Infinite-patch metapopulation models: branching, convergence and chaos

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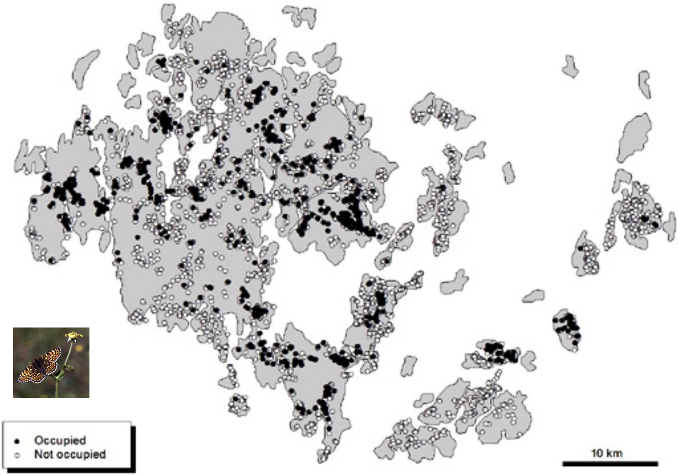
The University of Queensland

UWA Statistics Seminar

6th September 2019

Metapopulations



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

N-patch SPOM

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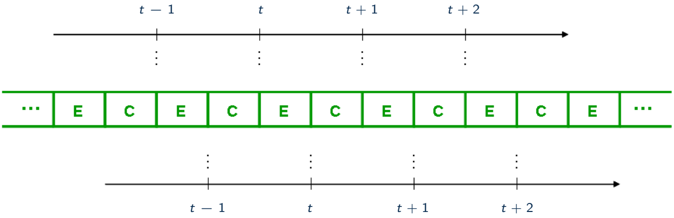
For many species the propensity for colonization and local extinction is markedly different in different phases of their life cycle. Examples:

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

Colonization and extinction happen in distinct, successive phases.



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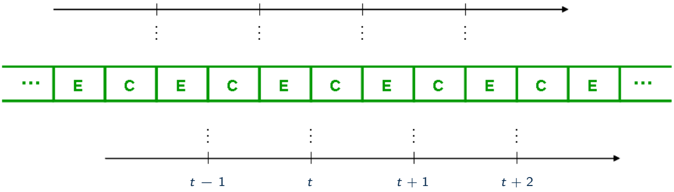

We will we assume that the population is *observed after successive extinction phases* (CE Model).

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Colonization and extinction happen in distinct, successive phases.

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]:

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

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

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

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The N-patch model:

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Theorem If $n_0/N \stackrel{p}{\to} x_0$ (a constant) as $N \to \infty$, then

$$n_t/N \stackrel{p}{\to} x_t, \quad \text{for all } t \geqslant 1,$$

with (x_t) determined by $x_{t+1} = f(x_t)$, where

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There are two possibilities:

- *Evanescence*: $c'(0) \leqslant (1-s)/s$; 0 is the unique fixed point of f in $[0,1]$. It is stable.
- *Quasi stationarity*: $c'(0) > (1-s)/s$; f has two fixed points in $[0,1]$: 0 (unstable) and $x^* \in (0,1)$ (stable).

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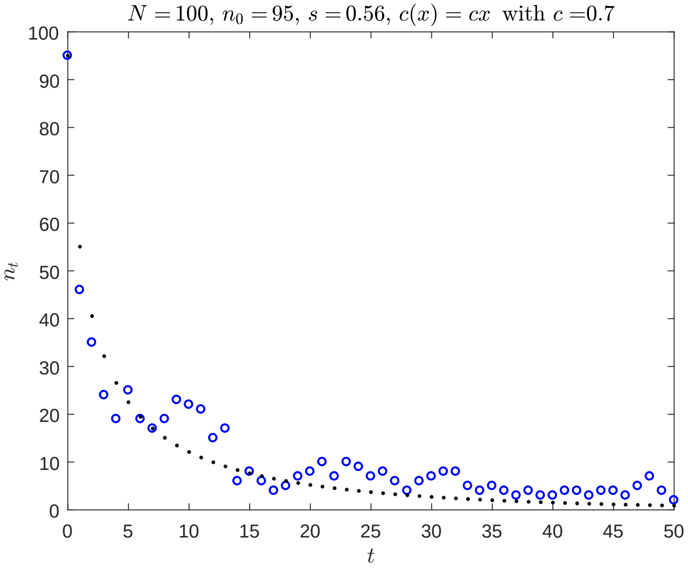

