# Infinite-patch metapopulation models: branching, convergence and chaos 

Phil Pollett

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



AUSTRALIAN RESEARCH COUNCIL Centre of Excellence for Mathematics and Statistics of Complex Systems

## Collaborator

## Fionnuala Buckley MASCOS PhD Scholar University of Queensland



[^0]\[

$$
\begin{gathered}
0^{\circ} \oplus \\
0 \\
0
\end{gathered}
$$
\]

## Metapopulations



$$
\begin{gathered}
0^{\circ} \\
0 \\
(\&)
\end{gathered}
$$

## Metapopulations



## Metapopulations



$$
\therefore 0_{0}
$$

## SPOM

A Stochastic Patch Occupancy Model (SPOM)

## SPOM

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

## SPOM

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 $t$.

## SPOM

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 $\left(n_{t}, t=0,1, \ldots\right)$ to be Markov chain.

## SPOM

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 $\left(n_{t}, t=0,1, \ldots\right)$ to be Markov chain.
Colonization and extinction happen in distinct, successive phases.

## SPOM - Phase structure

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



## SPOM - Phase structure

Colonization and extinction happen in distinct, successive phases.


We will we assume that the population is observed after successive extinction phases (CE Model).

## SPOM

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 $\left(n_{t}, t=0,1, \ldots\right)$ 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).

## SPOM

Colonization and extinction happen in distinct, successive phases.

Colonization: unoccupied patches become occupied independently with probability $c\left(n_{t} / N\right)$, where $c:[0,1] \rightarrow[0,1]$ is continuous, increasing and concave, and $c^{\prime}(0)>0$.

## SPOM

Colonization and extinction happen in distinct, successive phases.

Colonization: unoccupied patches become occupied independently with probability $c\left(n_{t} / N\right)$, where $c:[0,1] \rightarrow[0,1]$ is continuous, increasing and concave, and $c^{\prime}(0)>0$.

Extinction: occupied patches remain occupied independently with probability $s$.

## $N$-patch SPOM

We have the following Chain Binomial structure:

$$
n_{t+1} \stackrel{\mathrm{D}}{=} \operatorname{Bin}\left(n_{t}+\operatorname{Bin}\left(N-n_{t}, c\left(n_{t} / N\right)\right), s\right)
$$

## $N$-patch SPOM

We have the following Chain Binomial structure:

$$
n_{t+1} \stackrel{\mathrm{D}}{=} \operatorname{Bin}\left(n_{t}+\operatorname{Bin}\left(N-n_{t}, c\left(n_{t} / N\right)\right), s\right)
$$

Notation: $\operatorname{Bin}(m, p)$ is a binomial random variable with $m$ trials and success probability $p$.

## $N$-patch SPOM

We have the following Chain Binomial structure:

$$
n_{t+1} \stackrel{\mathrm{D}}{=} \operatorname{Bin}\left(n_{t}+\operatorname{Bin}\left(N-n_{t}, c\left(n_{t} / N\right)\right), s\right)
$$

## $N$-patch SPOM

We have the following Chain Binomial structure:


## $N$-patch SPOM

We have the following Chain Binomial structure:


## $N$-patch SPOM

We have the following Chain Binomial structure:

$$
n_{t+1} \stackrel{D}{=} \operatorname{Bin}\left(n_{t}+\operatorname{Bin}\left(N-n_{t}, c\left(n_{t} / N\right)\right), s\right)
$$

## $N$-patch SPOM

We have the following Chain Binomial structure:

$$
n_{t+1} \stackrel{D}{=} \operatorname{Bin}\left(n_{t}+\operatorname{Bin}\left(N-n_{t}, c\left(n_{t} / N\right)\right), s\right)
$$

## $N$-patch SPOM

We have the following Chain Binomial structure:

$$
n_{t+1} \xlongequal{D} \operatorname{Bin}\left(n_{t}+\operatorname{Bin}\left(N-n_{t}, c\left(n_{t} / N\right)\right), s\right)
$$

## $N$-patch SPOM

We have the following Chain Binomial structure:

$$
n_{t+1} \stackrel{\mathrm{D}}{=} \operatorname{Bin}\left(n_{t}+\operatorname{Bin}\left(N-n_{t}, c\left(n_{t} / N\right)\right), s\right)
$$

## CE Model



## CE Model



## CE Model - Evanescence



## CE Model - Quasi stationarity



## CE Model - Evanescence



## CE Model - Quasi stationarity



## CE Model $c^{\prime}(0)<(1-s) / s$



## CE Model $c^{\prime}(0)>(1-s) / s$



$$
\begin{gathered}
0^{\circ} \\
0 \\
(\&)
\end{gathered}
$$

Metapopulations

$$
\begin{aligned}
& \bigcirc \bigcirc \bigcirc \bigcirc \bigcirc \bigcirc \bigcirc \bigcirc \bigcirc \bigcirc \bigcirc \bigcirc \bigcirc \\
& \bigcirc \bigcirc \bigcirc \bigcirc \bigcirc \bigcirc \bigcirc \\
& \bigcirc \text { (b) } \bigcirc \bigcirc \bigcirc \bigcirc \bigcirc \bigcirc \bigcirc \\
& \text { (d) } \bigcirc \bigcirc \bigcirc \bigcirc \bigcirc \bigcirc \bigcirc
\end{aligned}
$$

