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AUTUMN COURSE ON MATHEMATICAL ECOLOGY

(16 November - 10 December 1982)

STOCHASTIC POPULATION THEORY
DIFFUSION PROCESSES II

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$$\begin{cases} \dfrac{dx}{dt} = x(1-x)\left[(w_{11}-w_{12})x + (w_{12}-w_{22})(1-x)\right] \\ \dfrac{dN}{dt} = \left[w_{11}x^2 + 2w_{12}\,x(1-x) + w_{22}(1-x)^2\right] \end{cases}$$

x = frequency of allele A_1
w_{ij} = fitness of genotype A_{ij} (in terms of Malthusian parameters).

No mutation
large population

$\longrightarrow$

$$\begin{cases} \dfrac{dx}{dt} = \alpha x\left[1-\phi(x)\right] \\ x(0) = x_0 \end{cases}$$

$\Phi(x)$ regulation function

$\Phi(x) = 0$ Malthusian growth

$\Phi(x) = \frac{\beta}{\alpha}x$, $\beta > 0$ logistic growth

$\Phi(x) = \frac{\beta}{\alpha}\ln x$ $\beta > 0$ Gompertz growth

Random environment

Lewontin, R.C. and Cohen, D. (1969). On a population growth in randomly varying environment. Proc. Nat. Ac. Sc. USA 62, 1056–1060

May, R. (1971). Stability in random fluctuating versus deterministic environments. Amer. Nat. 107, 621–650

May, R. (1973). Stability and Complexity in Model Ecosystems. Princeton Univ. Press.

Capocelli, R.M. and Ricciardi, L.M. (1974). A diffusion model for population growth in random environment. Theor. Pop. Biol. 5, 28–41

Malthusian

$$\begin{cases} \dfrac{dx}{dt} = rx + x\Lambda(t) \\ P_r\{x(0)=x_0\}=1 \end{cases}$$

$\Lambda(t)$ = white noise

$\langle \Lambda(t) \rangle = 0$

$\langle \Lambda(t)\Lambda(t') \rangle = \sigma^2 \delta(t-t')$

$r \to r + \Lambda(t)$

$X(t)$

May

$$\begin{cases} A_1 = rx \\ A_2 = \sigma^2 x^2 \end{cases}$$

Al.

$$\begin{cases} B_1 = \left(r + \dfrac{\sigma^2}{2}\right) x \\ B_2 = \sigma^2 x^2 \end{cases}$$

$$F(y,t|x_0) = \int_0^y dx\, f(x,t|x_0)$$

$$= \frac{1}{2} + \frac{1}{\sqrt{\pi}} \, Erf\left[\frac{\ln y/x_0}{\sigma\sqrt{2t}} - \left(m - \frac{\sigma^2}{2}\right)\sqrt{\frac{t}{2\sigma^2}} \right]$$

$m = r$ May

$m = r + \frac{\sigma^2}{2}$ Al.

$$M_1(t|x_0) = x_0 \, e^{mt}$$

$$\mu(t|x_0) = x_0 \, e^{\left(m - \frac{3}{2}\sigma^2\right)t}$$

. . . . .

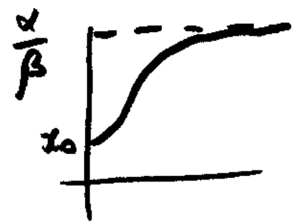
May $(m = r)$

$F(y,t|x_0) \to 1$, $0 < r < \frac{\sigma^2}{2}$

Al $\left(m = r + \frac{\sigma^2}{2}\right)$

$F(y,t|x_0) \to 0$, $0 < r < \frac{\sigma^2}{2}$

Logistic



$$\begin{cases} \dfrac{dx}{dt} = \alpha x - \beta x^2 + x\Lambda(t) \\ P_r\{x(0)=x_0\}=1 \end{cases}$$

May

$$\begin{cases} A_1 = \alpha x - \beta x^2 \\ A_2 = \sigma^2 x^2 \end{cases}$$

Al

$$\begin{cases} B_1 = \left(\alpha + \dfrac{\sigma^2}{2}\right) x - \beta x^2 \\ A_2 = \sigma^2 x^2 \end{cases}$$

