A Stochastic Model of a Pioneer/Climax Interaction

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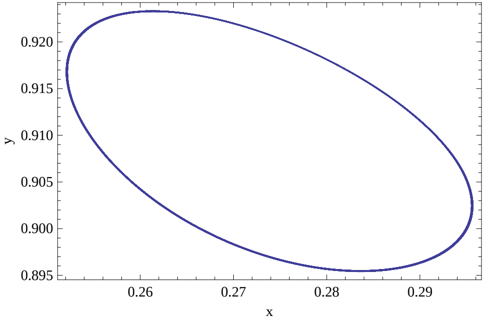
Deterministic Pioneer/Climax Model

$$
\begin{aligned}
x'(t) &= f(x(t), y(t)) \\
&= x(t)(1 - c_{11}x(t) - y(t)) \\
y'(t) &= g(x(t), y(t)) \\
&= -y(t)(1 - x(t) - c_{22}y(t))\left(\frac{9}{8} - x(t) - c_{22}y(t)\right)
\end{aligned}
$$

- Per capita reproduction rates for pioneer and climax species,
- Hopf bifurcations of equilibria,
- Variables x and y represent population density rather than numbers of individuals.

Background



- Asymptotic behaviors of pioneer/climax model explored in Buchanan (1999).
- For small populations, the behavior may be described by a stochastic process.
- Approach to the development of a stochastic model is based on the work of Klebaner and Liptser (2001) on the Lotka-Volterra model.

Integral Form of Deterministic Model

$$
\begin{aligned}
x(t) - x(0) &= \int_0^t f(x(s), y(s))\, ds \\
y(t) - y(0) &= \int_0^t g(x(s), y(s))\, ds.
\end{aligned}
$$

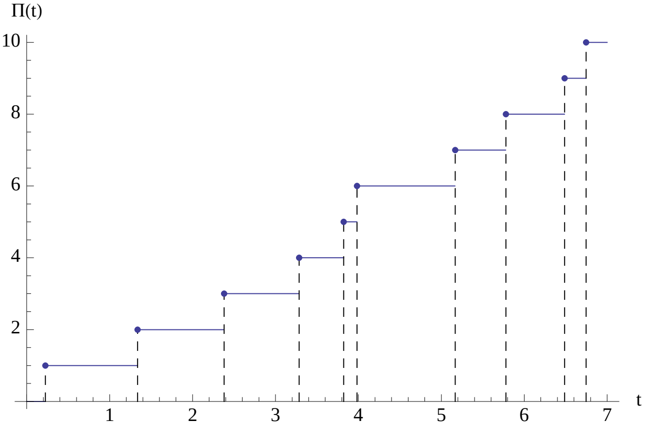
Let K be an integer and define

$$
\begin{aligned}
X(0) &= Kx(0) \\
Y(0) &= Ky(0),
\end{aligned}
$$

the initial values of random variables $X(t)$ and $Y(t)$.

Poisson Process

$\Pi^r(t)$ is a Poisson process with intensity (or rate) r.



Compensators and Martingales

Remarks:

- Poisson process $\Pi^r(t)$ is monotonic.
- $\mathrm{E}\left[\Pi^r(t)\right] = rt$.
- The compensator of $\Pi^r(t)$ is the deterministic expression rt.
- $\Pi^r(t) - rt$ is a martingale, *i.e.* it has no tendency to rise or fall.

$$\mathrm{E}\left[\Pi^r(t) - rt\right] = 0 \quad \text{for all } t.$$

Stochastic Integral

- $\{\Pi_n^r(t)\}_{n \in \mathbb{N}}$ is a sequence of independent Poisson processes with rate r.
- Let $r\left[X^i Y^j\right](t)$ denote the stochastic integral

$$r\left[X^i Y^j\right](t) = \int_0^t \sum_{n=1}^{\infty} \mathbb{I}\left(X^i(s-)Y^j(s-) \geq n\right) \, d\Pi_n^r(s). \tag{1}$$

- Define $A_r^{i,j}(t)$ to be

$$\begin{aligned} A_r^{i,j}(t) &= \int_0^t rX^i(s)Y^j(s)\, ds \\ &= \int_0^t \sum_{n=1}^{\infty} \mathbb{I}\left(X^i(s-)Y^j(s-) \geq n\right) r\, ds. \end{aligned} \tag{2}$$

