Limit theorems for chain-binomial population models

Phil Pollett

Department of Mathematics
The University of Queensland
http://www.maths.uq.edu.au/~pkp

AUSTRALIAN RESEARCH COUNCIL
Centre of Excellence for Mathematics and Statistics of Complex Systems
Fionnuala Buckley
Department of Mathematics
University of Queensland

Collaborators

Ross McVinish
Department of Mathematics
University of Queensland

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Metapopulations

Colonization
Metapopulations
Metapopulations

Local Extinction
Metapopulations
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Total Extinction
Metapopulations
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Colonization from the mainland
Metapopulations
A Stochastic Patch Occupancy Model (SPOM)
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Suppose that there are \( n \) patches.
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A Stochastic Patch Occupancy Model (SPOM)

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Colonization and extinction happen in distinct, successive phases.
For many species the propensity for colonization and local extinction is markedly different in different phases of their life cycle.
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The Vernal pool fairy shrimp (Branchinecta lynchi) and the California linderiella (Linderiella occidentalis), both listed under the Endangered Species Act (USA)

The Jasper Ridge population of Bay checkerspot butterfly (Euphydryas editha bayensis), now extinct
Colonization and extinction happen in distinct, successive phases.

\[ t - 1 \quad t \quad t + 1 \quad t + 2 \]

\[ \cdots \quad E \quad C \quad E \quad C \quad E \quad C \quad E \quad C \quad E \quad C \quad E \quad \cdots \]
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We will assume that the population is observed after successive extinction phases (CE Model).
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**Colonization**: unoccupied patches become occupied independently with probability \( c(n^{-1} \sum_{i=1}^{n} X_{i,t}^{(n)}) \), where \( c : [0, 1] \rightarrow [0, 1] \) is continuous, increasing and concave.
Examples of $c(x)$

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- $c(x) = c_0 + cx$, where $c_0 + c \in (0, 1]$ (mainland and island colonization).
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- $c(x) = 1 - \exp(-x\beta)$ \quad ($\beta > 0$).
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**Colonization:** unoccupied patches become occupied independently with probability \( c(n^{-1} \sum_{i=1}^{n} X_{i,t}^{(n)}) \), where \( c : [0, 1] \rightarrow [0, 1] \) is continuous, increasing and concave.

**Extinction:** occupied patch \( i \) remains occupied independently with probability \( S_i \) (random).
Thus, we have a Chain Bernoulli structure:

\[ X^{(n)}_{i,t+1} \overset{d}{=} Bin\left( X^{(n)}_{i,t} + Bin\left( 1 - X^{(n)}_{i,t}, c\left( \frac{1}{n} \sum_{j=1}^{n} X^{(n)}_{j,t} \right) \right), S_i \right) \]
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\[ n = 30, \; S_i \sim \text{Beta}(25.2, \; 19.8) \; (\mathbb{E}S_i = 0.56) \; \text{and} \; c(x) = 0.7x \]

\[
0 0 0 0 1 0 1 1 0 1 0 1 0 0 0 0 1 1 1 0 1 0 1 0 0 0 1 0 0 0
\]

\[
c(x) = c\left(\frac{11}{30}\right) = 0.7 \times 0.36 = 0.256
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\[
\begin{array}{cccccccccccccccccccccccccccc}
0 & 0 & 0 & 0 & 1 & 0 & 1 & 1 & 0 & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 1 & 1 & 0 & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0
\end{array}
\]

\[
\begin{array}{cccccccccccccccccccccccccccc}
C & 1 & 0 & 0 & 0 & 1 & 1 & 1 & 1 & 0 & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 0 & 0 & 0 & 1 & 0 & 1 & 0
\end{array}
\]

\[
\begin{array}{cccccccccccccccccccccccccccc}
E & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 1 & 0 & 1 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 & 1 & 1 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0
\end{array}
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\begin{array}{cccccccccccccccccccccccccccc}
C & 0 & 0 & 1 & 0 & 1 & 0 & 0 & 1 & 1 & 1 & 0 & 1 & 0 & 0 & 1 & 0 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0
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0 0 0 0 1 0 1 1 0 1 0 1 0 1 0 0 0 0 1 1 1 0 1 0 1 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0
C 1 0 0 0 1 1 1 1 0 1 0 1 0 0 0 0 0 1 1 1 1 1 1 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0
E 0 0 0 0 1 0 0 1 0 1 0 1 0 0 0 0 0 1 0 1 1 1 1 1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0
C 0 0 1 0 1 0 0 1 1 1 0 1 0 0 1 0 1 1 1 1 1 1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0
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.
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C 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
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```
SPOM - Homogeneous case

Compare this with the *homogeneous case*, where $S_i = s$ (non-random) is the same for each $i$, and we merely count the *number* $N_t^{(n)}$ of occupied patches at time $t$.