May

$$P(x_0) = P(\text{extinction}) = \lim_{t\to\infty} P_r\{X(t) \le 0 \mid X(0) = x_0\}$$

$$= 0 \quad \text{if} \quad \alpha > \frac{\sigma^2}{2} \quad \left(k > \frac{\sigma^2}{2\beta}\right)$$

$$= 1 \quad \text{if} \quad \alpha \le \frac{\sigma^2}{2} \quad \left(k \le \frac{\sigma^2}{2\beta}\right)$$

AI

$P(x_0) = 0$ always

Feldman, M. W. and Roughgarden, J. A population's stationary distribution and chance of extinction in stochastic environments with remarks on the theory of species packing (1975). Theor. Pop. Biol. 7, 197-207

$$\frac{dx}{dt} = f(x) + g(x)\,\Lambda(t) \qquad \Lambda(t) = \text{white noise}$$

$X(t)$ diffusion process $\qquad \langle \Lambda(t)\Lambda(t')\rangle = \sigma^2\delta(t-t')$

$$\begin{cases} A_1(x) = f(x) + \frac{1}{4}\frac{dA_2}{dx} \\ A_2(x) = \sigma^2 g^2(x) \end{cases}$$

$$dy = f(y)dt + g(y)\,dW(t) \qquad W(t) = \text{Wiener process}$$

$$\mathrm{cov}[W(t)W(t')] = \sigma^2 \min(t, t')$$

$Y(t)$ diffusion process

$$\begin{cases} B_1(y) = f(y) \\ B_2(y) = \sigma^2 g^2(y) \end{cases}$$

$X(t) \neq Y(t)$ if g is not constant

$$\frac{d}{dt}\langle x(t)\rangle \neq f(x)$$

$$X(t)\quad\begin{cases}\dfrac{dx}{dt} = f(x) + g(x)\,\Lambda(t)\\[2ex] dx = \left[f(x) + \dfrac{\sigma^2}{2}\, g(x)\, g'(x)\right]dt + g(x)\, dW(t)\end{cases}$$

$$Y(t)\quad\begin{cases}dy = f(y)\,dt + g(y)\, dW(t)\\[2ex] \dfrac{dy}{dt} = \left[f(y) - \dfrac{\sigma^2}{2}\, g(y)\, g'(y)\right] + g(y)\,\Lambda(t)\end{cases}$$

Ito- Stratonovich controversy. What calculus should be used? Either calculus is suitable provided one writes the correct equations.

$$\begin{cases}\dfrac{dx}{dt} = \alpha x - \beta x^2\\ x(0) = x_0\end{cases}$$

$$x(t) = \alpha x_0 \left[\alpha e^{-\alpha t} + \beta x_0 (1 - e^{-\alpha t})\right]^{-1}$$

Discrete analogue :

1) $y_{(n+1)\tau} - y_{n\tau} = \alpha\tau\, y_{n\tau} - \beta\tau\, y_{n\tau}^2 \;,\; \forall n$

$y_{k\tau}$ = population size at time $t = k\tau$

2) $$\frac{x_{(n+1)\tau} - x_{n\tau}}{x_{n\tau}} + 1 = \left[\frac{1-e^{-\alpha\tau}}{\alpha\tau}\,\beta\tau\, x_{n\tau} + e^{-\alpha\tau}\right]^{-1}$$

$(n = 0, 1, 2 \dots)$

$\alpha\tau \to \theta_0 , \theta_\tau , \theta_{2\tau} \dots$

$\langle \theta_{k\tau} \rangle = \alpha\tau \quad \forall k \;, \langle \theta_{k\tau}^2 \rangle = \sigma^2\tau$

$$\Theta_{n\tau} = \begin{bmatrix} \varepsilon & -\varepsilon \\ p & q \end{bmatrix} \to \theta_{n\tau} = \begin{bmatrix} \sigma\sqrt{\tau} & -\sigma\sqrt{\tau} \\ \frac{1}{2} + \frac{\alpha\sqrt{\tau}}{2\sigma} & \frac{1}{2} - \frac{\alpha\sqrt{\tau}}{2\sigma} \end{bmatrix}$$

$$Y_{(n+1)\tau} - Y_{n\tau} = \theta_{n\tau}\, Y_{n\tau} - \beta\tau\, Y_{n\tau}^2 \qquad (n = 0, 1, \dots)$$