State-dependent Intensity of Poisson Processes

$$r\left[X^i Y^j\right](t) - A_r^{i,j}(t) = \int_0^t \sum_{n=1}^{\infty} \mathbb{I}\left(X^i(s-)Y^j(s-) \geq n\right)\, d\left(\Pi_n^r(s) - rs\right)$$

- $r\left[X^i Y^j\right](t) - A_r^{i,j}(t)$ is a local martingale,
- $A_r^{i,j}(t)$ is a compensator for $r\left[X^i Y^j\right]_r(t)$,
- the intensity of $r\left[X^i Y^j\right](t)$ is $rX^i(t)Y^j(t)$.

Stochastic Analogue of Deterministic Model

$$
\begin{aligned}
X(t) &= X(0) + \left[X\,Y^0\right](t) \\
&\quad - \frac{c_{11}}{K}\left[X^2\,Y^0\right](t) - \frac{1}{K}[X\,Y](t) \qquad (3) \\
Y(t) &= Y(0) + \frac{17}{8K}[X\,Y](t) + \frac{17c_{22}}{8K}\left[X^0\,Y^2\right](t) \\
&\quad - \frac{9}{8}\left[X^0\,Y\right](t) - \frac{1}{K^2}\left[X^2\,Y\right](t) - \frac{2c_{22}}{K^2}\left[X\,Y^2\right](t) \\
&\quad - \frac{c_{22}^2}{K^2}\left[X^0\,Y^3\right](t). \qquad (4)
\end{aligned}
$$

Blow-up of Solutions

- The stochastic integrals defined in Eq. (1) exist so long as $X(t)$ and $Y(t)$ remain finite.
- The stochastic process $X(t)$ is said to be honest if $\mathrm{P}\left(X(t) < \infty\right) = 1$ for all t, similarly for $Y(t)$.
- Notation:
  - $a \wedge b = \min\{a, b\}$
  - $a \vee b = \max\{a, b\}$

Blow-up Time

Define

- $T_\infty = \inf\{t > 0 \,:\, X(t) \vee Y(t) = \infty\}$,
- for each $n \in \mathbb{N}$, $T_n^X = \inf\{t > 0 \,:\, X(t) \geq n\}$,
- $T_\infty^X = \lim_{n\to\infty} T_n^X$,
- for each $m \in \mathbb{N}$ define $T_m^Y = \inf\{t > 0 \,:\, Y(t) \geq m\}$ and,
- $T_\infty^Y = \lim_{m\to\infty} T_m^Y$.

Boundedness of $X(t)$ (1 of 3)

$$\begin{aligned} X(t \wedge T_n^X) &= X(0) + \left[X\,Y^0\right](t \wedge T_n^x) \\ &\quad - \frac{c_{11}}{K}\left[X^2\,Y^0\right](t \wedge T_n^X) - \frac{1}{K}\left[X\,Y\right](t \wedge T_n^X) \\ &\leq X(0) + \left[X\,Y^0\right](t \wedge T_n^x) \\ &= X(0) + \int_0^{t \wedge T_n^x} \sum_{m=1}^{\infty} \mathbb{I}(X(s-) \geq m)\, d\Pi_m^1(s). \end{aligned}$$

Boundedness of $X(t)$ (2 of 3)

Taking the expectation of both sides of the inequality yields

$$\begin{aligned}
\mathrm{E}\left[X(t \wedge T_n^X)\right] &\leq X(0) + \mathrm{E}\left[\int_0^{t \wedge T_n^X} \sum_{m=1}^{\infty} \mathbb{I}(X(s-) \geq m)\, d\Pi_m^1(s)\right] \\
&= X(0) + \mathrm{E}\left[\int_0^{t \wedge T_n^X} \sum_{m=1}^{\infty} \mathbb{I}(X(s-) \geq m)\, ds\right] \\
&= X(0) + \mathrm{E}\left[\int_0^{t \wedge T_n^X} X(s)\, ds\right] \\
&= X(0) + \mathrm{E}\left[\int_0^{t \wedge T_n^X} X(s \wedge T_n^X)\, ds\right] \\
&\leq X(0) + \mathrm{E}\left[\int_0^{t} X(s \wedge T_n^X)\, ds\right] \\
&= X(0) + \int_0^t \mathrm{E}\left[X(s \wedge T_n^X)\right]\, ds.
\end{aligned}$$

