Infinite-patch metapopulation models: branching, convergence and chaos

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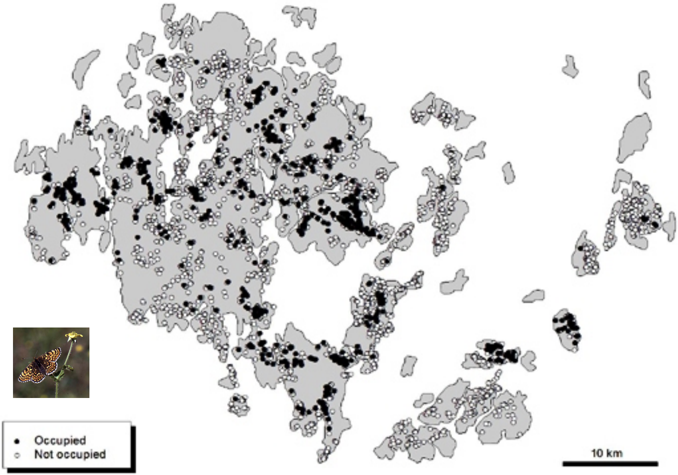
40th Conference on Stochastic Processes and their Applications

Chalmers University, June 2018

AUSTRALIAN RESEARCH COUNCIL CENTRE OF EXCELLENCE FOR MATHEMATICAL AND STATISTICAL FRONTIERS

Metapopulations



Glanville fritillary butterfly (Melitaea cinxia) in the Åland Islands in Autumn 2005.

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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

Phase structure

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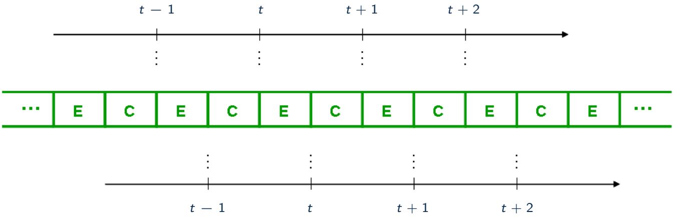

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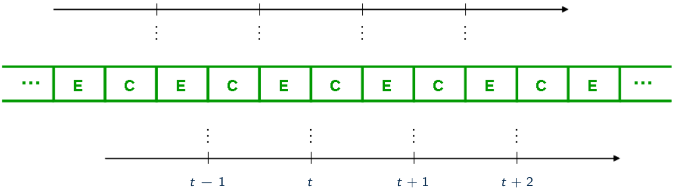

We will we assume that the population is *observed after successive extinction phases* (CE Model).

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Colonization: unoccupied patches become occupied independently with probability $c(n_t/N)$, where $c : [0,1] \to [0,1]$ is continuous, increasing and concave, with $c(0) = 0$ and $c'(0) > 0$.

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We thus have the following *Chain Binomial* structure[1]:

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

[$\mathrm{Bin}(m, p)$ is a binomial random variable with m trials and success probability p.]

