(0, \sigma_{\epsilon}^2)$ you'll get a different prediction!

Demographic stochasticity - Between-individual variation in per capita growth rate Analogy of flipping a coin (not perfect, but will do).

$$H = \text{birth and } T = \text{death}$$

Q: How many H and T in 1000 flips? How many in 100? How many in 4? For fair coin, P(H) = P(T) = 0.5 and P(H) + P(T) = 1 \Rightarrow Binomial distribution.

Class exercise in R

Number of extinctions as function of starting population size using binomial. Going to assume:

$$P(birth) = \frac{b}{b+d}$$

$$P(death) = \frac{d}{b+d}$$

where b and d are per capita birth and death rates, such that r = b - d.

For true population (no longer binomial):

$$P(birth) = \frac{b}{b+d+o}$$

$$P(death) = \frac{d}{b+d+o}$$

$$P(other) = 1 - [P(b) + P(d)]$$

Won't go through derivations, but expectation of N(t) is still:

$$\overline{N_t} = N_0 e^{\bar{r}t}$$

And for

$$\sigma_{N_T}^2 = \begin{cases} 2N_0\bar{b}T & \text{if } \bar{b} = \bar{d} \\ \frac{\bar{b} + \bar{d}}{\bar{b} - \bar{d}}N_0e^{\bar{r}T}(e^{\bar{r}T} - 1) & \text{if } \bar{b} \neq \bar{d} \end{cases}$$

Side note...Probability of extinction:

$$P(ext) = \left(\frac{d}{b}\right)^{N_0}$$

Of course, environmental and demographic stochasticity are not mutually exclusive! Temporal variation among individuals will also causes temporal variation in λ . See Case for example combining the two.