We have the following *Chain Binomial* structure:

$$N_{t+1}^{(n)} \overset{d}{=} Bin\left(N_t^{(n)} + Bin\left(n - N_t^{(n)}, c\left(\frac{1}{n}N_t^{(n)}\right)\right), s\right)$$
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A deterministic limit

**Theorem [BP]** If \( N_0^{(n)}/n \xrightarrow{p} x_0 \) (a constant), then

\[ N_t^{(n)}/n \xrightarrow{p} x_t, \quad \text{for all } t \geq 1, \]

with \((x_t)\) determined by \(x_{t+1} = f(x_t)\), where

\[ f(x) = s(x + (1 - x)c(x)). \]

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- **Stationarity**: \( c(0) > 0 \). There is a unique fixed point \( x^* \in [0, 1] \). It satisfies \( x^* \in (0, 1) \) and is stable.

- **Evanescence**: \( c(0) = 0 \) and \( 1 + c'(0) \leq 1/s \). Now \( 0 \) is the unique fixed point in \([0, 1]\). It is stable.

- **Quasi stationarity**: \( c(0) = 0 \) and \( 1 + c'(0) > 1/s \). There are two fixed points in \([0, 1]\): \( 0 \) (unstable) and \( x^* \in (0, 1) \) (stable).

[Notice that if \( c(0) = 0 \), we require \( c'(0) > 0 \) for quasi stationarity.]
CE Model simulation \( n = 100, \ s = 0.56, \ c(x) = cx \) with \( c = 0.7 \)
CE Model simulation \((n = 100, s = 0.8, c(x) = cx \text{ with } c = 0.7)\)
Theorem [BP] Further suppose that \( c(x) \) is twice continuously differentiable, and let

\[
Z_t^{(n)} = \sqrt{n}(N_t^{(n)}/n - x_t).
\]

If \( Z_0^{(n)} \xrightarrow{d} z_0 \), then \( Z_t^{(n)} \) converges weakly to the Gaussian Markov chain \( Z_t \) defined by

\[
Z_{t+1} = f'(x_t)Z_t + E_t \quad (Z_0 = z_0),
\]

with \((E_t)\) independent and \( E_t \sim \mathcal{N}(0, v(x_t))\), where

\[
v(x) = s[(1 - s)x + (1 - x)c(x)(1 - sc(x))].
\]
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Number of occupied patches

\[ N_{x^*} = 64.2857 \]
A deterministic limit

Returning to the general case, where patch survival probabilities are *random* and *patch dependent*, and we keep track of which patches are occupied . . .

\[ X_{i,t+1}^{(n)} \overset{d}{=} Bin\left(X_{i,t}^{(n)} + Bin\left(1 - X_{i,t}^{(n)}, c\left(\frac{1}{n}\sum_{j=1}^{n} X_{j,t}^{(n)}\right)\right), S_i\right) \]
A deterministic limit

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\]

First, . . .

*Notation:* If \( \sigma \) is a probability measure on \([0, 1)\) and let \( \bar{s}_k \) denote its \( k \)-th moment, that is,

\[
\bar{s}_k = \int_{0}^{1} x^k \sigma(dx).
\]
A deterministic limit

**Theorem** Suppose there is a probability measure $\sigma$ and deterministic sequence $\{d(0, k)\}$ such that

$$\frac{1}{n} \sum_{i=1}^{n} S_k^i \xrightarrow{p} \bar{s}_k \quad \text{and} \quad \frac{1}{n} \sum_{i=1}^{n} S_k^i X_{i,0}^{(n)} \xrightarrow{p} d(0, k)$$

for all $k = 0, 1, \ldots, T$. Then, there is a (deterministic) triangular array $\{d(t, k)\}$ such that, for all $t = 0, 1, \ldots, T$ and $k = 0, 1, \ldots, T - t$,

$$\frac{1}{n} \sum_{i=1}^{n} S_k^i X_{i,t}^{(n)} \xrightarrow{p} d(t, k),$$

where

$$d(t + 1, k) = d(t, k + 1) + c (d(t, 0)) (\bar{s}_{k+1} - d(t, k + 1)).$$
A deterministic limit $d(0,k)$
A deterministic limit $d(1,k)$
A deterministic limit $d(2, k)$
A deterministic limit $d(3,k)$
A deterministic limit $d(t,k)$
A deterministic limit $d(t,0)$
Remarks

- Typically, we are only interested in $d(t, 0)$, being the asymptotic proportion of occupied patches at time $t$:

$$\frac{1}{n} \sum_{i=1}^{n} X_{i,t}^{(n)} \xrightarrow{p} d(t, 0).$$
Remarks: \( d(t,0) \)
Remarks: $d(t,k)$
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Remarks

Typically, we are only interested in $d(t, 0)$, being the asymptotic proportion of occupied patches at time $t$:

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Typically, we are only interested in $d(t, 0)$, being the asymptotic proportion of occupied patches at time $t$:

$$\frac{1}{n} \sum_{i=1}^{n} X_{i,t}^{(n)} \xrightarrow{p} d(t, 0).$$

However, we may still interpret the ratio $d(t, k)/d(t, 0)$ ($k \geq 1$) as the $k$-th moment of the conditional distribution of the patch survival probability given that the patch is occupied. (From these moments, the conditional distribution could then be reconstructed.)
A deterministic limit

**Theorem** Suppose there is a probability measure \( \sigma \) and deterministic sequence \( \{d(0, k)\} \) such that

\[
\frac{1}{n} \sum_{i=1}^{n} S_{i}^{k} \overset{p}{\to} \bar{s}_{k} \quad \text{and} \quad \frac{1}{n} \sum_{i=1}^{n} S_{i}^{k} X_{i,0}^{(n)} \overset{p}{\to} d(0, k)
\]

for all \( k = 0, 1, \ldots, T \). Then, there is a (deterministic) triangular array \( \{d(t, k)\} \) such that, for all \( t = 0, 1, \ldots, T \) and \( k = 0, 1, \ldots, T - t \),

\[
\frac{1}{n} \sum_{i=1}^{n} S_{i}^{k} X_{i,t}^{(n)} \overset{p}{\to} d(t, k),
\]

where

\[
d(t + 1, k) = d(t, k + 1) + c(d(t, 0)) (\bar{s}_{k+1} - d(t, k + 1)) .
\]
Homogeneous case

When $\bar{s}_k = \bar{s}_1^k$ for all $k$, that is the patch survival probabilities are the same, then it is possible to simplify

$$d(t+1,k) = d(t, k+1) + c(d(t, 0)) (\bar{s}_{k+1} - d(t, k+1)) .$$

We can show by induction that $d(t, k) = \bar{s}_1^k x_t$, where

$$x_{t+1} = \bar{s}_1 (x_t + (1 - x_t) c(x_t)) .$$

Compare this with the earlier [BP] result....
**Theorem [BP]** If $N_0^{(n)}/n \xrightarrow{p} x_0$ (a constant), then

$$N_t^{(n)}/n \xrightarrow{p} x_t, \quad \text{for all } t \geq 1,$$

with $(x_t)$ determined by $x_{t+1} = f(x_t)$, where

$$f(x) = s(x + (1 - x)c(x)).$$

Theorem  Any fixed point $d = (d(0), d(1), \ldots)$ is given by

$$d(k) = \int_0^1 \frac{c(\psi)x^{k+1}}{1-x+c(\psi)x} \sigma(dx),$$

where $\psi (= d(0))$ solves

$$R(\psi) = \int_0^1 \frac{c(\psi)x}{1-x+c(\psi)x} \sigma(dx) = \psi. \tag{1}$$

If $c(0) > 0$, there is a unique $\psi > 0$. If $c(0) = 0$ and

$$c'(0) \int_0^1 \frac{x}{1-x} \sigma(dx) \leq 1,$$

then $\psi = 0$ is the unique solution to (1). Otherwise, (1) has two solutions, one of which is $\psi = 0$. 
Theorem  If $c(0) = 0$ and 

$$c'(0) \int_0^1 \frac{x}{1-x} \sigma(dx) \leq 1,$$

then $d(k) \equiv 0$ is a stable fixed point. Otherwise, the non-zero solution to 

$$R(\psi) = \int_0^1 \frac{c(\psi)x}{1-x+c(\psi)x} \sigma(dx) = \psi$$

provides the stable fixed point through 

$$d(k) = \int_0^1 \frac{c(\psi)x^{k+1}}{1-x+c(\psi)x} \sigma(dx).$$
CE Model simulation \( (n = 100, s = 0.56, c(x) = cx \text{ with } c = 0.7) \)
CE Model simulation \((n = 100, s_1 = 0.56, c(x) = cx \text{ with } c = 0.7)\)

\[
c'(0) \int_0^1 \frac{x}{1-x} \sigma(dx) = 0.9383
\]
CE Model simulation ($n = 100$, $s_1 = 0.56$, $c(x) = cx$ with $c = 0.7$)

$c'(0) \int_0^1 \frac{x}{1-x} \sigma(dx) = 1.2572$
CE Model simulation \((n = 100, s_1 = 0.56, c(x) = cx \text{ with } c = 0.7)\)


c'(0) \int_0^1 \frac{x}{1-x} \sigma(dx) = \infty

\beta(1.176, 0.924)
CE Model simulation \((n = 100, s_1 = 0.56, c(x) = cx \text{ with } c = 0.7)\)
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\[
c'(0) \int_0^1 \frac{x}{1-x} \sigma(dx) = \infty
\]
CE Model simulation \((n = 100, s_1 = 0.6, c(x) = cx \text{ with } c = 0.7)\)

\[ c'(0) \int_0^1 \frac{x}{1-x} \sigma(dx) = 2.1 \]