

Univariate AR(1) process

A deterministic model frequently used to describe density-dependent population growth is a discrete-time Gompertz model (Reddingius 1971, Dennis and Taper 1994)

$$n_t = n_{t-1} \exp[a + (b - 1) \ln n_{t-1}]. \quad (1)$$

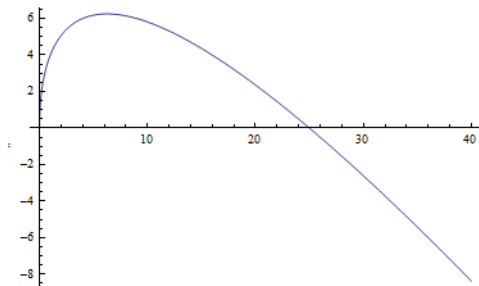
$$\begin{aligned} n_t &= n_{t-1} \exp(a + (b-1) \ln n_{t-1}) \\ &= e^a n_{t-1}^b \end{aligned}$$

$$n_t - n_{t-1} = (e^a n_{t-1}^{b-1} - 1) n_{t-1}$$

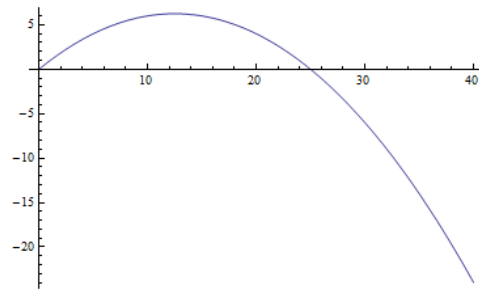
$$\frac{dn}{dt} = (\alpha n^\beta - 1)n$$

where $\alpha = e^a$ and $\beta = b - 1$. Compare with Logistic:

$$\frac{dn}{dt} = \alpha \left(1 - \frac{n}{K}\right)n$$



Gompertz



Logistic

Log form of Gompertz:

$$x_t = a + bx_{t-1}$$

where $x_t = \ln n_t$.

Provided $b \neq 1$, this model has an equilibrium point x_∞ given by

$$x_\infty = a/(1 - b). \quad (3)$$

In fact, $|b| < 1$ is the condition for stability of this deterministic system.

A stochastic version of Eq. 2 is the univariate AR(1) process

$$X_t = a + bX_{t-1} + E_t. \quad (5)$$

Here, the log abundance is now a random variable X due to the environmental (white) noise variable E , which is normally distributed with mean 0 and some finite variance σ^2 .

This AR(1) model has a stationary distribution (as $t \rightarrow \infty$) rather than a well defined equilibrium.

Mean:

$$\begin{aligned}\mu(X_t) &= \mu(a + bX_{t-1} + E_t) \\ &= a + b\mu(X_{t-1}) + \mu(E_t)\end{aligned}$$

Hence, taking $t \rightarrow \infty$ we see

$$\mu_\infty = \frac{a}{1-b}$$

Variance:

$$\begin{aligned}\text{Var}(X_t) &= \text{Var}(a + bX_{t-1} + E_t) \\ &= b^2 \text{Var}(X_{t-1}) + \text{Var}(E_t) + 2b \text{Cov}(X_{t-1}, E_t)\end{aligned}$$

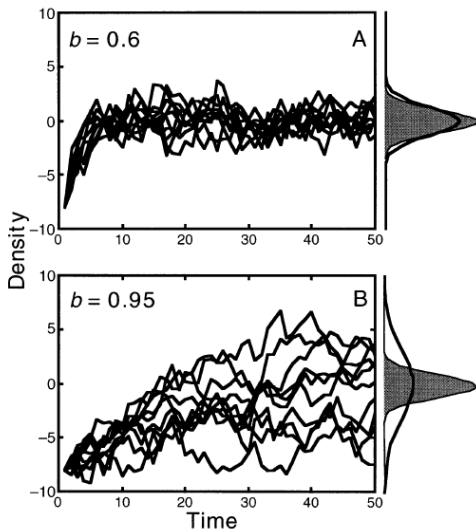
But X_{t-1} and E_t are uncorrelated, hence

$$v_\infty = \frac{\sigma^2}{1 - b^2}$$

Notice: the population variability is strictly greater than the environmental variability.

Turns out, the stationary distribution is normal (though I don't know why exactly).

