Modeling Pioneer/Climax Interactions Using Markov Processes

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Previous Work

- Studied the asymptotic behavior of pioneer/climax species interactions.

$$x'(t) = x(t)\, f(x(t), y(t)) \tag{1}$$
$$y'(t) = y(t)\, g(x(t), y(t)) \tag{2}$$

- Changes in qualitative behavior of solutions as model parameters are modified.
- Effects of external forcing (stocking/harvesting) on system.
- Poisson random variable model of the pioneer/climax interaction.

Probability Distribution

$X(t)$ random variable representing number of pioneer species individuals

$Y(t)$ random variable representing number of pioneer species individuals

$P_{x,y}(t)$ probability distribution

$$P_{x,y}(t) = \mathrm{P}\left(X(t) = x,\ Y(t) = y\right)$$

for $x = 0, 1, \ldots$ and $y = 0, 1, \ldots$

Assumption: $P_{x,y}(t) = 0$ whenever $x < 0$ or $y < 0$.

Transition Probabilities

If $(X(t), Y(t)) = (x, y)$ then during a short time interval $(t, t + \Delta t)$:

1. $\mathrm{P}\left(X(t+\Delta t) = x+1,\ Y(t+\Delta t) = y\right) = \beta_x \Delta t + o(\Delta t)$,
2. $\mathrm{P}\left(X(t+\Delta t) = x,\ Y(t+\Delta t) = y+1\right) = \beta_y \Delta t + o(\Delta t)$,
3. $\mathrm{P}\left(X(t+\Delta t) = x-1,\ Y(t+\Delta t) = y\right) = \delta_x \Delta t + o(\Delta t)$,
4. $\mathrm{P}\left(X(t+\Delta t) = x,\ Y(t+\Delta t) = y-1\right) = \delta_y \Delta t + o(\Delta t)$,
5. $\mathrm{P}\left(|X(t+\Delta t) - X(t)| > 1,\ Y(t+\Delta t) = y\right) = o(\Delta t)$,
6. $\mathrm{P}\left(X(t+\Delta t) = x,\ |Y(t+\Delta t) - Y(t)| > 1\right) = o(\Delta t)$,
7. $\mathrm{P}\left(X(t+\Delta t) = x, Y(t+\Delta t) = y\right) =$
   $1 - (\beta_x + \delta_x + \beta_y + \delta_y)\Delta t + o(\Delta t)$.

Differential Equation for Transition Probabilities

$$
\begin{aligned}
P_{x,y}(t+\Delta t) &= P_{x,y}(t)(1-\beta_x-\delta_x-\beta_y-\delta_y)\Delta t \\
&\quad + P_{x-1,y}(t)\lambda_{x-1}\Delta t + P_{x,y-1}\lambda_{y-1}\Delta t \\
&\quad + P_{x+1,y}(t)\mu_{x+1}\Delta t + P_{x,y+1}(t)\mu_{y+1}\Delta t \\
\frac{P_{x,y}(t+\Delta t)-P_{x,y}(t)}{\Delta t} &= -(\beta_x+\delta_x+\beta_y+\delta_y)P_{x,y}(t) \\
&\quad + \lambda_{x-1}P_{x-1,y}(t) + \lambda_{y-1}P_{x,y-1}(t) \\
&\quad + \mu_{x+1}P_{x+1,y}(t) + \mu_{y+1}P_{x,y+1}(t) \\
&= \frac{dP_{x,y}(t)}{dt} \qquad (3)
\end{aligned}
$$

Probability Generating Function

For $|r| \leq 1$ and $|s| \leq 1$ we define the **probability generating function**

$$F(r, s, t) = \sum_{x,y=0}^{\infty} P_{x,y}(t) r^x s^y$$

Note that

$$\frac{\partial F}{\partial t} = \sum_{x,y=0}^{\infty} \frac{dP_{x,y}(t)}{dt} r^x s^y$$

$$\frac{\partial F}{\partial r} = \sum_{x,y=0}^{\infty} x P_{x,y}(t) r^{x-1} s^y$$

$$\frac{\partial F}{\partial s} = \sum_{x,y=0}^{\infty} y P_{x,y}(t) r^x s^{y-1}$$

In general

$$\frac{\partial^{i+j} F}{\partial r^i \partial s^j} = \sum_{x,y=0}^{\infty} (x)_i (y)_j P_{x,y}(t) r^{x-i} s^{y-j}. \tag{4}$$