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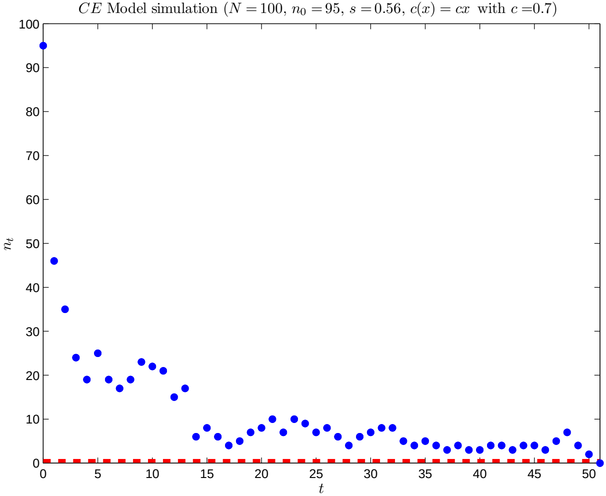
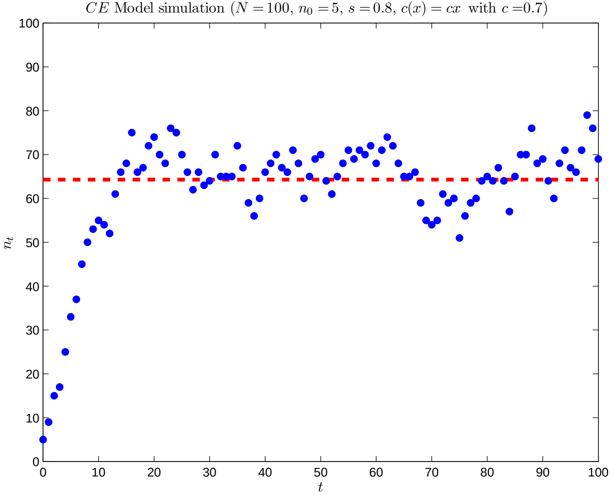
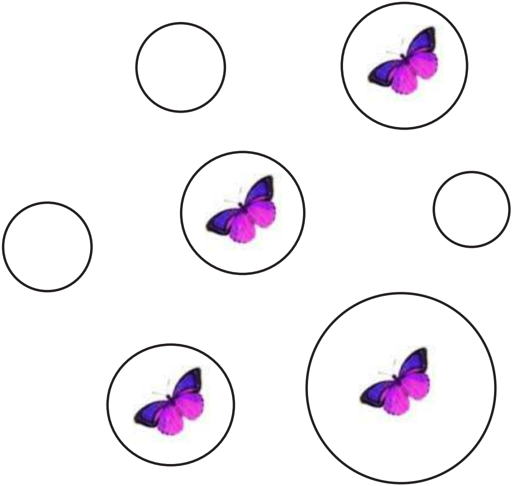
Evanescence: $c'(0) \leqslant (1-s)/s$



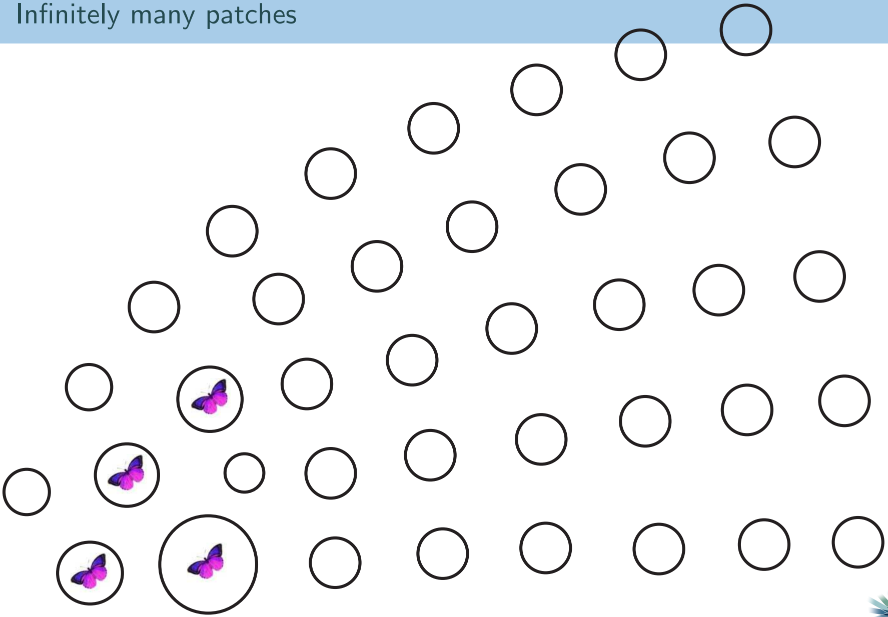
Quasi stationarity: $c'(0) > (1-s)/s$



N patches



Infinitely many patches



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Lemma If c has a continuous second derivative near 0, then, for fixed n,

$$\mathrm{Bin}(N - n, c(n/N)) \xrightarrow{d} \mathrm{Poi}(mn), \quad \text{as } N \to \infty,$$

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

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(Recall the earlier condition for evanescence: $c'(0) \leqslant (1 - s)/s$)

Infinite-patch SPOM with regulation

Assume the following structure:

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For some index N write $m(n) = N\mu(n/N)$, where μ is a continuous function. We may take N to be simply n_0 or, more generally, following Klebaner[2], we may interpret N as being a 'threshold' with the property that $n_0/N \to x_0$ as $N \to \infty$.

