Infinite-patch metapopulation models: branching, convergence and chaos

Phil Pollett

Department of Mathematics
The University of Queensland
http://www.maths.uq.edu.au/~pkp
Fionnuala Buckley
MASCOS PhD Scholar
University of Queensland

Metapopulations
Metapopulations

Colonization

[Diagram showing multiple circles connected by arrows, representing a metapopulation with colonization.]
Metapopulations
Metapopulations

Local Extinction
Metapopulations
Metapopulations
Metapopulations
A Stochastic Patch Occupancy Model (SPOM)
A Stochastic Patch Occupancy Model (SPOM)

Suppose that there are $N$ patches.
A Stochastic Patch Occupancy Model (SPOM)

Suppose that there are $N$ patches.

Let $n_t \in \{0, 1, \ldots, N\}$ be the number occupied at time $t$. 
A Stochastic Patch Occupancy Model (SPOM)

Suppose that there are $N$ patches.

Let $n_t \in \{0, 1, \ldots, N\}$ be the number occupied at time $t$.

Assume $(n_t, t = 0, 1, \ldots)$ to be Markov chain.
A Stochastic Patch Occupancy Model (SPOM)

Suppose that there are \( N \) patches.

Let \( n_t \in \{0, 1, \ldots, N\} \) be the number occupied at time \( t \).

Assume \((n_t, t = 0, 1, \ldots)\) to be Markov chain.

Colonization and extinction happen in distinct, successive phases.
Colonization and extinction happen in distinct, successive phases.

$\cdots \ E \ C \ E \ C \ E \ C \ E \ C \ E \ C \ E \ \cdots$

$t - 1 \quad t \quad t + 1 \quad t + 2$
Colonization and extinction happen in distinct, successive phases.

We will assume that the population is observed after successive extinction phases (CE Model).
A Stochastic Patch Occupancy Model (SPOM)

Suppose that there are $N$ patches.

Let $n_t \in \{0, 1, \ldots, N\}$ be the number occupied at time $t$.

Assume $(n_t, t = 0, 1, \ldots)$ to be Markov chain.

Colonization and extinction happen in distinct, successive phases.

We will assume that the population is observed after successive extinction phases (CE Model).
Colonization and extinction happen in distinct, successive phases.

**Colonization**: unoccupied patches become occupied independently with probability \( c(\frac{n_t}{N}) \), where \( c : [0, 1] \to [0, 1] \) is continuous, increasing and concave, and \( c'(0) > 0 \).
Colonization and extinction happen in distinct, successive phases.

**Colonization**: unoccupied patches become occupied independently with probability \( c \left( \frac{n_t}{N} \right) \), where \( c : [0, 1] \to [0, 1] \) is continuous, increasing and concave, and \( c'(0) > 0 \).

**Extinction**: occupied patches remain occupied independently with probability \( s \).
We have the following *Chain Binomial* structure:

\[ n_{t+1} \overset{D}{=} \text{Bin} \left( n_t + \text{Bin} \left( N - n_t, c\left( \frac{n_t}{N} \right) \right), s \right) \]
We have the following *Chain Binomial* structure:

\[ n_{t+1} \overset{D}{=} \operatorname{Bin} \left( n_t + \operatorname{Bin} \left( N - n_t, c(n_t/N) \right), s \right) \]

**Notation:** $\operatorname{Bin}(m, p)$ is a binomial random variable with $m$ trials and success probability $p$. 
We have the following *Chain Binomial* structure:

\[ n_{t+1} \overset{D}{=} \text{Bin} \left( n_t + \text{Bin} \left( N - n_t, c \left( \frac{n_t}{N} \right) \right), s \right) \]
We have the following *Chain Binomial* structure:

\[ n_{t+1} \overset{D}{=} \text{Bin}(n_t + \text{Bin}(N - n_t, c(n_t/N)), s) \]
We have the following *Chain Binomial* structure:

\[ n_{t+1} \overset{D}{=} \text{Bin}\left(n_t + \text{Bin}\left(N - n_t, c(n_t/N)\right), s\right) \]
We have the following \textit{Chain Binomial} structure:

\[ n_{t+1} \overset{\text{d}}{=} \text{Bin} \left( n_t + \text{Bin} \left( N - n_t, c \left( \frac{n_t}{N} \right) \right), s \right) \]
We have the following *Chain Binomial* structure:

\[ n_{t+1} \overset{D}{=} \text{Bin}\left( n_t + \text{Bin}\left( N - n_t, c\left( n_t/N \right) \right), s \right) \]
We have the following \textit{Chain Binomial} structure:

\[
n_{t+1} \overset{D}{=} \text{Bin}\left(n_t + \text{Bin}\left(N - n_t, c\left(n_t/N\right)\right), s\right)
\]
We have the following *Chain Binomial* structure:

\[ n_{t+1} \overset{D}{=} \text{Bin} \left( n_t + \text{Bin} \left( N - n_t, c(n_t/N) \right), s \right) \]
CE Model simulation ($N = 100$, $n_0 = 95$, $s = 0.56$, $c(x) = cx$ with $c = 0.7$)
CE Model simulation \((N = 100, n_0 = 5, s = 0.8, c(x) = cx \text{ with } c = 0.7)\)
CE Model simulation ($N=100$, $n_0=95$, $s=0.56$, $c(x) = cx$ with $c=0.7$)
CE Model simulation \( (N = 100, n_0 = 5, s = 0.8, c(x) = cx \text{ with } c = 0.7) \)
CE Model simulation ($N = 100, n_0 = 95, s = 0.56, c(x) = cx$ with $c = 0.7$)
CE Model simulation \((N = 100, n_0 = 5, s = 0.8, c(x) = cx \text{ with } c = 0.7)\)
CE Model simulation ($N = 100$, $n_0 = 95$, $s = 0.56$, $c(x) = cx$ with $c = 0.7$)
CE Model \( c'(0) > (1 - s)/s \)

\[
CE \text{ Model simulation } (N = 100, \ n_0 = 5, \ s = 0.8, \ c(x) = cx \ \text{with } c = 0.7)
\]
Prelude  If \( c(0) = 0 \) and \( c \) has a continuous second derivative near 0, then, for fixed \( n \),

\[
\text{Bin}(N - n, c(n/N)) \xrightarrow{D} \text{Poi}(mn), \quad \text{as } N \to \infty,
\]

where \( m = c'(0) \).
We have the following structure:

\[ n_{t+1} \overset{D}{=} \text{Bin} \left( n_t + \text{Poi} \left( mn_t \right), s \right) \]
We have the following structure:

\[ n_{t+1} \overset{D}{=} \text{Bin}\left( n_t + \text{Bin}\left( N - n_t, c(n_t/N) \right), s \right) \]

\[ \text{Bin}(N - n, c(n/N)) \overset{D}{\rightarrow} \text{Poi}(mn) \quad \text{(as } N \rightarrow \infty) \]
We have the following structure:

\[ n_{t+1} \overset{D}{=} \text{Bin}(n_t + \text{Poi}(mn_t), s) \]
We have the following structure:

\[ n_{t+1} \overset{\text{D}}{=} \text{Bin}(n_t + \text{Poi}(mn_t), s) \]

**Claim** The process \((n_t, t = 0, 1, \ldots)\) is a branching process (Galton-Watson process) whose offspring distribution has pgf \(G(z) = (1 - s + sz)e^{-ms(1-z)}\).
We have the following structure:

\[ n_{t+1} \overset{\text{D}}{=} \text{Bin}(n_t + \text{Poi}(mn_t), s) \]

**Claim** The process \((n_t, t = 0, 1, \ldots)\) is a branching process (Galton-Watson process) whose offspring distribution has pgf \(G(z) = (1 - s + sz)e^{-ms(1-z)}\).