AR(1) process runs:



Important points

These autoregressive processes are “stochastic”. E.g. processes which evolve according to probabilistic mechanisms.

Any particular time series arising out of a stochastic process is just a single realization of the underlying probabilistic mechanism.

(show code)

Multivariate AR(1) process

If there are p interacting species, a multivariate version of the univariate AR(1) model (Eq. 5) is

$$\mathbf{X}_t = \mathbf{A} + \mathbf{B}\mathbf{X}_{t-1} + \mathbf{E}_t \quad (10)$$

where \mathbf{X}_t is a $p \times 1$ vector of (log-transformed) population abundances at time t , \mathbf{A} is a $p \times 1$ vector of constants, \mathbf{B} is a $p \times p$ matrix whose elements b_{ij} give the effect of the abundance of species j on the per capita population growth rate of species i , and \mathbf{E}_t is a $p \times 1$ vector of process errors that has a multivariate normal distribution with mean vector $\mathbf{0}$ and covariance matrix Σ . The vectors \mathbf{E}_t represent stochastic environmental factors and are assumed to be independent through time. Nonetheless, the elements in \mathbf{E}_t may covary with each other, as measured by the off-diagonal elements

When the process error of the MAR(1) process is normally distributed, the stationary distribution is a multivariate normal distribution with mean vector $\boldsymbol{\mu}_\infty$ and covariance matrix \mathbf{V}_∞ given by

$$\boldsymbol{\mu}_\infty = (\mathbf{I} - \mathbf{B})^{-1}\mathbf{A} \quad (15)$$

$$\mathbf{V}_\infty = \mathbf{B}\mathbf{V}_\infty\mathbf{B}' + \boldsymbol{\Sigma} \quad (16)$$

where \mathbf{I} is the $p \times p$ identity matrix, and \mathbf{B}' denotes the transpose of \mathbf{B} . Eq. 16 is a matrix equation that

The condition for the MAR(1) process to have a stationary distribution (i.e., the stability condition) is that the all eigenvalues λ (real or complex) of the community matrix B must satisfy $|\lambda| < 1$. (Explain why this makes sense.)

The equation for the mean of the distribution is found in the same way we found the mean for the AR(1) model:

$$\begin{aligned}\mu(\vec{X}_t) &= \mu(\vec{A} + B\vec{X}_{t-1} + \vec{E}_t) \\ &= \vec{A} + B\mu(\vec{X}_{t-1}) + \mu(\vec{E}_t)\end{aligned}$$

Hence, taking $t \rightarrow \infty$ we see

$$(I - B)\vec{\mu}_\infty = \vec{A}$$

We assume $I - B$ is invertible, though I don't see why it has to be.

The derivation of the covariance matrix equation is also similar, and relies on the following:

$$\text{Cov}(B\vec{X}) = B \text{Cov}(\vec{X}) B^T$$

$$\text{Cov}(\vec{X} + \vec{Y}) = \text{Cov}(\vec{X}) + \text{Cov}(\vec{Y}) \text{ if } \vec{X} \text{ and } \vec{Y} \text{ are uncorrelated.}$$

Hence,

$$\begin{aligned} \text{Cov}(\vec{X}_t) &= \text{Cov}(\vec{A} + B\vec{X}_{t-1} + \vec{E}_t) \\ &= B \text{Cov}(\vec{X}_{t-1}) B^T + \text{Cov}(\vec{E}_t) \end{aligned}$$

so that taking $t \rightarrow \infty$ results in

$$V_\infty = B V_\infty B^T + \Sigma$$

There is a way to extract V_∞ from this equation using non-standard linear algebra.

STABILITY of the system in terms of the variance of the stationary distribution.

Essentially, the closer the eigenvalues of B are to 0 the less variability there will be in the system above that due to the environmental variability.