$\therefore$

$$\Delta Y_{n\tau} = Y_{(n+1)\tau} - Y_{n\tau}$$

$$\frac{1}{\tau}\langle \Delta Y_{n\tau} \mid Y_{n\tau} = x \rangle = \alpha x - \beta x^2$$

$$\frac{1}{\tau}\langle (\Delta Y_{n\tau})^2 \mid Y_{n\tau} = x \rangle = \sigma^2 x^2 + o(\tau)$$

$$\frac{1}{\tau}\langle (\Delta Y_{n\tau})^{2+p} \mid Y_{n\tau} = x \rangle = o(\tau) \qquad p = 1, 2, \dots$$

$$Y_{n\tau} \to Y(t) \qquad \begin{cases} A_1 = \alpha x - \beta x^2 \\ A_2 = \sigma^2 x^2 \end{cases}$$

$$\Longrightarrow$$

$$\frac{X_{(n+1)\tau} - X_{n\tau}}{X_{n\tau}} + 1 = \left[\beta\tau X_{n\tau} \frac{(1 - e^{-\theta_{n\tau}})}{\theta_{n\tau}} + e^{-\theta_{n\tau}}\right]^{-1}$$

$(n = 0, 1, \dots)$

$$\xi_{n\tau} = \left\{\left[\beta\tau X_{n\tau} \frac{1 - e^{-\theta_{n\tau}}}{\theta_{n\tau}} + e^{-\theta_{n\tau}}\right]^{-1} \middle| X_{n\tau} = x\right\}$$

$n = 0, 1, \dots$

$$\varepsilon \equiv \sigma\sqrt{\tau}$$

$$\begin{cases} P_r\left\{\xi_{n\tau} = \left[\frac{\beta\varepsilon^2 x}{\sigma^2}\, \frac{1 - e^{-\varepsilon}}{\varepsilon} + e^{-\varepsilon}\right]^{-1}\right\} = \frac{1}{2} + \frac{\alpha\varepsilon}{2\sigma^2} \\ \\ P_r\left\{\xi_{n\tau} = \left[\frac{\beta\varepsilon^2 x}{\sigma^2}\, \frac{e^{\varepsilon} - 1}{\varepsilon} + e^{\varepsilon}\right]^{-1}\right\} = \frac{1}{2} - \frac{\alpha\varepsilon}{2\sigma^2} \end{cases}$$

$$\langle (\Delta X_{n\tau})^r \mid X_{n\tau} = x \rangle = x^r E\left[(\xi_{n\tau} - 1)^r\right]$$

$r = 1, 2, \dots$

$$B_1 \equiv \lim_{\tau \to 0} \frac{1}{\tau}\langle \Delta X_{n\tau} \mid X_{n\tau} = x \rangle = \left(\alpha + \frac{\sigma^2}{2}\right)x - \beta x^2$$

$$B_2 \equiv \lim_{\tau \to 0} \frac{1}{\tau}\langle (\Delta X_{n\tau})^2 \mid X_{n\tau} = x \rangle = \sigma^2 x^2$$

$$B_m = 0 \qquad m > 2$$

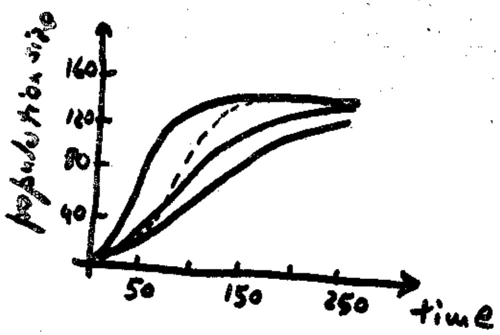
$$X_{n\tau} \to X(t)$$

L.M. Ricciardi (1979). On a conjecture concerning population growth in random environment. Biol. Cybernetics __32__, 95-99

$$\begin{cases} \dfrac{dx}{dt} = \alpha x - \beta x \ln x \quad , \beta > 0 \\ x(0) = x_0 \end{cases}$$