Boundedness of $X(t)$ (3 of 3)

According to Gronwall's inequality

$$\mathrm{E}\left[X(t \wedge T_n^X)\right] \leq X(0)e^t \quad \text{for all } n \in \mathbb{N},\ t > 0.$$

Fatou's Lemma implies

$$\begin{aligned} \mathrm{E}\left[X(t \wedge T_\infty^X)\right] &= \mathrm{E}\left[\lim_{n\to\infty} X(t \wedge T_n^X)\right] \\ &\leq \lim_{n\to\infty} \mathrm{E}\left[X(t \wedge T_n^X)\right] \\ &\leq X(0)e^t. \end{aligned}$$

It follows that $\mathrm{P}\left(T_\infty^X \leq t\right) = 0$ for all $t > 0$, so $X(t)$ is honest.

Boundedness of $Y(t)$ (1 of 4)

$$
\begin{aligned}
& Y(t \wedge T_n^X \wedge T_m^Y) \\
\leq \quad & Y(0) + \frac{17}{8K} [X\, Y] (t \wedge T_n^X \wedge T_m^Y) + \frac{17 c_{22}}{8K} \left[X^0\, Y^2\right] (t \wedge T_n^X \wedge T_m^Y) \\
& - \frac{2 c_{22}}{K^2} \left[X\, Y^2\right] (t \wedge T_n^X \wedge T_m^Y) \\
= \quad & Y(0) + \int_0^{t \wedge T_n^X \wedge T_m^Y} \sum_{j=1}^{\infty} \mathbb{I}(X(s-)Y(s-) \geq j)\, d\Pi_j^{17/8K}(s) \\
& + \int_0^{t \wedge T_n^X \wedge T_m^Y} \sum_{j=1}^{\infty} \mathbb{I}(Y^2(s-) \geq j)\, d\Pi_j^{17 c_{22}/8K}(s) \\
& - \int_0^{t \wedge T_n^X \wedge T_m^Y} \sum_{j=1}^{\infty} \mathbb{I}(X(s-)Y^2(s-) \geq j)\, d\Pi_j^{2 c_{22}/K^2}(s).
\end{aligned}
$$

Boundedness of $Y(t)$ (2 of 4)

Taking expectations of both sides of the inequality above produces

$$
\begin{aligned}
\mathrm{E}\left[Y(t \wedge T_n^X \wedge T_m^Y)\right] &\leq Y(0) + \int_0^t \frac{17}{8K}\mathrm{E}\left[X(s \wedge T_n^X \wedge T_m^Y)Y(s \wedge T_n^X \wedge T_m^Y)\right]\,ds \\
&\quad + \int_0^t \frac{17c_{22}}{8K}\mathrm{E}\left[Y^2(s \wedge T_n^X \wedge T_m^Y)\right]\,ds \\
&\quad - \int_0^t \frac{2c_{22}}{K^2}\mathrm{E}\left[X(s \wedge T_n^X \wedge T_m^Y)Y^2(s \wedge T_n^X \wedge T_m^Y)\right]\,ds \\
&\leq Y(0) + \int_0^t \frac{17n}{8K}\mathrm{E}\left[Y(s \wedge T_n^X \wedge T_m^Y)\right]\,ds \\
&\quad + \int_0^t \frac{17c_{22}}{8K}\mathrm{E}\left[Y^2(s \wedge T_n^X \wedge T_m^Y)\right]\,ds \\
&\quad - \int_0^t \frac{2nc_{22}}{K^2}\mathrm{E}\left[Y^2(s \wedge T_n^X \wedge T_m^Y)\right]\,ds
\end{aligned}
$$

Boundedness of $Y(t)$ (3 of 4)

$$\begin{aligned}
& \mathrm{E}\left[Y(t \wedge T_n^X \wedge T_m^Y)\right] \\
& \quad \leq \quad Y(0) + \int_0^t \frac{17n}{8K} \mathrm{E}\left[Y(s \wedge T_n^X \wedge T_m^Y)\right] \, ds \\
& \qquad\quad + \frac{c_{22}}{K}\left(\frac{17}{8} - \frac{2n}{K}\right) \int_0^t \mathrm{E}\left[Y^2(s \wedge T_n^X \wedge T_m^Y)\right] \, ds \\
& \quad \leq \quad Y(0) + \frac{17n}{8K} \int_0^t \mathrm{E}\left[Y(s \wedge T_n^X \wedge T_m^Y)\right] \, ds
\end{aligned}$$

for $n \geq 17K/16$.