## Infinite-patch SPOM

Prelude If $c(0)=0$ and $c$ has a continuous second derivative near 0 , then, for fixed $n$,

$$
\operatorname{Bin}(N-n, c(n / N)) \xrightarrow{\mathrm{D}} \mathrm{Poi}(m n), \quad \text { as } N \rightarrow \infty,
$$

where $m=c^{\prime}(0)$.

## Infinite-patch SPOM

We have the following structure:

$$
n_{t+1} \stackrel{\mathrm{D}}{=} \operatorname{Bin}\left(n_{t}+\operatorname{Poi}\left(m n_{t}\right), s\right)
$$

## $N$-patch SPOM

We have the following structure:

$$
n_{t+1} \stackrel{\mathrm{D}}{=} \operatorname{Bin}\left(n_{t}+\operatorname{Bin}\left(N-n_{t}, c\left(n_{t} / N\right)\right), s\right)
$$

$\operatorname{Bin}(N-n, c(n / N)) \xrightarrow{\mathrm{D}} \operatorname{Poi}(m n) \quad($ as $N \rightarrow \infty)$

## Infinite-patch SPOM

We have the following structure:

$$
n_{t+1} \stackrel{\mathrm{D}}{=} \operatorname{Bin}\left(n_{t}+\operatorname{Poi}\left(m n_{t}\right), s\right)
$$

## Infinite-patch SPOM

We have the following structure:

$$
n_{t+1} \stackrel{\mathrm{D}}{=} \operatorname{Bin}\left(n_{t}+\operatorname{Poi}\left(m n_{t}\right), s\right)
$$

Claim The process $\left(n_{t}, t=0,1, \ldots\right)$ is a branching process (Galton-Watson process) whose offspring distribution has pgf $G(z)=(1-s+s z) \mathrm{e}^{-m s(1-z)}$.

## Infinite-patch SPOM

We have the following structure:

$$
n_{t+1} \stackrel{\mathrm{D}}{=} \operatorname{Bin}\left(n_{t}+\operatorname{Poi}\left(m n_{t}\right), s\right)
$$

Claim The process $\left(n_{t}, t=0,1, \ldots\right)$ is a branching process (Galton-Watson process) whose offspring distribution has pgf $G(z)=(1-s+s z) \mathrm{e}^{-m s(1-z)}$.
(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.)

## Infinite-patch SPOM

We have the following structure:

$$
n_{t+1} \stackrel{\mathrm{D}}{=} \operatorname{Bin}\left(n_{t}+\operatorname{Poi}\left(m n_{t}\right), s\right)
$$

Claim The process $\left(n_{t}, t=0,1, \ldots\right)$ is a branching process (Galton-Watson process) whose offspring distribution has pgf $G(z)=(1-s+s z) \mathrm{e}^{-m s(1-z)}$.

## Infinite-patch SPOM

We have the following structure:

$$
n_{t+1} \stackrel{D}{=} \operatorname{Bin}\left(n_{t}+\operatorname{Poi}\left(m n_{t}\right), s\right)
$$

Claim The process $\left(n_{t}, t=0,1, \ldots\right)$ is a branching process (Galton-Watson process) whose offspring distribution has pgf $G(z)=(1-s+s z) \mathrm{e}^{-m s(1-z)}$.

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

## Infinite-patch SPOM

We have the following structure:

$$
n_{t+1} \stackrel{\mathrm{D}}{=} \operatorname{Bin}\left(n_{t}+\operatorname{Poi}\left(m n_{t}\right), s\right)
$$

Claim The process $\left(n_{t}, t=0,1, \ldots\right)$ is a branching process (Galton-Watson process) whose offspring distribution has pgf $G(z)=(1-s+s z) \mathrm{e}^{-m s(1-z)}$.

The mean number of offspring is $\mu=(1+m) s$.
So, for example, $\mathrm{E}\left(n_{t} \mid n_{0}\right)=n_{0} \mu^{t}(t \geq 1)$.

## Infinite-patch SPOM

We have the following structure:

$$
n_{t+1} \stackrel{\mathrm{D}}{=} \operatorname{Bin}\left(n_{t}+\operatorname{Poi}\left(m n_{t}\right), s\right)
$$

Claim The process $\left(n_{t}, t=0,1, \ldots\right)$ is a branching process (Galton-Watson process) whose offspring distribution has pgf $G(z)=(1-s+s z) \mathrm{e}^{-m s(1-z)}$.