Differential Equation for the PGF

Multiply both sides of Eq. (3) by $r^x s^y$ and sum over x and y.

$$\begin{aligned}
\sum_{x,y=0}^{\infty} \frac{dP_{x,y}(t)}{dt} r^x s^y = & -\sum_{x,y=0}^{\infty} (\beta_x + \delta_x + \beta_y + \delta_y) P_{x,y}(t) r^x s^y \\
& + \sum_{x,y=0}^{\infty} \lambda_{x-1} P_{x-1,y}(t) r^x s^y \\
& + \sum_{x,y=0}^{\infty} \lambda_{y-1} P_{x,y-1}(t) r^x s^y \\
& + \sum_{x,y=0}^{\infty} \mu_{x+1} P_{x+1,y}(t) r^x s^y \\
& + \sum_{x,y=0}^{\infty} \mu_{y+1} P_{x,y+1}(t) r^x s^y
\end{aligned}$$

Re-index Summations

Re-index the summations.

$$\begin{aligned}\frac{\partial F}{\partial t} &= -\sum_{x,y=0}^{\infty}(\beta_x+\delta_x+\beta_y+\delta_y)P_{x,y}(t)r^x s^y \\ &+ \sum_{x,y=0}^{\infty}\beta_x P_{x,y}(t)r^{x+1}s^y + \sum_{x,y=0}^{\infty}\beta_y P_{x,y}(t)r^x s^{y+1} \\ &+ \sum_{x,y=0}^{\infty}\delta_x P_{x,y}(t)r^{x-1}s^y + \sum_{x,y=0}^{\infty}\delta_y P_{x,y}(t)r^x s^{y-1}.\end{aligned} \tag{5}$$

Assumptions About the Birth and Death Functions

To simplify the differential equation for $F(r, s, t)$ it is necessary to make further assumptions about the functions β_x, β_y, δ_x, δ_y. We will assume that

$$\begin{aligned}
\beta_x &= x \\
\beta_y &= (1+\lambda)y(x+c_{22}y) \\
\delta_x &= c_{11}x^2 + xy \\
\delta_y &= \lambda y + y(x+c_{22}y)^2.
\end{aligned}$$

Derivation of PDE for $F(r, s, t)$

Making these substitutions in Eq. (5) produces

$$
\begin{aligned}
\frac{\partial F}{\partial t} &= (r-1)\sum_{x,y=0}^{\infty} xP_{x,y}(t)r^x s^y + \lambda(s^{-1}-1)\sum_{x,y=0}^{\infty} yP_{x,y}(t)r^x s^y \\
&+ c_{11}(r^{-1}-1)\sum_{x,y=0}^{\infty} x^2 P_{x,y}(t)r^x s^y \\
&+ [(\lambda+1)(s-1)+r^{-1}-1]\sum_{x,y=0}^{\infty} xyP_{x,y}(t)r^x s^y \\
&+ c_{22}(1+\lambda)(s-1)\sum_{x,y=0}^{\infty} y^2 P_{x,y}(t)r^x s^y \\
&+ (s^{-1}-1)\sum_{x,y=0}^{\infty} x^2 yP_{x,y}(t)r^x s^y + 2c_{22}(s^{-1}-1)\sum_{x,y=0}^{\infty} xy^2 P_{x} \\
&+ c_{22}^2(s^{-1}-1)\sum_{x,y=0}^{\infty} y^3 P_{x,y}(t)r^x s^y .
\end{aligned}
$$

Replace the summations on the RHS with the appropriate partial derivatives using Eq. (4) and use the following identities:

$$
\begin{aligned}
x^2 &= x(x-1) + x \\
y^2 &= y(y-1) + y \\
x^2 y &= xy(x-1) + xy \\
xy^2 &= xy(y-1) + xy \\
y^3 &= y(y-1)(y-2) + 3y(y-1) + y
\end{aligned}
$$