Boundedness of $Y(t)$ (4 of 4)

Gronwall's inequality implies

$$\mathrm{E}\left[Y(t \wedge T_n^X \wedge T_m^Y)\right] \leq Y(0)e^{17nt/(8K)}$$

for all $t > 0$ when $n \geq 17K/16$.
Fatou's Lemma implies

$$\mathrm{E}\left[Y(t \wedge T_n^X \wedge T_\infty^Y)\right] \leq Y(0)e^{17nt/(8K)}.$$

Therefore $\mathrm{P}\left(T_\infty^Y \leq T_n^X \wedge t\right) = 0$ for all $t > 0$ when $n \geq 17K/16$.
Since $T_n^X \to \infty$ as $n \to \infty$ then

$$\lim_{n\to\infty} \left(T_n^X \wedge t\right) = t$$

for all $t > 0$ and thus $\mathrm{P}\left(T_m^Y \leq t\right) = 0$.

Boundedness of $(X(t), Y(t))$

Since $T_\infty = T_\infty^X \wedge T_\infty^Y$ then

$$\begin{aligned} \mathrm{P}\left(T_\infty \leq t\right) &= \mathrm{P}\left(T_\infty^X \wedge T_\infty^Y \leq t\right) \\ &\leq \mathrm{P}\left(T_\infty^X \leq t\right) + \mathrm{P}\left(T_\infty^Y \leq t\right) \\ &= 0. \end{aligned}$$

Quadratic Variation and Martingales

Define

$$M_r^{i,j}(t) = r\left[X^i Y^j\right](t) - A_r^{i,j}(t)$$

which is a local martingale.

The quadratic variation process of $N(t)$ is defined as

$$[N,N](t) = \lim_{\|P\|\to 0} \sum_{i=0}^{n-1} \left(N(t_{i+1}^n) - N(t_i^n)\right)^2$$

where $\left\{t_i^n\right\}_{i=0}^n$ is any partition of $[0,t]$.

The sharp bracket process is the compensator of $[N,N](t)$.

$$\left\langle M_r^{i,j}(t), M_r^{i,j}(t)\right\rangle = A_r^{i,j}(t)$$

Normalized Stochastic Random Variables

Define:

$$
\begin{aligned}
x^K(t) &= \frac{X(t)}{K} \\
y^K(t) &= \frac{Y(t)}{K} \\
m(t) &= \frac{1}{K}\left(M_1^{1,0}(t) - M_{\frac{c_{11}}{K}}^{2,0}(t) - M_{\frac{1}{K}}^{1,1}(t)\right) \\
\hat{m}(t) &= \frac{1}{K}\left(M_{\frac{17}{8K}}^{1,1}(t) - M_{\frac{17c_{22}}{8K}}^{0,2}(t) - M_{\frac{9}{8}}^{0,1}(t) - M_{\frac{1}{K^2}}^{2,1}(t)\right. \\
&\qquad \left. - M_{\frac{2c_{22}}{K^2}}^{1,2}(t) - M_{\frac{c_{22}^2}{K^2}}^{0,3}(t)\right)
\end{aligned}
$$

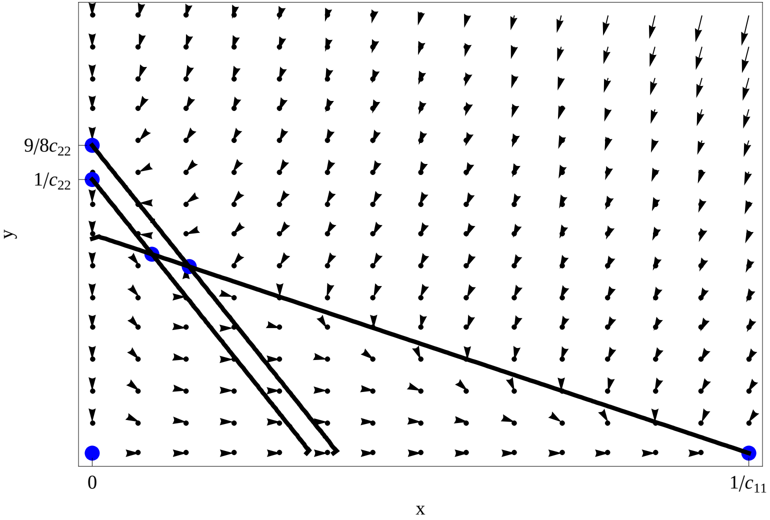
Stochastic Integral Equations

Dividing Eqs. (3) and (4) by K produces a pair of integral equations for the stochastic process $(x^K(t), y^K(t))$.