Gompertz

$$x(t) = \exp\left[\frac{\alpha}{\beta} - \left(\frac{\alpha}{\beta} - \ln x_0\right) e^{-\beta t}\right] \qquad k = e^{\alpha/\beta}$$



$$\alpha\tau \longrightarrow \Theta_{n\tau}$$

$$\langle \Theta_{n\tau} \rangle = \alpha\tau$$
$$\langle \Theta_{n\tau}^2 \rangle = \sigma^2\tau$$

1)

$$\begin{cases} Y_{(n+1)\tau} - Y_{n\tau} = \left(\Theta_{n\tau} - \beta\tau \ln Y_{n\tau}\right) Y_{n\tau} \\ \Pr\{Y_0 = x_0\} = 1 \qquad\qquad n = 0, 1, 2, \dots \end{cases}$$

2)

$$\begin{cases} X_{(n+1)\tau} - X_{n\tau} = X_{n\tau}\left\{\exp\left[\dfrac{\beta\tau \ln X_{n\tau} - \Theta_{n\tau}}{\beta\tau}\left(e^{-\beta\tau} - 1\right)\right] - 1\right\} \\ \Pr\{X_0 = x_0\} = 1 \qquad\qquad n = 0, 1, \dots \end{cases}$$

A.G. Nobile and L.M. Ricciardi (1980). Growth and extinction in random environment. In __Applications of Information and Control Systems__ (D.G. Lainiotis and N.S. Tzannes eds.), Reidel 455-465

$$Y_{n\tau} \longrightarrow \begin{cases} A_1 = \alpha x - \beta x \ln x \\ A_2 = \sigma^2 x^2 \end{cases}$$

$$X_{n\tau} \longrightarrow \begin{cases} B_1 = \left(\alpha + \dfrac{\sigma^2}{2}\right) x - \beta x \ln x \\ B_2 = \sigma^2 x^2 \end{cases}$$

$$W(x) \equiv \lim_{t\to\infty} f(x,t\,|\,x_0) \text{ exists.}$$

$$\lim_{t\to\infty} P_r\{\,X(t)\le 0\,|\,X(0)=x_0\} = 1-\int_0^\infty W(x)\,dx = 0$$

$\longrightarrow$

$x(t)$ = # of individuals at time t in a population growing in an environment having finite carrying capacity

$x_{n\tau}$ observed numbers at time $t=n\tau$ $(\tau>0)$
$n=0,1,2\ldots$

$$\Delta x_{n\tau} = A\tau\, f(x_{n\tau}) \quad , n=0,1,\ldots$$

or

$$\frac{dx}{dt} = B\,f(x)$$

A and B to be determined.

$$x(t)\Big|_{t=n\tau} = x_{n\tau}$$

$\therefore$

$$\begin{cases} B = \dfrac{A\,f(x_{n\tau})}{\Delta x_{n\tau}} \displaystyle\int_{x_{n\tau}}^{x_{(n+1)\tau}} \frac{dz}{f(z)} \\[2ex] \Delta x_{n\tau} = A\tau\, f(x_{n\tau}) \end{cases}$$

Expanding r.h.s.:

$$B = A - \frac{1}{2} f'(x_{n\tau})A^2\tau + o(\tau)$$

B is generally density-dependent.

$$\Delta x_{n\tau} = A\tau\, f(x_{n\tau}) \quad n=0,1,2\ldots$$

"random environment" assumption:

$$A\tau \longrightarrow A'_{n\tau}$$

$$A'_{n\tau} : \quad \begin{aligned} &P_r\{A'_{n\tau} = \sigma\sqrt{\tau}\} = \frac{1}{2} + \frac{A\sqrt{\tau}}{2\sigma} \\ &P_r\{A'_{n\tau} = -\sigma\sqrt{\tau}\} = \frac{1}{2} - \frac{A\sqrt{\tau}}{2\sigma} \quad , \sigma > 0 \end{aligned}$$

$$\langle A'_{n\tau} \rangle = A\tau$$

$$\langle (A'_{n\tau})^2 \rangle = \sigma^2 \tau$$

$$\langle (A'_{n\tau})^{2+p} \rangle = o(\tau) \qquad p = 1, 2, \ldots$$

$$\therefore$$

$$x_{n\tau} \to X_{n\tau} \quad : \quad \Delta X_{n\tau} = A'_{n\tau} \, f(X_{n\tau}) \quad \forall n$$