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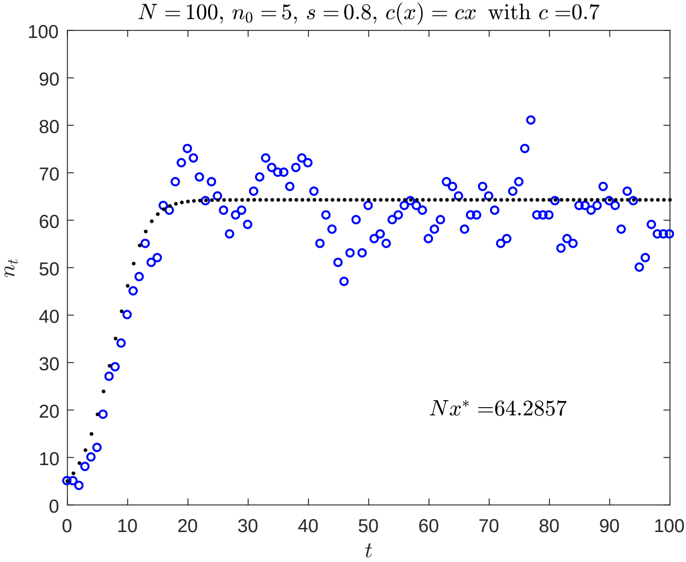


Theorem Further suppose that $c(x)$ is twice continuously differentiable, and let

$$Z_t^N = \sqrt{N}(n_t/N - x_t).$$

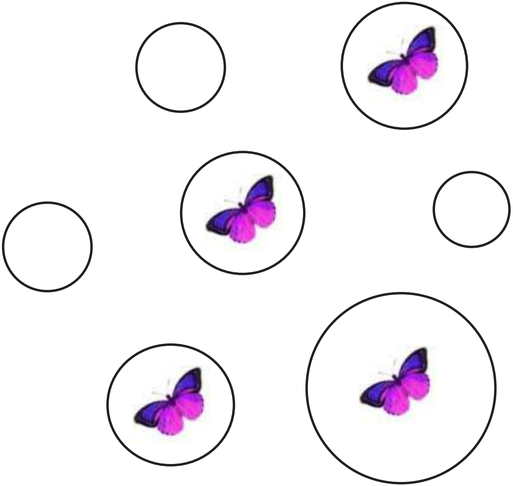
If $Z_0^N \xrightarrow{d} z_0$, then Z^N converges weakly to the Gaussian Markov chain Z defined by

$$Z_{t+1} = f'(x_t)Z_t + E_t \qquad (Z_0 = z_0),$$

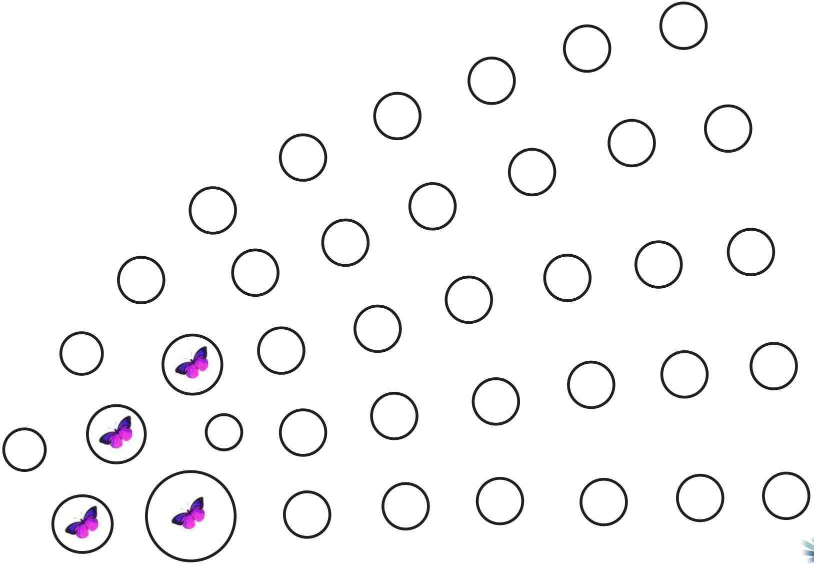
with (E_t) independent and $E_t \sim \mathrm{N}(0, v(x_t))$, where

$$v(x) = s\big[(1-s)x + (1-x)c(x)\big(1 - sc(x)\big)\big].$$

N patches



Infinitely many patches



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

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

where $m = c'(0)$.

