Metapopulations with dynamic extinction probabilities

Phil Pollett

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

Ross McVinish
Department of Mathematics
University of Queensland

Yui Sze (Jessica) Chan
Department of Mathematics
University of Queensland
Metapopulations
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Colonization
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Local Extinction
Metapopulations
A stochastic patch occupancy model (SPOM)
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Suppose that there are \( n \) patches.

Let \( X^{(n)}_t = (X^{(n)}_{1,t}, \ldots, X^{(n)}_{n,t}) \), where \( X^{(n)}_{i,t} \) is a binary variable indicating whether or not patch \( i \) is occupied at time \( t \).
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. 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
Colonization and extinction happen in distinct, successive phases.

We will assume that the population is observed after successive extinction phases (CE Model).
Colonization: unoccupied patch $i$ becomes occupied with probability

$$c \left( \frac{1}{n} \sum_{j=1}^{n} X_{j,t}^{(n)} d(\tilde{z}, z_j) a_j \right),$$

where $d(\tilde{z}, \tilde{z}) \geq 0$ measures the ease of movement between patches located at $\tilde{z}$ 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 $c'(0) > 0$. 
For simplicity, take $d \equiv 1$ and $a \equiv 1$. So, …

*Colonization*: unoccupied patch $i$ becomes occupied with probability $c(n^{-1} \sum_{j=1}^{n} X_{j,t}^{(n)})$, where $c : [0, 1] \rightarrow [0, 1]$ (called the *colonisation function*) is increasing and Lipschitz continuous, with $c(0) = 0$ and $c'(0) > 0$. 
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Extinction: occupied patch \( i \) remains occupied with probability \( s_{i,t} \).
**SPOM - Phase structure**

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**Extinction**: occupied patch $i$ remains occupied with probability $s_{i,t}$.

Then, given the current state $X_t^{(n)}$ and survival probabilities $s_t$, the $X_{i,t+1}^{(n)}$ ($i = 1, \ldots, n$) are independent with transitions

$$\Pr(X_{i,t+1}^{(n)} = 1 \mid X_t^{(n)}, s_t) = s_{i,t} X_{i,t}^{(n)} + s_{i,t} c\left(n^{-1} \sum_{j=1}^{n} X_{j,t}^{(n)}\right) \left(1 - X_{i,t}^{(n)}\right).$$
**Extinction**: occupied patch $i$ remains occupied with probability $s_{i,t}$.

We will assume that $(s_{i,t})_{t=0}^{\infty}$ ($i = 1, \ldots, n$) are independent Markov chains taking values in $[0, 1]$ with common transition kernel $P(s, dr)$.

This covers the simple but important case where patches are classified as being suitable or unsuitable for occupancy.
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, and, letting the initial number $N_0^{(n)}$ of occupied patches grow at the same rate as $n$ we arrive at:

**Theorem** 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

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

**Survival probability**

**Colonization probability**
CE Model simulation \((n = 100, s = 0.56, c(x) = cx \text{ with } c = 0.7)\)
CE Model simulation ($n = 100$, $s = 0.8$, $c(x) = cx$ with $c = 0.7$)
Stability

\[ x_{t+1} = f(x_t), \text{ where } f(x) = s(x + (1 - x)c(x)). \]

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

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

CE Model simulation \((n = 100, s = 0.8, c(x) = cx \text{ with } c = 0.7)\)
Return now to the general case, where patch survival probabilities evolve in time, and we keep track of which patches are occupied . . .

\[
\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).
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Treat the collection of patch survival probabilities and those of *occupied patches* at time $t$ as point processes on $[0, 1]$. 
Our approach - Point processes

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

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

$$\sigma_{n,t}(B) = \#\{s_{i,t} \in B\}/n, \quad B \in \mathcal{B}([0, 1]),$$

$$\mu_{n,t}(B) = \#\{s_{i,t} \in B : X^{(n)}_{i,t} = 1\}/n, \quad B \in \mathcal{B}([0, 1]).$$
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We are going to suppose that $\sigma_{n,0} \xrightarrow{d} \sigma_0$ for some non-random (probability) measure $\sigma_0$. 


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We are going to suppose that $\sigma_{n,0} \overset{d}{\rightarrow} \sigma_0$ for some non-random (probability) measure $\sigma_0$.

Think of $\sigma_0$ as being the initial distribution of survival probabilities.
Equivalently, we may define $(\sigma_{n,t})$ and $(\mu_{n,t})$ by

$$\int h(s)\sigma_{n,t}(ds) = \frac{1}{n} \sum_{i=1}^{n} h(s_{i,t})$$

$$\int h(s)\mu_{n,t}(ds) = \frac{1}{n} \sum_{i=1}^{n} X_{i,t}^{(n)} h(s_{i,t}),$$

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 \((h \equiv 1)\),

\[
\int \mu_{n,t}(ds) = \frac{1}{n} \sum_{i=1}^{n} X_{i,t}^{(n)} \quad \text{(proportion occupied)}.
\]
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 times.

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

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

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

$$
\int h(s)\mu_{t+1}(ds) = c_t \int s \int h(r)P(s,dr)\sigma_t(ds) \\
(1 - c_t) \int s \int h(r)P(s,dr)\mu_t(ds),
$$

where $c_t = c(\mu_t([0,1])) = c\left(\int \mu_t(ds)\right)$. 
Survival probability simulation

Survival probability \((p = 0.62 \text{ with Beta}(1,30) \text{ proportional jumps})\)
CE Model simulation \((n = 100, p = 0.62, c(x) = cx \text{ with } c = 0.7)\)
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