$$\lim_{\tau \to 0} \frac{1}{\tau} \langle \Delta X_{n\tau} \,|\, X_{n\tau} = z \rangle = A f(z)$$

$$\lim_{\tau \to 0} \frac{1}{\tau} \langle (\Delta X_{n\tau})^2 \,|\, X_{n\tau} = z \rangle = \sigma^2 f^2(z)$$

$$\ldots \quad \ldots \quad = 0$$

$$dX = A f \, dt + f \, dW$$

$$\frac{dx}{dt} = \left[A - \frac{\sigma^2}{2} f f'\right] \Lambda$$

$$\frac{dx}{dt} = B f(x)$$

$$B\tau = \int_{x_{n\tau}}^{x_{(n+1)\tau}} \frac{dz}{f(z)} \qquad n = 0, 1, \ldots$$

$$B\tau \to B'_{n\tau}$$

$$\begin{cases} P_r\{B'_{n\tau} = \sigma\sqrt{\tau}\} = \frac{1}{2} + \frac{B\sqrt{\tau}}{2\sigma} \\ P_r\{B'_{n\tau} = -\sigma\sqrt{\tau}\} = \frac{1}{2} - \frac{B\sqrt{\tau}}{2\sigma} \end{cases}$$

$$B'_{n\tau} = \int_{Y_{n\tau}}^{Y_{(n+1)\tau}} \frac{dz}{f(z)} \qquad n = 0, 1, \ldots$$

By Taylor expansion of r.h.s. :

$$Y_{n\tau} \to Y(t) \qquad \begin{cases} A_1 = f(y)\left[B + \frac{\sigma^2}{2} f'(y)\right] \\ A_2 = \sigma^2 f^2(y) \end{cases}$$

$$\begin{cases} \frac{dY}{dt} = [B + \Lambda(t)] f(Y) \\ dY = \left[B + \frac{\sigma^2}{2} f'(Y)\right] f(Y) dt + f(Y) dW \end{cases}$$

- $dX(t) = A f(X)dt + f(X)\, dW(t)$
- $\frac{dY}{dt} = [B + \Lambda(t)]\, f(Y)$

A and B are related $\left(B = A - \frac{1}{2} f' A^2 \tau + \dots\right)$

Example

$$\frac{dx}{dt} = m x \left(1 - \frac{x}{K}\right) \qquad \begin{cases} B \to m \\ f(x) = x\left(1 - \frac{x}{K}\right) \end{cases}$$

$$\Delta x_{n\tau} = w\tau\, x_{n\tau}\left(1 - \frac{x_{n\tau}}{K}\right) \qquad A \to w$$

$n = 0, 1 \dots$

$$\begin{cases} m = w \dfrac{f(x_{n\tau})}{\Delta x_{n\tau}} \displaystyle\int_{x_{n\tau}}^{x_{(n+1)\tau}} \frac{dz}{f(z)} \\ \Delta x_{n\tau} = w\tau\, f(x_{n\tau}) \end{cases}$$

$$w = \frac{1 - e^{-m\tau}}{(1 - e^{-m\tau}) K^{-1} x_{n\tau} + e^{-m\tau}}$$

Random environment assumption:

$$\begin{cases} w\tau \to W_{n\tau} & \langle W_{n\tau} \rangle = w\tau \\ m\tau \to M_{n\tau} & \langle M_{n\tau} \rangle = m\tau \end{cases}$$

$W_{n\tau}$ indep.:

$$\langle M_{n\tau} \rangle \equiv \underbrace{\langle W_{n\tau} \rangle}_{w\tau} - \frac{\sigma^2}{2}\left(1 - \frac{2x}{K}\right)\tau + o(\tau)$$

$M_{n\tau}$ indep.:

$$\langle W_{n\tau} \rangle = m\tau + \frac{\sigma^2}{2}\left(1 - \frac{2x}{K}\right)\tau + o(\tau)$$

$\therefore$

$$m = \lim_{\tau \to 0} \frac{\langle M_{n\tau} \rangle}{\tau} = w - \frac{\sigma^2}{2}\left(1 - 2\frac{x}{K}\right)$$

$$w = \lim_{\tau \to 0} \frac{\langle W_{n\tau} \rangle}{\tau} = m + \frac{\sigma^2}{2}\left(1 - 2\frac{x}{K}\right)$$