$$
\begin{aligned}
x^K(t) - x(0) &= \int_0^t f(x^K(s), y^K(s))\, ds + m(t) \\
y^K(t) - y(0) &= \int_0^t g(x^K(s), y^K(s))\, ds + \hat{m}(t)
\end{aligned}
$$

Limiting Case as $K \to \infty$

Question: does the behavior of $(x^K(t), y^K(t))$ resemble the behavior of $(x(t), y(t)$ as $K \to \infty$?



Difference of Solutions

Define:

$$\begin{aligned} T_n &= \inf\{t > 0 \,:\, X(t) \vee Y(t) \geq n\} \\ T_n^K &= \inf\{t > 0 \,:\, x^K(t) \vee y^K(t) \geq n\} \end{aligned}$$

Note: $T_n^K = T_{nK}$

Fix $T > 0$ and $n \in \mathbb{N}$ and consider the differences

$$f(x^K(t), y^K(t)) - f(x(t), y(t)) \quad \text{and} \quad g(x^K(t), y^K(t)) - g(x(t), y(t)),$$

for $0 \leq t \leq T_n^K \wedge T$.

Deviation of Solutions

There exists constant $L_n > 0$ depending on n and T such that

$$\begin{aligned}
&\left|f(x^K(t), y^K(t)) - f(x(t), y(t))\right| \\
&\quad\leq L_n \left(\left|x^K(t) - x(t)\right| + \left|y^K(t) - y(t)\right|\right) \\
&\left|g(x^K(t), y^K(t)) - g(x(t), y(t))\right| \\
&\quad\leq L_n \left(\left|x^K(t) - x(t)\right| + \left|y^K(t) - y(t)\right|\right),
\end{aligned}$$

for $0 \leq t \leq T_n^K \wedge T$, which implies

$$\begin{aligned}
&\left|x^K(t) - x(t)\right| + \left|y^K(t) - y(t)\right| \\
&\quad\leq 2L_n \int_0^t \left(\left|x^K(s) - x(s)\right| + \left|y^K(s) - y^K(s)\right|\right) ds \\
&\qquad + |m(t)| + |\hat{m}(t)|.
\end{aligned}$$

Supremum of the Deviation

$$\begin{aligned}
&\sup_{t \leq T \wedge T_n^K} \left(\left| x^K(t) - x(t) \right| + \left| y^K(t) - y(t) \right| \right) \\
&\leq \quad 2L_n \int_0^t \sup_{s \leq T \wedge T_n^K} \left(\left| x^K(s) - x(s) \right| + \left| y^K(s) - y^K(s) \right| \right) \, ds \\
&\quad + \sup_{t \leq T \wedge T_n^K} |m(t)| + \sup_{t \leq T \wedge T_n^K} |\hat{m}(t)|
\end{aligned}$$

Gronwall's inequality implies

$$\begin{aligned}
&\sup_{t \leq T \wedge T_n^K} \left(\left| x^K(t) - x(t) \right| + \left| y^K(t) - y(t) \right| \right) \\
&\leq \quad \left(\sup_{t \leq T \wedge T_n^K} |m(t)| + \sup_{t \leq T \wedge T_n^K} |\hat{m}(t)| \right) e^{2L_n T}. \qquad (5)
\end{aligned}$$

Bounding the Normalized Martingales (1 of 4)

Compute the sharp brackets:

$$
\begin{aligned}
&\langle m, m \rangle (t) \\
&= \left\langle \frac{1}{K}\left(M_1^{1,0} - M_{c_{11}/K}^{2,0} - M_{1/K}^{1,1}\right), \frac{1}{K}\left(M_1^{1,0} - M_{c_{11}/K}^{2,0} - M_{1/K}^{1,1}\right) \right\rangle (t) \\
&= \frac{1}{K}\int_0^t x^K(s)\left(1 + c_{11}x^K(s) + y^K(s)\right)\, ds \\
&\langle \hat{m}, \hat{m} \rangle (t) \\
&= \frac{1}{K}\int_0^t y^K(s)\left(1 + x^K(s) + c_{22}y^K(s)\right)\left(\frac{9}{8} + x^K(s) + c_{22}y^K(s)\right)\, ds
\end{aligned}
$$

The bilinearity of the sharp bracket and the independence of the jumps in the state-dependent Poisson random variables has been used.