[2] Klebaner, F.C. (1993) Population-dependent branching processes with a threshold. Stochastic Process. Appl. 46, 115–127.

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By choosing μ appropriately, we may allow for a degree of regulation in the colonization process.

For example, $\mu(x)$ might be of the form

- $\mu(x) = rx(a - x)$ $(0 \leqslant x \leqslant a)$ (logistic growth);
- $\mu(x) = x\mathrm{e}^{r(1-x)}$ $(x \geqslant 0)$ (Ricker dynamics);
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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.

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Theorem 2 If $X_0^N \xrightarrow{p} x_0$ as $N \to \infty$, then $X_t^N \xrightarrow{p} x_t$ for all $t \geqslant 1$, where (x_t) is determined by $x_{t+1} = f(x_t)$ $(t \geqslant 0)$ with $f(x) = s(x + \mu(x))$.

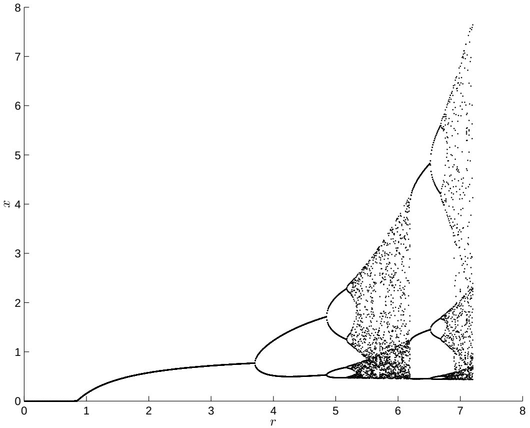
The proof uses the following very useful result.

Lemma[3] Let U_n, V_n, and u be random variables, where U_n and u are scalar. If $\mathbb{E}(U_n|V_n) \xrightarrow{p} u$ and $\mathrm{Var}\,(U_n|V_n) \xrightarrow{p} 0$ then $U_n \xrightarrow{p} u$.

[3] McVinish, R. and Pollett, P.K. (2012) The limiting behaviour of a mainland-island metapopulation. Journal of Mathematical Biology 64, 775–801.

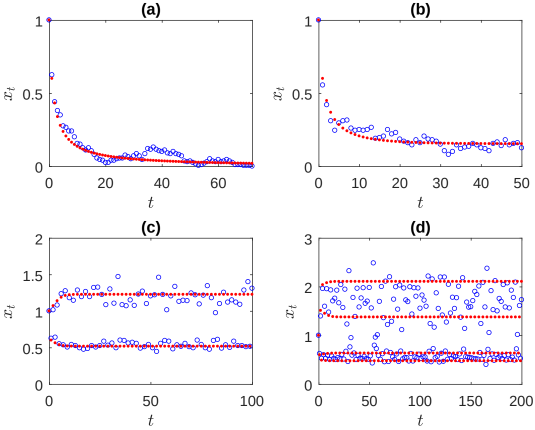
Proof: We will use mathematical induction. Suppose $X_t^N \xrightarrow{p} x_t$ for some $t \geqslant 0$. Since $n_{t+1} \stackrel{\mathrm{D}}{=} \mathrm{Bin}\big(n_t + \mathrm{Poi}\big(m(n_t)\big), s\big)$, a simple calculation gives $\mathbb{E}(n_{t+1}|n_t) = s(n_t + m(n_t))$. But, $m(n) = N\mu(n/N)$. So, dividing by N gives $\mathbb{E}(X_{t+1}^N|X_t^N) = f(X_t^N)$, where $f(x) = s(x + \mu(x))$. Since μ is continuous, so is f, and so $\mathbb{E}(X_{t+1}^N|X_t^N) \xrightarrow{p} f(x_t) = x_{t+1}$. Another simple calculation yields $\mathrm{Var}\,(n_{t+1}|n_t) = s((1-s)n_t + m(n_t))$, and so $N\,\mathrm{Var}\,(X_{t+1}^N|X_t^N) = v(X_t^N)$, where $v(x) = s((1-s)x + \mu(x))$. Since v is continuous, $v(X_t^N) \xrightarrow{p} v(x_t)$, and hence $\mathrm{Var}\,(X_{t+1}^N|X_t^N) \xrightarrow{p} 0$. Using the technical lemma we arrive at $X_{t+1}^N \xrightarrow{p} x_{t+1}$, and the proof is complete.