(We think of the census times as marking the ‘generations’, the ‘particles’ being the occupied patches, and the ‘offspring’ being the occupied patches that they notionally replace in the succeeding generation.)
We have the following structure:

\[ n_{t+1} \overset{\text{D}}{=} \text{Bin}(n_t + \text{Poi}(mn_t), s) \]

**Claim**  The process \((n_t, t = 0, 1, \ldots)\) is a *branching process* (Galton-Watson process) whose offspring distribution has pgf \(G(z) = (1 - s + sz)e^{-ms(1-z)}\).
We have the following structure:

\[ n_{t+1} \overset{D}{=} \text{Bin}(n_t + \text{Poi}(mn_t), s) \]

Claim  The process \((n_t, t = 0, 1, \ldots)\) is a branching process (Galton-Watson process) whose offspring distribution has pgf \(G(z) = (1 - s + sz)e^{-ms(1-z)}\).

The mean number of offspring is \(\mu = (1 + m)s\).
We have the following structure:

\[ n_{t+1} \overset{D}{=} \text{Bin}(n_t + \text{Poi}(mn_t), s) \]

**Claim** The process \((n_t, t = 0, 1, \ldots)\) is a *branching process* (Galton-Watson process) whose offspring distribution has pgf \(G(z) = (1 - s + sz)e^{-ms(1-z)}\).

The mean number of offspring is \(\mu = (1 + m)s\).

So, for example, \(E(n_t|n_0) = n_0\mu^t (t \geq 1)\).
We have the following structure:

\[ n_{t+1} \overset{D}{=} \text{Bin}(n_t + \text{Poi}(mn_t), s) \]

**Claim** The process \((n_t, t = 0, 1, \ldots)\) is a *branching process* (Galton-Watson process) whose offspring distribution has pgf \(G(z) = (1 - s + sz)e^{-ms(1-z)}\).
We have the following structure:

\[ n_{t+1} \overset{\text{D}}{=} \text{Bin}(n_t + \text{Poi}(mn_t), s) \]

**Claim** The process \((n_t, t = 0, 1, \ldots)\) is a branching process (Galton-Watson process) whose offspring distribution has pgf \(G(z) = (1 - s + sz)e^{-ms(1-z)}\).

**Theorem** Extinction occurs with probability 1 if and only if \(m \leq (1 - s)/s\); otherwise total extinction occurs with probability \(\eta^{n_0}\), where \(\eta\) is the unique fixed point of \(G\) on the interval \((0, 1)\).
CE Model simulation \(N = 100, n_0 = 95, s = 0.56, c(x) = cx \text{ with } c = 0.7\)
CE Model $c'(0) > (1 - s)/s$ ($\eta^{n_0} = 0.0020837$)

CE Model simulation ($N = 100$, $n_0 = 5$, $s = 0.8$, $c(x) = cx$ with $c = 0.7$)
Assume the following structure:

\[ n_{t+1} \overset{D}{=} \text{Bin}(n_t + \text{Poi}(m(n_t)), s) \]

where \( m(n) \geq 0 \).
Assume the following structure:

\[ n_{t+1} \overset{D}{=} \text{Bin}(n_t + \text{Poi}(m(n_t)), s) \]

where \( m(n) \geq 0 \). A moment ago we had \( m(n) = mn \).
Assume the following structure:

\[ n_{t+1} \overset{D}{=} \text{Bin}(n_t + \text{Poi}(m(n_t)), s) \]

where \( m(n) \geq 0 \).
Infinite-patch SPOM with regulation

\[ n_{t+1} \overset{D}{=} \text{Bin}(n_t + \text{Poi}(m(n_t)), s) \]
\[ n_{t+1} \overset{D}{=} \text{Bin}(n_t + \text{Poi}(m(n_t)), s) \]

We will consider what happens when the initial number of occupied patches \( n_0 \) becomes large.
\[ n_{t+1} \overset{D}{=} \text{Bin}(n_t + \text{Poi}(m(n_t)), s) \]

We will consider what happens when the initial number of occupied patches \( n_0 \) becomes large.

