Chances are good
Modeling stochastic forces in ecology

Ecologists have a love-hate relationship with mathematical models

“The current popularity in population ecology of models so abstract that it is difficult to see how a testable hypothesis might be deduced from them is a more serious matter. How much weight and epistemological status do the authors and supporters of such models attach to the conclusions that might be drawn from them? Does the popularity of such models mark the first step toward Scholasticism?”
— Andrewartha and Birch (1954)

Part of the problem was that mathematical models in ecology were deterministic, consisting of differential equations, difference equations, etc. Ecological data, by contrast, typically revealed wild fluctuations (see Figures):
The claim (May 1974) that such wild fluctuations might in fact be deterministic and explained with some low-dimensional mathematical model (if only we knew the form of the model) was the ultimate provocation. (In the '70s, in practically the same breath, the mathematical ecologists claimed that dynamic models, “linearized around equilibrium,” explained population abundance patterns in ecological communities.)

What were ecologists to make of mathematical models? Were these differential equations in their textbooks intended to be taken seriously as scientific hypotheses? In all of the “biomathematics” literature, was there a single mathematical model that “stuck” as a successful explanation of a real system?
Stochasticity

population processes are fundamentally births, deaths, migrations

stochasticity is the random variability in such processes

“random”: unexplained, high-dimensional variability that is conveniently modeled by probability distributions
Importance of stochasticity

noise is pervasive in ecological data, and satisfactory explanations (ecological theory) must accommodate such variability.

connecting deterministic models with data requires explicit modeling of stochastic forces (departures of data from model).

deterministic concepts, such as point equilibria, cycles, and chaos must be rethought in stochastic contexts.

accurate modeling and estimation of stochastic forces crucial to species preservation efforts in conservation biology.
**Deterministic model:**

\[ n_1 = pn_0 \]

\( n_0 \): number of individuals in a cohort at year \( t = 0 \)

\( p \): survival fraction

\( n_1 \): number of individuals in cohort alive 1 year later

**Demographic stochasticity**

each individual in cohort experiences an independent random experiment to determine a life table outcome

e.g. for each of \( n_0 \) individuals, roll the “dice of life” to determine whether the individual lives or dies

\( p \): probability of survival

\( N_1 \): number of survivors is a *random variable*
\[
\Pr[N_1 = n_1] = \binom{n_0}{n_1} p^{n_1} (1 - p)^{n_0-n_1},
\]
\[
n_1 = 0, 1, 2, ...
\]

notation:
\[
N_1 \sim \text{binomial}(n_0, p)
\]

expected value:
\[
E(N_1) = \sum_{n_1=0}^{n_0} n_1 \Pr[N_1 = n_1]
\]
\[
= pn_0
\]

variance:
\[
V(N_1) = \sum_{n_1=0}^{n_0} (n_1 - E(N_1))^2 P[N_1 = n_1]
\]
\[
= p(1 - p)n_0 \quad ( = \alpha n_0 )
\]

coefficient of variation:
\[
CV(N_1) = \frac{\sqrt{V(N_1)}}{E(N_1)} = \frac{1}{\sqrt{n_0}} \sqrt{\frac{(1-p)}{p}}
\]

note: \(CV(N_1) \to 0\) as \(n_0\) becomes large
(model becomes essentially deterministic)
Environmental stochasticity

good years and bad years: survival probability varies

model: $P$ taken to be a random variable with continuous distribution on $(0, 1)$

$$N_1 = Pn_0$$

expected value:
$$E(N_1) = E(P)n_0$$

variance:
$$V(N_1) = V(P)n_0^2 \quad (= \beta n_0^2)$$

coefficient of variation:
$$CV(N_1) = CV(P)$$

note: $CV(N_1)$ does not go to zero as $n_0$ increases
Both demo and enviro stochasticity

\[ f_P(p): \text{ probability density function for } P \]

\[ \int_0^1 f_P(p) \, dp = 1 \]

first draw value of \( P \) (say, \( p \)); then draw value of \( N_1 \)

\[ N_1 \mid P = p \sim \text{binomial}(n_0, p) \]

\[ \Pr[N_1 = n_1] = \]

\[ \int_0^1 \binom{n_0}{n_1} p^{n_1} (1 - p)^{n_0 - n_1} f_P(p) \, dp \]

from conditional probability:

\[ E(N_1) = E[E(N_1 \mid P = p)] \]

\[ V(N_1) = E[V(N_1 \mid P = p)] \]

\[ + V[E(N_1 \mid P = p)] \]

expected value:

\[ E(N_1) = E(n_0 P) = n_0 E(P) \]
variance:
\[ V(N_1) = E[n_0 P(1 - P)] + V(n_0 P) \]
\[ = n_0 E[P(1 - P)] + n_0^2 V(P) \]
\[ (= \alpha n_0 + \beta n_0^2) \]