Bounding the Normalized Martingales (2 of 4)

By definition of T_n^K,

$$\sup_{t \le T \wedge T_n^K} \left(x^K(t) \vee y^K(t) \right) \le n + 1$$

which implies

$$\begin{aligned}
& \mathrm{E}\left[\langle m, m \rangle (T \wedge T_n^K) \right] \\
= \;& \frac{1}{K} \mathrm{E}\left[\int_0^{T \wedge T_n^K} x^K(s) \left(1 + c_{11} x^K(s) + y^K(s) \right) \, ds \right] \\
\le \;& \frac{T}{K} (n+1) \left(1 + (c_{11} + 1)(n+1) \right) \\
& \mathrm{E}\left[\langle \hat{m}, \hat{m} \rangle (T \wedge T_n^K) \right] \\
\le \;& \frac{T}{K} (n+1) \left(1 + (c_{22} + 1)(n+1) \right) \left(\frac{9}{8} + (c_{22} + 1)(n+1) \right).
\end{aligned}$$

Bounding the Normalized Martingales (3 of 4)

Applying Doob's martingale inequality twice yields

$$\mathrm{E}\left[\left(\sup_{t\leq T\wedge T_n^K} m(t)\right)^2\right] \leq 4\mathrm{E}\left[\langle m, m\rangle \left(T \wedge T_n^K\right)\right] \quad \text{and}$$

$$\mathrm{E}\left[\left(\sup_{t\leq T\wedge T_n^K} \hat{m}(t)\right)^2\right] \leq 4\mathrm{E}\left[\langle \hat{m}, \hat{m}\rangle \left(T \wedge T_n^K\right)\right].$$

This implies

$$\begin{aligned}\lim_{K\to\infty} \mathrm{E}\left[\left(\sup_{t\leq T\wedge T_n^K} m(t)\right)^2\right] &= \lim_{K\to\infty} \frac{4T}{K}(n+1)\left(1+(c_{11}+1)(n+1)\right) \\ &= 0 \quad \text{and likewise} \\ \lim_{K\to\infty} \mathrm{E}\left[\left(\sup_{t\leq T\wedge T_n^K} \hat{m}(t)\right)^2\right] &= 0\end{aligned}$$

Bounding the Normalized Martingales (4 of 4)

The limits on the previous slide confirm

$$\lim_{K\to\infty}\left(\sup_{t\leq T\wedge T_n^K} m(t) + \sup_{t\leq T\wedge T_n^K} \hat{m}(t)\right) = 0. \tag{6}$$

Fluid Approximation

If $\epsilon > 0$ then by Eq. (6) and inequality (5) it follows that

$$\lim_{K\to\infty} \mathrm{P}\left(\sup_{t \leq T \wedge T_n^K} \left(\left| x^K(t) - x(t) \right| + \left| y^K(t) - y(t) \right| \right) > \epsilon \right) = 0.$$

If $T > 0$,

$$\lim_{n\to\infty} \mathrm{P}\left(T_n \leq T\right) = 0 \quad \Longrightarrow \quad \lim_{n\to\infty} \limsup_{K\to\infty} \mathrm{P}\left(T_n^K \leq T\right) = 0.$$

Hence with almost certainty, $T_n^K \wedge T = T$ and thus for all $\epsilon > 0$

$$\lim_{K\to\infty} \mathrm{P}\left(\sup_{t \leq T} \left(\left| x^K(t) - x(t) \right| + \left| y^K(t) - y(t) \right| \right) > \epsilon \right) = 0.$$

Summary

- The deterministic model is the limiting result of the stochastic model for large populations.
- Future work: explore the possibility of extinction of one or both of the species for small to moderately sized populations.