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Claim The process $(n_t,\ t = 0, 1, \ldots)$ 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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The mean number of offspring is $\mu = (1 + m)s$. So, for example, $\mathbb{E}(n_t | n_0) = n_0 \mu^t$.

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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:

$$n_{t+1} \stackrel{d}{=} \mathrm{Bin}\big(n_t + \mathrm{Poi}\big(m(n_t)\big), s\big)$$

where $m(n) \geqslant 0$.

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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.

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);
- $\mu(x) = \lambda x/(1+ax)^b$ $(x \geqslant 0)$ (Hassell 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 $t = 1, 2, \ldots$, where (x_t) is determined by $x_{t+1} = f(x_t)$ $(t = 0, 1, \ldots)$ with $f(x) = s(x + \mu(x))$.

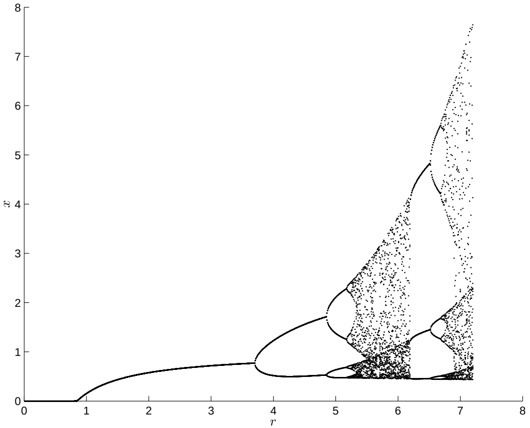
The proof uses the following very useful result.

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 $t \in \{0, 1, \dots\}$. Since $n_{t+1} \stackrel{d}{=} \mathrm{Bin}\big(n_t + \mathrm{Poi}\big(m(n_t)\big), s\big)$, 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).

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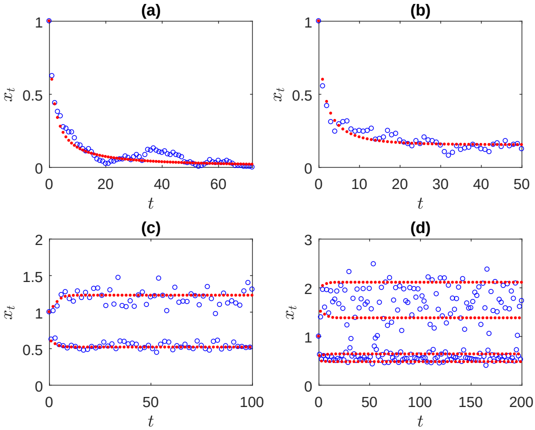
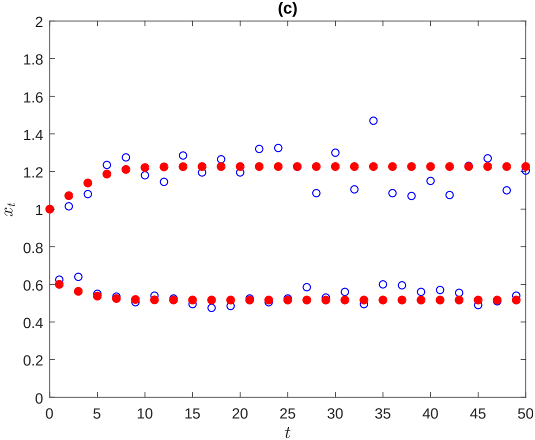
Infinite-patch SPOM with regulation



Simulation (blue circles) of the infinite-patch model with colonization following Ricker growth dynamics ($x_{t+1} = 0.3\, x_t(1 + \mathrm{e}^{r(1-x_t)})$), 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) $r = 5$.

Infinite-patch SPOM with regulation



Simulation (blue circles) of the infinite-patch model with colonization following Ricker growth dynamics ($x_{t+1} = 0.3\, x_t(1 + \mathrm{e}^{r(1-x_t)})$), together with the corresponding limiting deterministic trajectories (solid red). Here $s = 0.3$, $N = 200$, and $r = 4$.