## Infinite-patch SPOM

We have the following structure:

$$
n_{t+1} \stackrel{\mathrm{D}}{=} \operatorname{Bin}\left(n_{t}+\operatorname{Poi}\left(m n_{t}\right), s\right)
$$

Claim The process $\left(n_{t}, t=0,1, \ldots\right)$ is a branching process (Galton-Watson process) whose offspring distribution has pgf $G(z)=(1-s+s z) \mathrm{e}^{-m s(1-z)}$.

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 $c^{\prime}(0)<(1-s) / s \quad(\eta=1)$



## CE Model $c^{\prime}(0)>(1-s) / s \quad\left(\eta^{n_{0}}=0.0020837\right)$



## Infinite-patch SPOM with regulation

Assume the following structure:

$$
n_{t+1} \stackrel{\mathrm{D}}{=} \operatorname{Bin}\left(n_{t}+\operatorname{Poi}\left(m\left(n_{t}\right)\right), s\right)
$$

where $m(n) \geq 0$.

## Infinite-patch SPOM with regulation

Assume the following structure:

$$
n_{t+1} \stackrel{\mathrm{D}}{=} \operatorname{Bin}\left(n_{t}+\operatorname{Poi}\left(m\left(n_{t}\right)\right), s\right)
$$

where $m(n) \geq 0$. A moment ago we had $m(n)=m n$.

## Infinite-patch SPOM with regulation

Assume the following structure:

$$
n_{t+1} \stackrel{\mathrm{D}}{=} \operatorname{Bin}\left(n_{t}+\operatorname{Poi}\left(m\left(n_{t}\right)\right), s\right)
$$

where $m(n) \geq 0$.

## Infinite-patch SPOM with regulation

$$
n_{t+1} \stackrel{\mathrm{D}}{=} \operatorname{Bin}\left(n_{t}+\operatorname{Poi}\left(m\left(n_{t}\right)\right), s\right)
$$

## Infinite-patch SPOM with regulation

$$
n_{t+1} \stackrel{\mathrm{D}}{=} \operatorname{Bin}\left(n_{t}+\operatorname{Poi}\left(m\left(n_{t}\right)\right), s\right)
$$

We will consider what happens when the initial number of occupied patches $n_{0}$ becomes large.

## Infinite-patch SPOM with regulation

$$
n_{t+1} \stackrel{\mathrm{D}}{=} \operatorname{Bin}\left(n_{t}+\operatorname{Poi}\left(m\left(n_{t}\right)\right), s\right)
$$

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.

## Infinite-patch SPOM with regulation

$$
n_{t+1} \stackrel{\mathrm{D}}{=} \operatorname{Bin}\left(n_{t}+\operatorname{Poi}\left(m\left(n_{t}\right)\right), s\right)
$$

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 $n_{0} / N \rightarrow x_{0}$ as $N \rightarrow \infty$.
*Klebaner (1993) Population-dependent branching processes with a threshold. Stochastic Process. Appl. 46, 115-127.

## Infinite-patch SPOM with regulation

By choosing $\mu$ appropriately, we may allow for a degree of regulation in the colonisation process.

## 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

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


## 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

- $\mu(x)=r x(a-x)(0 \leq x \leq a)$ (logistic growth);
- $\mu(x)=x \mathrm{e}^{r(1-x)}(x \geq 0)$ (Ricker dynamics);
- $\mu(x)=\lambda x /(1+a x)^{b}(x \geq 0)$ (Hassell dynamics);
- $\mu(x)=m x(x \geq 0)$ (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

- $\mu(x)=r x(a-x)(0 \leq x \leq a)$ (logistic growth);
- $\mu(x)=x \mathrm{e}^{r(1-x)}(x \geq 0)$ (Ricker dynamics);
- $\mu(x)=\lambda x /(1+a x)^{b}(x \geq 0)$ (Hassell dynamics);
- $\mu(x)=m x(x \geq 0)$ (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.

## Infinite-patch SPOM - Convergence

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 $N \rightarrow \infty$, then $X_{t}^{(N)} \xrightarrow{2} x_{t}$ for all $t \geq 1$, where $\left(x_{t}\right)$ is determined by $x_{t+1}=f\left(x_{t}\right)(t \geq 0)$, where $f(x)=s(x+\mu(x))$.

## Infinite-patch SPOM - Ricker dynamics



Bifurcation diagram for the infinite-patch deterministic CE model with Ricker growth dynamics: $x_{n+1}=0.3 x_{n}\left(1+\mathrm{e}^{r\left(1-x_{n}\right)}\right)(r$ ranges from 0 to 7.2$)$.

## Infinite-patch SPOM - Ricker dynamics

(a)

(c)

(b)

(d)


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) $r=5$.


[^0]:    *Buckley, F.M. and Pollett, P.K. (2010) Limit theorems for discrete-time metapopulation models. Probability Surveys 7, 53-83.