Infinite-patch SPOM with regulation



Bifurcation diagram for the infinite-patch deterministic model with colonization following Ricker growth dynamics: $x_{t+1} = 0.3\, x_t(1 + \mathrm{e}^{r(1-x_t)})$ (r ranges from 0 to 7.2).

Infinite-patch SPOM with regulation



Simulation (blue circles) of the infinite-patch model with colonization following Ricker growth dynamics, together with the corresponding limiting deterministic trajectories (solid red). Here $s = 0.3$, $N = 200$, and (a) $r = 0.84$, (b) $r = 1$ (c) $r = 4$, (d) $r = 5$.

We can also get a handle on the fluctuations of (X_t^N) about (x_t). Define Z^N by $Z_t^N = \sqrt{N}(X_t^N - x_t)$ $(t \geqslant 0)$.

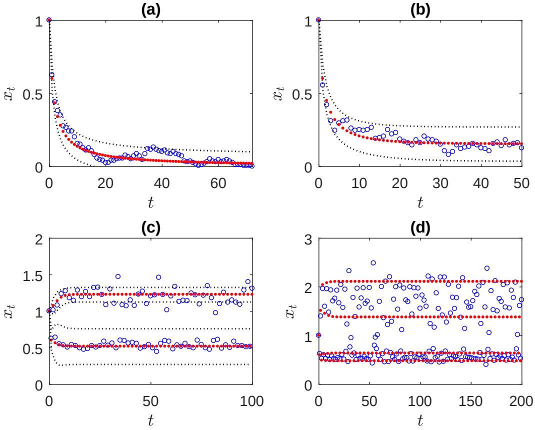
Theorem 3 Suppose that μ is twice continuously differentiable with bounded second derivative, and suppose that $Z_0^N \xrightarrow{d} z_0$. Then, Z^N converges weakly to the Gaussian Markov chain Z defined by $Z_{t+1} \stackrel{\mathrm{D}}{=} s(1+\mu'(x_t))Z_t + E_t$, starting at $(Z_0 =)$ z_0, with (E_t) independent and $E_t \sim \mathrm{N}(0, v(x_t))$, where $v(x) = s((1-s)x + \mu(x))$.

The proof follows the programme laid out in the proof of Theorem 1 of

> Klebaner, F.C. and Nerman, O. (1994) Autoregressive approximation in branching processes with a threshold. Stochastic Process. Appl. 51, 1–7,

but note that (n_t) is not a *population-dependent branching processes with threshold*; see last slide.

Infinite-patch SPOM with regulation



Same graphs as earlier, but now in (a), (b) and (c), the black dotted lines indicate ± 2 standard deviations of the Gaussian approximation (in (c) every *second* point is proximate, thus indicating the extent of variation about each of the two limit cycle values).

Infinite-patch SPOM with regulation - stability

Recall that $f(x) = s(x + \mu(x))$. Notice that x^* will be a fixed point of f if and only if $\mu(x^*) = \rho x^*$, where $\rho = (1 - s)/s$. Clearly 0 is a fixed point, but there might be others. If there *is* a unique positive fixed point x^*, it will be stable if $\mu'(x^*) < 1$ and unstable if $\mu'(x^*) > 1$ (need to consider higher derivatives when $\mu'(x^*) = 1$).