For some index \( N \) write \( m(n) = N \mu(n/N) \), and assume \( \mu \) is continuous with bounded first derivative.
$n_{t+1} \overset{D}{=} \text{Bin}(n_t + \text{Poi}(m(n_t)), s)$

We will consider what happens when the initial number of occupied patches $n_0$ becomes large.

For some index $N$ write $m(n) = N\mu(n/N)$, and assume $\mu$ is continuous with bounded first derivative.

We may take $N$ to be simply $n_0$ or, more generally, following Klebaner*, we may interpret $N$ as being a ‘threshold’ with the property that $n_0/N \to x_0$ as $N \to \infty$.

By choosing $\mu$ appropriately, we may allow for a degree of regulation in the colonisation process.
By choosing \( \mu \) appropriately, we may allow for a degree of regulation in the colonisation process. For example, \( \mu(x) \) might be of the form

- \( \mu(x) = rx(a - x) \ (0 \leq x \leq a) \) (logistic growth);
- \( \mu(x) = xe^{r(1-x)} \ (x \geq 0) \) (Ricker dynamics);
- \( \mu(x) = \lambda x/(1 + ax)^b \ (x \geq 0) \) (Hassell dynamics).

By choosing $\mu$ appropriately, we may allow for a degree of regulation in the colonisation process. For example, $\mu(x)$ might be of the form

- $\mu(x) = rx(a - x) \ (0 \leq x \leq a)$ (logistic growth);
- $\mu(x) = x e^{r(1-x)} \ (x \geq 0)$ (Ricker dynamics);
- $\mu(x) = \lambda x / (1 + ax)^b \ (x \geq 0)$ (Hassell dynamics);
- $\mu(x) = mx \ (x \geq 0)$ (branching).
Infinite-patch SPOM with regulation

By choosing $\mu$ appropriately, we may allow for a degree of regulation in the colonisation process. For example, $\mu(x)$ might be of the form

- $\mu(x) = rx(a - x) \ (0 \leq x \leq a)$ (logistic growth);
- $\mu(x) = xe^{r(1-x)} \ (x \geq 0)$ (Ricker dynamics);
- $\mu(x) = \lambda x/(1 + ax)^b \ (x \geq 0)$ (Hassell dynamics);
- $\mu(x) = mx \ (x \geq 0)$ (branching).

We can establish a law of large numbers for $X_t^{(N)} = n_t/N$, the number of occupied patches at census $t$ measured relative to the threshold.
**Theorem** For the infinite-patch CE model with parameters $s$ and $\mu(x)$, let $X_t^{(N)} = n_t/N$ be the number of occupied patches at census $t$ relative to the threshold $N$.

Suppose that $\mu$ is continuous with bounded first derivative.

If $X_0^{(N)} \xrightarrow{2} x_0$ as $N \to \infty$, then $X_t^{(N)} \xrightarrow{2} x_t$ for all $t \geq 1$, where $(x_t)$ is determined by $x_{t+1} = f(x_t)$ ($t \geq 0$), where $f(x) = s(x + \mu(x))$. 
Bifurcation diagram for the infinite-patch deterministic CE model with Ricker growth dynamics: \( x_{n+1} = 0.3 \cdot x_n \cdot (1 + e^{r(1-x_n)}) \) (\( r \) ranges from 0 to 7.2).
Simulation (open circles) of the infinite-patch CE model with Ricker growth dynamics, together with the corresponding limiting deterministic trajectories (solid circles). Here $s = 0.3$, $N = 200$ and (a) $r = 0.84$, (b) $r = 1$ (c) $r = 4$, (d) $r = 5$. 