Simplified Form of PDE for $F(r, s, t)$

$$
\begin{aligned}
\frac{\partial F}{\partial t} \quad = \quad & (r-1)(r-c_{11})\frac{\partial F}{\partial r} + (c_{22}(\lambda+1)s - \lambda - c_{22}^2)(s-1)\frac{\partial F}{\partial s} \\
& - c_{11} r(r-1)\frac{\partial^2 F}{\partial r^2} \\
& + (r(s-1)((\lambda+1)s - 2c_{22} - 1) - s(r-1))\frac{\partial^2 F}{\partial r \partial s} \\
& + c_{22}((1+\lambda)s - 3c_{22})s(s-1)\frac{\partial^2 F}{\partial s^2} \\
& - r^2(s-1)\frac{\partial^3 F}{\partial r^2 \partial s} - 2c_{22} rs(s-1)\frac{\partial^3 F}{\partial r \partial s^2} \\
& - c_{22}^2 s^2(s-1)\frac{\partial^3 F}{\partial s^3} \qquad (6)
\end{aligned}
$$

Cumulant Generating Function

Let $r = e^u$ and $s = e^v$ and define the **cumulant generating function**

$$K(u, v, t) = \ln F(e^u, e^v, t).$$

Note that

$$K(0, 0, t) = \ln F(1, 1, t) = \ln \sum_{x,y=0}^{\infty} P_{x,y}(t)(1^x)(1^y) = \ln 1 = 0,$$

and we may expand $K(u, v, t)$ as a Taylor series about $(u_0, v_0) = (0, 0)$.

Taylor Series for $K(u, v, t)$

$$
\begin{aligned}
K(u,v,t) &= uK_u(0,0,t) + vK_v(0,0,t) \\
&\quad + \frac{1}{2}u^2K_{uu}(0,0,t) + \frac{1}{2}v^2K_{vv}(0,0,t) + uvK_{uv}(0,0,t) \\
&\quad + \frac{1}{6}u^3K_{uuu}(0,0,t) + \frac{1}{6}v^3K_{vvv}(0,0,t) \\
&\quad + \frac{1}{2}u^2vK_{uuv}(0,0,t) + \frac{1}{2}uv^2K_{uvv}(0,0,t) + \cdots
\end{aligned}
$$

Coefficients of Taylor Series

$$
\begin{aligned}
K(u,v,t) &= \ln \sum_{x,y=0}^{\infty} P_{x,y}(t) e^{ux} e^{vy} \\
\frac{\partial K}{\partial u}(u,v,t) &= \frac{\sum_{x,y=0}^{\infty} P_{x,y}(t) x e^{ux} e^{vy}}{\sum_{x,y=0}^{\infty} P_{x,y}(t) e^{ux} e^{vy}} \\
K_u(0,0,t) &= \sum_{x,y=0}^{\infty} x\, P_{x,y}(t) = \mathrm{E}\left[X(t)\right] \equiv \mu_x(t)
\end{aligned}
$$

Product Moments

$$
\begin{aligned}
\mu_y(t) &\equiv \mathrm{E}\left[Y(t)\right] = \frac{\partial K}{\partial v}(0,0,t) \\
m_{20}(t) &\equiv \mathrm{E}\left[(X(t)-\mu_x(t))^2\right] = \frac{\partial^2 K}{\partial u^2}(0,0,t) \\
m_{02}(t) &\equiv \mathrm{E}\left[(Y(t)-\mu_y(t))^2\right] = \frac{\partial^2 K}{\partial v^2}(0,0,t) \\
m_{11}(t) &\equiv \mathrm{E}\left[(X(t)-\mu_x(t))(Y(t)-\mu_y(t))\right] = \frac{\partial^2 K}{\partial u \partial v}(0,0,t) \\
m_{21}(t) &\equiv \mathrm{E}\left[(X(t)-\mu_x(t))^2(Y(t)-\mu_y(t))\right] = \frac{\partial^3 K}{\partial u^2 \partial v}(0,0,t) \\
m_{12}(t) &\equiv \mathrm{E}\left[(X(t)-\mu_x(t))(Y(t)-\mu_y(t))^2\right] = \frac{\partial^3 K}{\partial u \partial v^2}(0,0,t) \\
m_{30}(t) &\equiv \mathrm{E}\left[(X(t)-\mu_x(t))^3\right] = \frac{\partial^3 K}{\partial u^3}(0,0,t) \\
m_{03}(t) &\equiv \mathrm{E}\left[(Y(t)-\mu_y(t))^3\right] = \frac{\partial^3 K}{\partial v^3}(0,0,t)
\end{aligned}
$$