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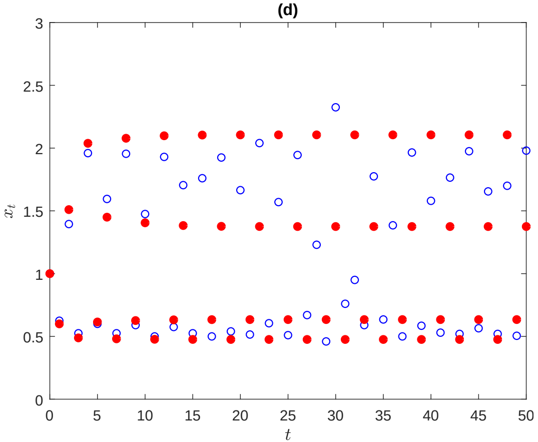

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We can also get a handle on the fluctuations of (X_t^N) about (x_t). Define Z^N by $Z_t^N = \sqrt{N}(X_t^N - x_t)$ $(t = 0, 1, \dots)$.

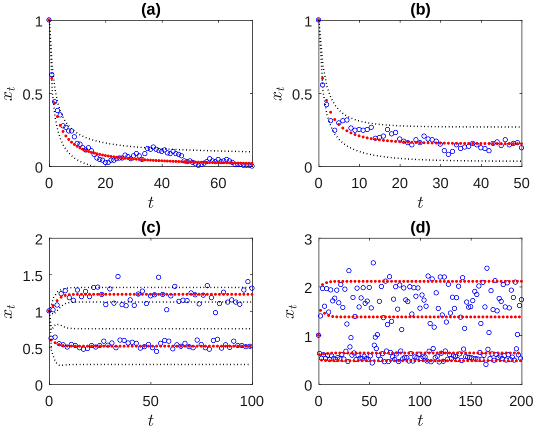
Theorem 3 Suppose that μ is twice continuously differentiable with bounded second derivative, and suppose that $Z_0^N \xrightarrow{d} z_0$. Then, Z^N converges weakly to the Gaussian Markov chain Z defined by $Z_{t+1} \stackrel{d}{=} s(1 + \mu'(x_t))Z_t + E_t$, starting at $(Z_0 =)\ z_0$, with (E_t)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

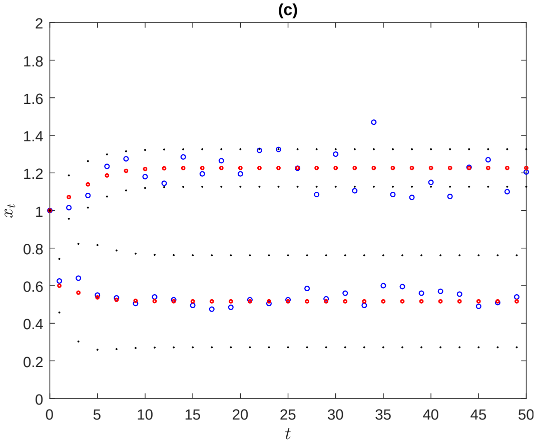
But, note that (n_t) is not a *population-dependent branching processes with threshold*; see note later.

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



Same graph as earlier, but now the black dotted lines indicate ± 2 standard deviations of the Gaussian approximation (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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Infinite-patch SPOM with regulation - stability

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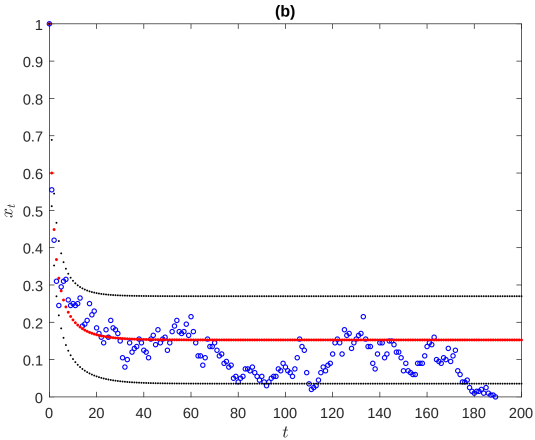
Corollary 1 Suppose that f admits a unique positive stable fixed point x^*. Then, if $X_0^N \xrightarrow{p} x^*$, $x_t = x^*$ for all t and, assuming $Z_0^N \to z_0$, the limit process Z is an AR-1 process of the form $Z_{t+1} \stackrel{d}{=} s(1 + \mu'(x^*))Z_t + E_t$, starting at $(Z_0 =)z_0$, with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

Infinite-patch SPOM with regulation - stable equilibrium



Simulation (blue circles) of the infinite-patch model with colonization following Ricker growth dynamics ($x_{t+1} = 0.3\, x_t(1 + \mathrm{e}^{r(1-x_t)})$), together with the corresponding limiting deterministic trajectories (solid red). The black dotted lines indicate ± 2 standard deviations of the Gaussian approximation. Here $s = 0.3$, $N = 200$, and $r = 1$, and x^*(stable)$\simeq 0.152704$.