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Corollary 1 Suppose that f admits a unique positive stable fixed point x^*. Then, if $X_0^N \xrightarrow{p} x^*$, $x_t = x^*$ for all t and, assuming $Z_0^N \to z_0$, the limit process Z is an AR-1 process of the form $Z_{t+1} \stackrel{\mathrm{D}}{=} s(1 + \mu'(x^*))Z_t + E_t$, starting at $(Z_0 =)$ z_0, with iid errors $E_t \sim \mathrm{N}(0, (1 - s^2)x^*)$.

Corollary 2 Suppose that f admits a stable limit cycle $x_0^*, x_1^*, \ldots, x_{d-1}^*$ with $X_0^N \xrightarrow{p} x_0^*$. Then, $x_{nd+j} = x_j^*$ $(n \geqslant 0,\ j = 0, \ldots, d-1)$ and, assuming $Z_0^N \to z_0$, the limit process Z has the following representation: $(\boldsymbol{Y}_n,\ n \geqslant 0)$, where $\boldsymbol{Y}_n = (Z_{nd}, Z_{nd+1}, \ldots, Z_{(n+1)d-1})^\top$ with $Z_0 = z_0$, is a d-variate AR-1 process of the form $\boldsymbol{Y}_{n+1} \stackrel{\mathrm{D}}{=} A\boldsymbol{Y}_n + \boldsymbol{E}_n$, with iid errors $\boldsymbol{E}_n \sim \mathrm{N}(\mathbf{0}, \Sigma_d)$; A is the $d \times d$ matrix

$$A = \begin{pmatrix} 0 & 0 & \cdots & a_1 \\ 0 & 0 & \cdots & a_2 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & a_d \end{pmatrix},$$

where $a_j = s^j \prod_{i=0}^{j-1}(1 + \mu'(x_i^*))$, $\Sigma_d = (\sigma_{ij})$ is the $d \times d$ symmetric matrix with entries

$$\sigma_{ij} = a_i a_j \sum_{k=0}^{i-1} v(x_k^*)/a_{k+1}^2 \qquad (1 \leqslant i \leqslant j \leqslant d),$$

where $v(x) = s((1-s)x + \mu(x))$, and the random entries, $(Z_1, \ldots, Z_{d-1})$, of $\boldsymbol{Y}_0$ have a Gaussian $\mathrm{N}(\boldsymbol{a}z_0, \Sigma_{d-1})$ distribution, where $\boldsymbol{a} = (a_1, \ldots, a_{d-1})$. Furthermore, $(\boldsymbol{Y}_n)$ has a Gaussian $\mathrm{N}(\mathbf{0}, V)$ stationary distribution, where $V = (v_{ij})$ has entries $v_{ij} = \sigma_{ij}/(1 - a_d^2)$.

Note added

Recall that $n_{t+1} \stackrel{\mathrm{D}}{=} \mathrm{Bin}\big(n_t + \mathrm{Poi}(m(n_t)), s\big)$. Whilst (n_t) does not exhibit the branching property (required for it to be a *population-dependent branching processes with threshold*), we can say the following.

Theorem $n_{t+1} \stackrel{\mathrm{D}}{=} \mathrm{Bin}(n_t, s) + \mathrm{Poi}\big(sm(n_t)\big)$ (independent RVs).

Proof:

$$\begin{aligned}
\mathbb{E}(z^{n_{t+1}}|n_t) &= \mathbb{E}\Big(\mathbb{E}\Big(z^{n_{t+1}}\Big|\mathrm{Poi}(m(n_t)), n_t\Big)\Big|n_t\Big) \\
&= \mathbb{E}\Big((1-s+sz)^{n_t+\mathrm{Poi}(m(n_t))}\Big|n_t\Big) \\
&= (1-s+sz)^{n_t}\,\mathbb{E}\Big((1-s+sz)^{\mathrm{Poi}(m(n_t))}\Big|n_t\Big) \\
&= (1-s(1-z))^{n_t}\, e^{-sm(n_t)(1-z)}
\end{aligned}$$