What we want is a measure of relative variance (relative to the environment).

the “volume” of covariance matrices. For example, in two-dimensional space the area of the parallelogram defined by any two vectors equals the determinant of the matrix containing the two vectors as columns. Since the covariance matrices \mathbf{V}_∞ and $\mathbf{\Sigma}$ give the variances of the stationary distribution and process errors, respectively, the volume of the difference $\mathbf{V}_\infty - \mathbf{\Sigma}$ measures the degree to which species interactions increase the variance of the stationary distribution relative to the variance of the process error. From Eq. 16

$$\det(\mathbf{V}_\infty - \mathbf{\Sigma}) = \det(\mathbf{V}_\infty)\det(\mathbf{B})^2. \quad (24)$$

This last equation follows from

$$V_{\infty} = B V_{\infty} B^T + \Sigma$$

$$\det(XY) = \det(X) \det(Y)$$

$$\det(B^T) = \det(B)$$

That is,

$$\det(V_{\infty} - \Sigma) = \det(B V_{\infty} B^T) = \det(V_{\infty}) \det(B)^2$$

Hence, the "proportion of the volume of V_{∞} attributable to species interactions" is

$$\frac{\det(V_{\infty} - \Sigma)}{\det V_{\infty}} = \det(B)^2$$

Something from Math 270: The determinant of a matrix is the product of all its real and complex eigenvalues (with multiplicity). Hence,

$$\det(B)^2 = (\lambda_1 \cdots \lambda_p)^2 \quad (1)$$

So that we see in this equation confirmation of the notion that systems with eigenvalues closer to zero will be more stable.

But notice that just having more eigenvalues (i.e., more species) makes (1) smaller. So instead they use the term

$$\det(B)^{2/p} = \sqrt[p]{(\lambda_1 \cdots \lambda_p)^2}$$

Parameter Estimation!!! (Discussion of linear least squares)

This boils down to trying to “solve” an overdetermined linear system:

$$X\vec{b} = \vec{y}$$

Where X is a $T \times p$ matrix, \vec{b} is a $p \times 1$ column vector, and \vec{y} is a $T \times 1$ column vector. Here “overdetermined” means $T > p$.

X and \vec{y} are known (observed) and we want to find \vec{b} that minimizes the objective function

$$\begin{aligned} S(\vec{b}) &= \|\vec{y} - X\vec{b}\|^2 \\ &= \sum_{t=1}^T (y_t - \sum_{j=1}^p X_{t,j} b_j)^2 \end{aligned}$$

We define the t th residual as the term

$$r_t = y_t - \sum_{j=1}^p X_{t,j} b_j$$

This is the difference between the observation y_t and what our model (based on our choice of \vec{b}) predicts y_t should be. So we can write

$$S(\vec{b}) = \sum_{t=1}^T r_t^2$$

This is a multivariable function (a function of $p > 1$ variables).

From Math 210: multivariable functions attain maxes and mins where their gradient is zero. For us, this means we need $\partial S / \partial b_j = 0$ for all j .

We compute

$$\begin{aligned}\partial S / \partial b_j &= \sum_{t=1}^T 2r_t \partial r_t / \partial b_j \\ &= \sum_{t=1}^T 2(y_t - \sum_{j=1}^p X_{t,j} b_j) (-X_{t,j})\end{aligned}$$

So we need to find \vec{b} so that

$$\sum_{t=1}^T (y_t - \sum_{j=1}^p X_{t,j} b_j) X_{t,j} = 0 \quad \text{for all } j$$

Rearranging results in the matrix equation

$$X^T X \vec{b} = X^T \vec{y}$$

Thus the solution to the least squares problem is given by

$$\vec{b} = (X^T X)^{-1} X^T \vec{y}$$

The particular equation given in Ives is similar ...

matrices of estimated parameters. Letting $\mathbf{Z} = [\mathbf{1}, \mathbf{X}, \mathbf{U}]$ be the $T \times (1 + p + q)$ matrix with $\mathbf{1}$, \mathbf{X} , and \mathbf{U} concatenated horizontally as columns, and $\hat{\mathbf{D}}_i = [\hat{a}_i, \hat{\mathbf{B}}_i, \hat{\mathbf{C}}_i]$ be the $1 \times (1 + p + q)$ vector containing the estimates of a_i , \mathbf{B}_i , and \mathbf{C}_i , the CLS estimates are given by the formula

$$\hat{\mathbf{D}}'_i = (\mathbf{Z}'\mathbf{Z})^{-1}\mathbf{Z}'\mathbf{Y}_i. \quad (31)$$

(show code)

Other important/interesting points:

- 1 Adding environmental covariates (does not change math problem significantly, but increases the need for a larger data set)
- 2 Maximum likelihood estimator (equation in Ives is close to a standard one)
- 3 Model selection (CONDITIONAL least squares)
- 4 Parameter confidence
- 5 Replicated experiments data – how to handle this?
- 6 Interpolating/extrapolating data sets (don't think this will work)