# Metapopulations with dynamic extinction probabilities 

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australian research council centre of excellence for MATHEMATICAL AND STATISTICAL FRONTIERS

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## Metapopulations



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## SPOM - Phase structure

## For many species the propensity for colonization and local extinction is markedly different in different phases of their life cycle. Examples:

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


## 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 - Phase structure

Colonization: unoccupied patch $i$ becomes occupied with probability

$$
c\left(\frac{1}{n} \sum_{j=1}^{n} X_{j, t}^{(n)} d\left(z_{i}, z_{j}\right) a_{j}\right),
$$

where $d(z, \tilde{z}) \geq 0$ measures the ease of movement between patches located at $z$ and $\tilde{z}, a_{j}$ is a weight related to the size of the patch $j$ and $c:[0, \infty) \rightarrow[0,1]$ (called the colonisation function) is increasing and Lipschitz continuous, with $c(0)=0$ and $c^{\prime}(0)>0$.

## SPOM - Phase structure

For simplicity, take $d \equiv 1$ and $a \equiv 1$. So, $\ldots$
Colonization: unoccupied patch $i$ becomes occupied with probability $c\left(n^{-1} \sum_{j=1}^{n} X_{j, t}^{(n)}\right)$, where $c:[0,1] \rightarrow[0,1]$ (called the colonisation function) is increasing and Lipschitz continuous, with $c(0)=0$ and $c^{\prime}(0)>0$.

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Proportion of patches occupied

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Extinction: occupied patch $i$ remains occupied from time $t$ to time $t+1$ with probability $s_{i, t}$.

Then, given the current state $X_{t}^{(n)}$ and survival probailities $s_{t}$, the $X_{i, t+1}^{(n)}(i=1, \ldots, n)$ are independent with transitions
$\operatorname{Pr}\left(X_{i, t+1}^{(n)}=1 \mid X_{t}^{(n)}, s_{t}\right)=s_{i, t} X_{i, t}^{(n)}+s_{i, t} c\left(n^{-1} \sum_{j=1}^{n} X_{j, t}^{(n)}\right)\left(1-X_{i, t}^{(n)}\right)$.

## SPOM - Landscape dynamics

Suppose that $\left(s_{i, t}\right)_{t=0}^{\infty}(i=1, \ldots, n)$ are independent Markov chains taking values in $[0,1]$ with common transition kernel $P(s, d r)$, assumed to satisfy the weak Feller property: for every continuous function $h$ on $[0,1]$, the function defined by

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P h(s):=\int h(r) P(s, d r), \quad s \in[0,1],
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This Markov chain model for the survival probabilities can incorporate the suitable/unsuitable approach to landscape dynamics.

## SPOM - Homogeneous case

In the homogeneous case, where $s_{i}=s$ is the same for each $i$, the number $N_{t}^{(n)}$ of occupied patches at time $t$ is Markovian. It has the following Chain Binomial structure:

$$
N_{t+1}^{(n)} \stackrel{d}{=} \operatorname{Bin}\left(N_{t}^{(n)}+\operatorname{Bin}\left(n-N_{t}^{(n)}, c\left(\frac{1}{n} N_{t}^{(n)}\right)\right), s\right) .
$$

## A deterministic limit

Letting the initial number $N_{0}^{(n)}$ of occupied patches grow at the same rate as $n \ldots$

Theorem If $N_{0}^{(n)} / n \xrightarrow{p} x_{0}$ (a constant), then

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N_{t}^{(n)} / n \xrightarrow{p} x_{t}, \quad \text { for all } t \geq 1,
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with $\left(x_{t}\right)$ determined by $x_{t+1}=f\left(x_{t}\right)$, where

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f(x)=s(x+(1-x) c(x)) .
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## CE Model - Evanescence



## CE Model - Quasi stationarity



## Stability

$x_{t+1}=f\left(x_{t}\right)$, where $f(x)=s(x+(1-x) c(x))$.
Evanescence: $1+c^{\prime}(0) \leq 1 / s$. 0 is the unique fixed point in $[0,1]$. It is stable.
Quasi stationarity: $1+c^{\prime}(0)>1 / s$. There are two fixed points in $[0,1]: 0$ (unstable) and $x^{*} \in(0,1)$ (stable).