Cumulant in Terms of Product Moments

$$
\begin{aligned}
K(u,v,t) &= u\mu_x(t) + v\mu_y(t) \\
&+ \frac{1}{2}u^2 m_{20}(t) + \frac{1}{2}v^2 m_{02}(t) + uvm_{11}(t) \\
&+ \frac{1}{6}u^3 m_{30}(t) + \frac{1}{6}v^3 m_{03}(t) \\
&+ \frac{1}{2}u^2 v m_{21}(t) + \frac{1}{2}uv^2 m_{12}(t) + \cdots
\end{aligned} \tag{7}
$$

Convert the PDE for $F(r,s,t)$ into a PDE for $K(u,v,t)$.

$$
\begin{aligned}
\frac{\partial F}{\partial t} &= e^K \frac{\partial K}{\partial t} \\
\frac{\partial F}{\partial r} &= e^{K-u} \frac{\partial K}{\partial u} \\
\frac{\partial F}{\partial s} &= e^{K-v} \frac{\partial K}{\partial v}
\end{aligned}
$$

Higher order partial derivatives are readily found.

Differential Equation for $K(u, v, t)$

$$
\begin{aligned}
K_t = \; & (e^u - 1)K_u + \lambda(e^{-v} - 1)K_v \\
& + c_{11}(e^{-u} - 1)\left[K_{uu} + (K_u)^2\right] \\
& + c_{22}(1 + \lambda)(e^v - 1)\left[K_{vv} + (K_v)^2\right] \\
& + ((e^{-u} - 1) + (\lambda + 1)(e^v - 1))\left[K_u K_v + K_{uv}\right] \\
& + (e^{-v} - 1)\left[K_u\left(K_u K_v + 2K_{uv}\right) + K_{uu}K_v + K_{uuv}\right] \\
& + 2c_{22}(e^{-v} - 1)\left[K_v\left(K_u K_v + 2K_{uv}\right) + K_u K_{vv} + K_{uvv}\right] \\
& + c_{22}^2(e^{-v} - 1)\left[(K_v)^3 + 3K_v K_{vv} + K_{vvv}\right]
\end{aligned} \tag{8}
$$

Taylor Series Expansion

Expand Eq. (8) in terms of u and v using Eq. (7) and equate coefficients of like terms on the LHS and RHS.

For terms of $O(u)$:

$$
\begin{aligned}
\frac{d\mu_x}{dt} &= \mu_x(1 - c_{11}\mu_x - \mu_y) - m_{11} - c_{11}m_{20} \\
&= \mu_x - c_{11}\mu_{x^2} - \mu_{xy} \\
&= \mu_x - \mu_{c_{11}x^2} - \mu_{xy}
\end{aligned}
$$

Taylor Series Expansion

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$$
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&= \mu_x - c_{11}\mu_{x^2} - \mu_{xy} \\
&= \mu_x - \mu_{c_{11}x^2} - \mu_{xy}
\end{aligned}
$$

Comparison with deterministic model:

$$
\frac{dx}{dt} = x(1 - c_{11}x - y) = x - c_{11}x^2 - xy
$$

Terms of $O(v)$

$$
\begin{aligned}
\frac{d\mu_y}{dt} &= (1+\lambda)(\mu_{xy} + c_{22}\mu_{y^2}) - \lambda\mu_y \\
&\quad - (\mu_{x^2y} + 2c_{22}\mu_{xy^2} + c_{22}^2\mu_{y^3}) \\
&\quad + \mu_y(3\mu_x^2 - \mu_{x^2}) + 2c_{22}(3\mu_x\mu_y^2 - \mu_x\mu_{y^2})
\end{aligned}
$$

Terms of $O(v)$

$$
\begin{aligned}
\frac{d\mu_y}{dt} &= (1+\lambda)(\mu_{xy} + c_{22}\mu_{y^2}) - \lambda\mu_y \\
&\quad - (\mu_{x^2y} + 2c_{22}\mu_{xy^2} + c_{22}^2\mu_{y^3}) \\
&\quad + \mu_y(3\mu_x^2 - \mu_{x^2}) + 2c_{22}(3\mu_x\mu_y^2 - \mu_x\mu_{y^2})
\end{aligned}
$$

Comparison with deterministic model:

$$
\frac{dy}{dt} = (1+\lambda)y(x + c_{22}y) - \lambda y - y(x + c_{22}y)^2
$$