Variance stabilizing transformations

\[ V(N_1) = v(n_0) \] (conditional on \( n_0 \))

want to find transformation \( X_1 = g(N_1) \)
such that the variance of \( X_1 \) is a constant (i.e. does not depend on \( n_0 \))

such a transformation represents the scale on which the stochasticity in \( N_1 \) can be modeled as “additive noise”

\[ X_1 = g(N_1) \approx g(n_0) + (N_1 - n_0)g'(n_0) \]

\[ V(X_1) \approx V[g(n_0) + (N_1 - n_0)g'(n_0)] \]
\[ V(N_1 g'(n_0)) = [g'(n_0)]^2 v(n_0) \]

Set \([g'(n)]^2 v(n) = c_0\) (a positive constant) and solve for \(g(n)\)

\[ g(n) = c_1 \int \frac{dn}{\sqrt{v(n)}} + c_2 \]

where \(c_1\) \(=\ \sqrt{c_0}\) and \(c_2\) are arbitrary constants

**demographic**: take \(v(n) = \alpha n\)

\[ g(n) = \frac{c_1}{2 \sqrt{\alpha}} \sqrt{n} + c_2 \]

or just

\[ g(n) = \sqrt{n} \]
environmental: take \( v(n) = \beta n^2 \)

\[
g(n) = \frac{c_1}{\beta} \ln n + c_2
\]

or just

\[
g(n) = \ln n
\]

both d & e: take \( v(n) = \alpha n + \beta n^2 \)

\[
g(n) = \frac{c_1}{2 \sqrt{\beta}} \ln \left( \sqrt{\beta n} + \sqrt{\beta n + \alpha} \right) + c_2
\]

reparameterize as

\[
v(n) = \alpha n + \beta n^2
\]

\[
= \phi [(1 - \psi)4n + \psi n^2]
\]

\( \psi \): relative “weight” of enviro stochasticity component
\[ g(n) = \frac{2}{\sqrt{\psi}} \ln \left[ \frac{1}{2} \sqrt{\psi n} + \frac{1}{2} \sqrt{\psi n + 4(1 - \psi)} \right] \]

(\( c_1 = \sqrt{\phi} \) and \( c_2 = -(2/\sqrt{\psi}) \ln (2\sqrt{\psi}) \))

if \( \psi = 1 \), \( g(n) = \ln n \)

if \( \psi \to 0 \), \( g(n) \to \sqrt{n} \)
Stochastic dynamic models

deterministic survival as a dynamic model:
\[ n_t = pn_{t-1} \]

where \( t = 0, 1, 2, \ldots \).

1. Chains of conditional distributions (Markov, etc.)

\[ \Pr[N_t = n_t \mid N_{t-1} = n_{t-1}] = p(n_t \mid n_{t-1}) \]

\( p(\cdot) \): probability mass (or density) function for \( N_t \) given the fixed size of the previous population

demographic stochastic model of survival

\[ p(n_t \mid n_{t-1}) = \binom{n_{t-1}}{n_t} p^n_t (1 - p)^{n_{t-1} - n_t} \]

Start with \( n_0 \), pick \( N_1 \), then pick \( N_2, \ldots \).
ex. demo plus enviro

\[ p(n_t | n_{t-1}) = \int_0^{1} \binom{n_0}{n_1} p^n (1 - p)^{n_0 - n_1} f_P(p) \, dp \]

**Nonlinear autoregressive (NLAR) processes**

deterministic population model:

\[ n_t = f(n_{t-1}) \]

ex. Ricker model:

\[ n_t = n_{t-1} \exp (a - bn_{t-1}) \]

stochastic version: transform and add “noise”:

\[ x_t = g(n_t) = g(f(n_{t-1})) = h(x_{t-1}) \]
\[ X_t = h(X_{t-1}) + E_t \]

where \( E_t \) has a normal distribution with mean 0 and variance \( \sigma^2 \) \( (E_t \sim \text{normal}(0, \sigma^2)) \), with \( E_1, E_2, \ldots \), uncorrelated.

The above implies that the conditional distribution of \( X_t \) given \( X_{t-1} = x_{t-1} \) is normal\( (h(x_{t-1}), \sigma^2) \). \( X_t \) is called a nonlinear autoregressive (NLAR) process.

Conditional pdf for \( X_t \) is:

\[
p(x_t \mid x_{t-1}) = \left( \sigma^2 2\pi \right)^{-\frac{1}{2}} \exp \left[ -\frac{(x_t - h(x_{t-1}))^2}{2\sigma^2} \right]
\]
ex. environmental stochastic Ricker:

\[
\ln N_t = \ln N_{t-1} + a + bN_{t-1} + E_t
\]

\[
X_t = X_{t-1} + a + be^{X_{t-1}} + E_t
\]

The conditional pdf for \( X_t \) is:

\[
p(x_t|x_{t-1}) = \\
(\sigma^2 2\pi)^{-\frac{1}{2}} \exp \left[ -\frac{(x_t - x_{t-1} - a + b e^{x_{t-1}})^2}{2\sigma^2} \right]
\]