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## CE Model - Evanescence



## CE Model - Quasi stationarity



## SPOM - General case

Return now to the general case, where patch survival probabilities evolve in time, and we keep track of which patches are occupied...
$\operatorname{Pr}\left(X_{i, t+1}^{(n)}=1 \mid X_{t}^{(n)}, s_{t}\right)=s_{i, t} X_{i, t}^{(n)}+s_{i, t} c\left(n^{-1} \sum_{j=1}^{n} X_{j, t}^{(n)}\right)\left(1-X_{i, t}^{(n)}\right)$.

## Our approach - Point processes

Treat the collection of patch survival probabilities and those of occupied patches at time $t$ as point processes on $[0,1]$.

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Define sequences ( $\sigma_{n, t}$ ) and ( $\mu_{n, t}$ ) of random measures by

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\begin{gathered}
\sigma_{n, t}(B)=\#\left\{s_{i, t} \in B\right\} / n, \quad B \in \mathcal{B}([0,1]), \\
\mu_{n, t}(B)=\#\left\{s_{i, t} \in B: X_{i, t}^{(n)}=1\right\} / n, \quad B \in \mathcal{B}([0,1]) .
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Think of $\sigma_{0}$ as being the initial distribution of survival probabilities.

## Our approach - Point processes

Equivalently, we may define ( $\sigma_{n, t}$ ) and ( $\mu_{n, t}$ ) by

$$
\begin{gathered}
\int h(s) \sigma_{n, t}(d s)=\frac{1}{n} \sum_{i=1}^{n} h\left(s_{i, t}\right) \\
\int h(s) \mu_{n, t}(d s)=\frac{1}{n} \sum_{i=1}^{n} X_{i, t}^{(n)} h\left(s_{i, t}\right),
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for $h$ in $C^{+}([0,1])$, the class of continuous functions that map $[0,1]$ to $[0, \infty)$.

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for $h$ in $C^{+}([0,1])$, the class of continuous functions that map $[0,1]$ to $[0, \infty)$. For example $(h \equiv 1)$,

$$
\left.\int \mu_{n, t}(d s)=\frac{1}{n} \sum_{i=1}^{n} X_{i, t}^{(n)} \quad \text { (proportion occupied }\right) .
$$

## Our approach - Point processes

Suppose that $\sigma_{n, 0} \xrightarrow{d} \sigma_{0}$ for some non-random (probability) measure $\sigma_{0}$. Although this assumption concerns only the initial variation in the survival probabilities, it implies a similar 'law of large numbers' for them at all subsequent times.

Lemma $\quad \sigma_{n, t} \xrightarrow{d} \sigma_{t}$, where $\sigma_{t}$ is defined by the recursion

$$
\int h(s) \sigma_{t+1}(d s)=\int h(s) \int P(r, d s) \sigma_{t}(d r),
$$

for all $h \in C^{+}([0,1])$.

## A measure-valued difference equation

Theorem Suppose that $\mu_{n, 0} \xrightarrow{d} \mu_{0}$ for some non-random measure $\mu_{0}$. Then, $\mu_{n, t} \xrightarrow{d} \mu_{t}$ for all $t=1,2, \ldots$, where $\mu_{t}$ is defined by the following recursion: for $h \in C^{+}([0,1])$,

$$
\begin{array}{r}
\int h(s) \mu_{t+1}(d s)=c_{t} \int s \int h(r) P(s, d r) \sigma_{t}(d s) \\
\left(1-c_{t}\right) \int s \int h(r) P(s, d r) \mu_{t}(d s)
\end{array}
$$

where $c_{t}=c\left(\mu_{t}([0,1])\right)=c\left(\int \mu_{t}(d s)\right)$.

## Stationary survival probabilities

Suppose $\lim _{t \rightarrow \infty} \sigma_{t}=\sigma$, for some (necessarily invariant) measure $\sigma$. It is easy to show that $\mu_{t}$ is absolutely continuous with respect to $\sigma$, and so one might hope to obtain a recursion for the Radon-Nikodym derivative of $\mu_{t}$ with respect to $\sigma$.

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\frac{\partial \mu_{t+1}}{\partial \sigma}(s)=\int r \frac{\partial \mu_{t}}{\partial \sigma}(r) P(s, d r)+c_{t} \int r\left(1-\frac{\partial \mu_{t}}{\partial \sigma}(r)\right) P(s, d r)
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## For aficionados

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## Survival probability simulation



## CE Model - Evanescence



## CE Model - Persistence



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## CE Model - Evanescence



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## CE Model - Persistence