Infinite-patch SPOM with regulation - stability

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 $\boldsymbol{Y}_{n+1} \stackrel{d}{=} A\boldsymbol{Y}_n + \boldsymbol{E}_n$, with iid errors $\boldsymbol{E}_n \sim \mathrm{N}(\mathbf{0}, \Sigma_d)$; A is the $d \times d$ matrix

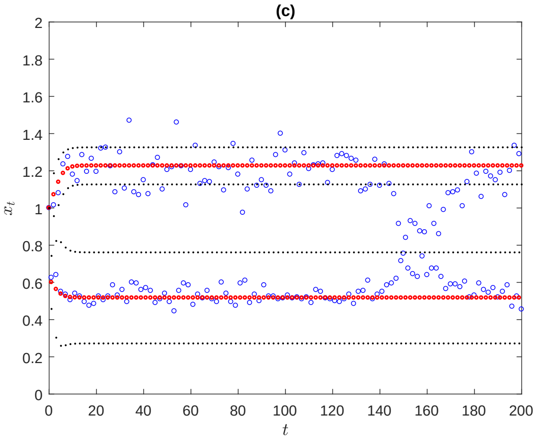
$$A = \begin{pmatrix} 0 & 0 & \cdots & a_1 \\ 0 & 0 & \cdots & a_2 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & a_d \end{pmatrix},$$

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 $v_{ij} = \sigma_{ij}/(1 - a_d^2)$.

Infinite-patch SPOM with regulation - limit cycle ($d = 2$)



Simulation (blue circles) of the infinite-patch model with colonization following Ricker growth dynamics ($x_{t+1} = 0.3\, x_t(1 + \mathrm{e}^{r(1-x_t)})$), together with the corresponding limiting deterministic trajectories (solid red). The black dotted lines indicate ± 2 standard deviations of the Gaussian approximation. Here $s = 0.3$, $N = 200$, and $r = 4$, and, $x_0^* \simeq 0.516661$, $x_1^* \simeq 1.22645$.

Note

Recall that $n_{t+1} \stackrel{d}{=} \mathrm{Bin}\big(n_t + \mathrm{Poi}(m(n_t)), s\big)$. 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 $n_{t+1} \stackrel{d}{=} \mathrm{Bin}(n_t, s) + \mathrm{Poi}\big(sm(n_t)\big)$ (independent RVs).

Proof:

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

Future directions

An *inhomogeneous* SPOM keeps track of which patches are occupied: $\boldsymbol{X}_t^N = (X_{1,t}^N, X_{2,t}^N, \dots)$, where $X_{i,t}^N$ is a binary variable indicating whether or not patch i is occupied at time t. (Again we consider a sequence of models indexed by a threshold N.)

Assume that $(\boldsymbol{X}_t^N,\ t = 0, 1, \dots)$ is a (countable-state) Markov chain with

$$X_{i,t+1}^N \stackrel{d}{=} \mathrm{Bin}\Big(X_{i,t}^N + \mathrm{Bin}\Big(1 - X_{i,t}^N, c\big(\boldsymbol{X}_t^N\big)\Big), s_i\Big),$$

a "*Chain Bernoulli*" structure.

Approach: Following

McVinish, R. and Pollett, P.K. (2010) Limits of large metapopulations with patch dependent extinction probabilities. Adv. Appl. Probab. 42, 1172–1186.

use *point processes* $(\mathcal{S}_t^N = \{s_i : X_{i,t}^N = 1\})$ and *probability generating functionals* $G_{\mathcal{S}_t^N}(\xi) = \mathbb{E}\left[\prod_{s_i \in \mathcal{S}_t^N} \xi(s_i)\right]$, and hope that $(\mathcal{S}_t^N)$ converges weakly to a point process $\mathcal{S}_t$, with $G_{\mathcal{S}_{t+1}}(\xi) = G_{\mathcal{S}_t}(H(\xi))$ for suitable H.