**Multivariate NLAR process**

Deterministic model now is a system of difference equations

\[
n_t = f(n_{t-1})
\]

where \( n_t \) is a vector of state variables, and \( f(\cdot) \) is a vector of functions
ex. LPA model of laboratory flour beetle populations

\[ L_t = b A_{t-1} \exp(-c_{el} L_{t-1} - c_{ea} A_{t-1}) \]

\[ P_t = L_{t-1}(1 - \mu_l) \]

\[ A_t = P_{t-1} \exp(-c_{pa} A_{t-1}) + A_{t-1}(1 - \mu_a) \]

\( L_t \) = feeding larvae at time \( t \), \( P_t \) = non-feeding larvae, pupae, & callow adults at time \( t \), \( A_t \) = sexually mature adults at time \( t \)
Stochastic version:

\[ X_t = h(X_{t-1}) + E_t \]

where \( X_t \) is the vector of transformed variables, \( h(\cdot) \) is the map on the transformed scale, and \( E_t \) is a random vector with a multivariate normal distribution having mean vector 0 and variance-covariance matrix \( \Sigma \).

Ex. LPA model, demographic stochasticity

\[
\begin{align*}
\sqrt{L_t} &= \sqrt{bA_{t-1}\exp(-c_{el}L_{t-1} - c_{ea}A_{t-1})} + E_{1t} \\
\sqrt{P_t} &= \sqrt{L_{t-1}(1 - \mu_l)} + E_{2t} \\
\sqrt{A_t} &= \sqrt{P_{t-1}\exp(-c_{pa}A_{t-1}) + A_{t-1}(1 - \mu_a)} + E_{3t}
\end{align*}
\]
Joint distribution of $X_1, X_2, ..., X_q$

starting from $x_0$

$$p(x_1, x_2, ..., x_q | x_0)$$

$$= p(x_1 | x_0)p(x_2 | x_1) \cdots p(x_q | x_{q-1})$$

joint pdf of the trajectory $x_1, x_2, ..., x_q$

starting at fixed size $x_0$

Advantages of “chain” models

These types of “chain” models are excellent for analyzing time series data

Many discrete time ecological processes
2. Diffusion processes (stochastic differential equations)

deterministic model:

\[
\frac{dn_t}{dt} = m(n_t)
\]

\[dn_t = m(n_t)dt\]

stochastic version:

\[dN_t = m(N_t)dt + \sqrt{v(N_t)}dW_t\]

here \(dW_t \sim \text{normal}(0, dt)\), \(m(n)\) is the “infinitesimal mean” function, and \(v(n)\) is the “infinitesimal variance” function.

\(dN_t\) is defined rigorously in terms of an Ito stochastic integral

\(v(n)\) scales the noise, e.g.,

\[v(n) = \alpha n \text{ demographic}\]

\[v(n) = \beta n^2 \text{ environmental, etc.}\]
ex. Stochastic logistic equation with environmental noise

\[ dN_t = \left( rN_t - \frac{r}{k}N_t^2 \right) dt + \sqrt{\beta N_t^2} dW_t \]

Conditional pdf ("transition distribution") is solution to a PDE:

\[
\Pr[a < N_t < b] = \int_a^b p(n, t \mid n_0) dn
\]

\[
\frac{\partial p}{\partial n} = \frac{1}{2} \frac{\partial^2 [vp]}{\partial n^2} - \frac{\partial [mp]}{\partial n}
\]

Note: in “chain” models, it is usually not possible to write down the form of \( p(n, t \mid n_0) \). But in diffusion processes,

\[
p(n_t \mid n_{t-1}) = p(n_t, 1 \mid n_{t-1})
\]
Advantages of diffusion processes:

Many closed formulas for statistical properties of diffusion processes have been derived

Many other stochastic processes can be approximated by diffusion processes
Stationary distributions

In some stochastic models, the transition distribution converges to a “stationary distribution” (independent of time and initial condition)

\[ p(n, t \mid n_0) \to p(n) \text{ as } t \to \infty \]

In some other stochastic models, such as in models where extinction is possible, the transition distribution can become quasi-stationary for a long time

In diffusion processes, if a stationary distribution exists, it is given by

\[ p(n) = \frac{C}{v(n)} \exp \left[ 2 \int \frac{m(n)}{v(n)} \, dn \right] \]
ex. stochastic logistic, enviro noise

\[ p(n) = \frac{\lambda^s}{\Gamma(s)} n^{s-1} e^{-\lambda n}, \quad 0 < n < \infty \]

\[ \lambda = \frac{2r}{\beta k}, \quad s = \frac{2r}{\beta} - 1 \]

(gamma distribution; special case is the chi-square distribution)
First passage properties

\[ \xi(n; a, b) : \text{probability of reaching } a \text{ before } b, \]
starting from \( n \), where \( a \leq n \leq b \)

\[ \xi(n; a, b) = \frac{\int_n^b \exp[-w(x)] \, dx}{\int_a^b \exp[-w(x)] \, dx} \]

where \( w(x) = 2 \int \frac{m(x)}{v(x)} \, dx \)

Interestingly, stable and unstable equilibria in \( m(n) \) correspond to inflection points in \( \xi \)
taken as a function of \( n \)
These presentation notes may be downloaded at:

http://www.webpages.uidaho.edu/~brian/reprints/BDennis_reprint_list.htm

My email address:

brian@uidaho.edu