

Stochastic models for population networks

II: Discrete-time patch occupancy models [Exact results]

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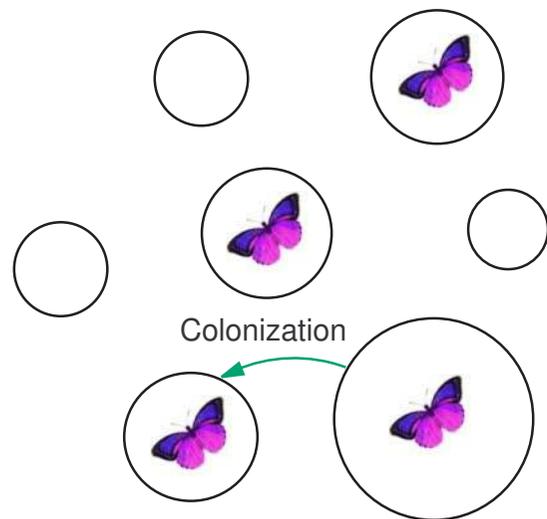


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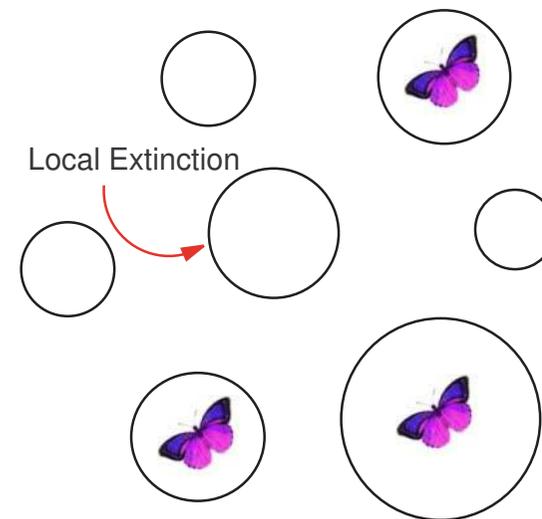
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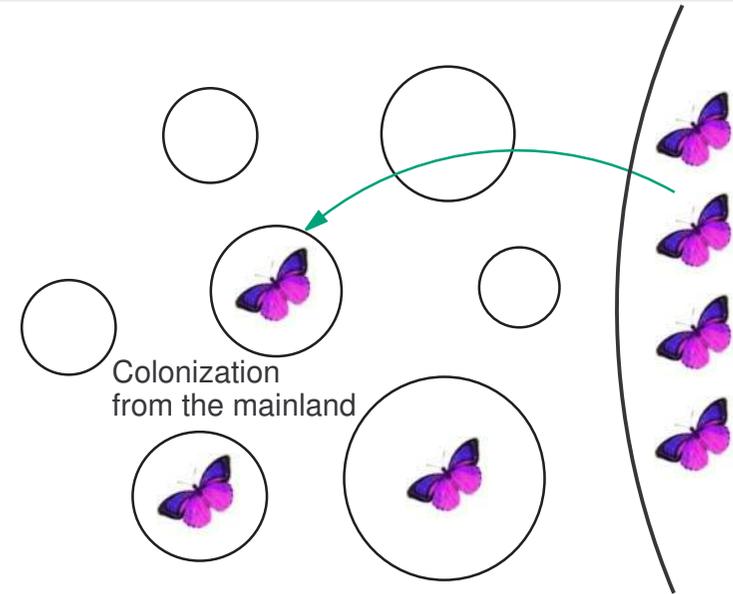
Metapopulations



Metapopulations



- A metapopulation is a population that is confined to a network of geographically separated habitat patches (for example a group of islands).
- Individual patches may suffer local extinction.
- Recolonization can occur through dispersal of individuals from other patches.
- In some instances there is an external source of immigration (mainland-island configuration).



Given an appropriate model ...

- Assessing population viability:
 - What is the expected time to (total) extinction* ?
 - What is the probability of extinction by time t^* ?
- Can we improve population viability ?
- How do we estimate the parameters of the model ?
- Can we determine the stationary/quasi-stationary distributions ?

*Or *first* total extinction in the mainland-island setup.

We record the *number* n_t of occupied patches at each time t and suppose that $(n_t, t \geq 0)$ is a Markov chain in discrete or continuous time.

In Lecture 1 we looked at the *stochastic logistic (SL) model* of Feller*.

*Feller, W. (1939) Die grundlagen der volterraschen theorie des kampfes ums dasein in wahrscheinlichkeitstheoretischer behandlung. Acta Biotheoretica 5, 11–40.

A continuous-time model

There are J patches. Each occupied patch becomes empty at rate e and colonization of empty patches occurs at rate c/J for each occupied-unoccupied pair.

The state space of the Markov chain $(n_t, t \geq 0)$ is $S = \{0, 1, \dots, J\}$ and the transitions are:

$$\begin{aligned} n \rightarrow n + 1 & \quad \text{at rate} \quad \frac{c}{J}n(J - n) \\ n \rightarrow n - 1 & \quad \text{at rate} \quad en \end{aligned}$$

Mainland-island version (v is the immigration rate):

$$\begin{aligned} n \rightarrow n + 1 & \quad \text{at rate} \quad v(J - n) + \frac{c}{J}n(J - n) \\ n \rightarrow n - 1 & \quad \text{at rate} \quad en \end{aligned}$$

The SL model

We identified an approximating deterministic model for the *proportion*, $X_t^{(J)} = n_t/J$, of occupied patches at time t . A *functional law of large numbers* established convergence of the family $(X_t^{(J)})$ to the unique trajectory (x_t) satisfying

$$x_t' = cx_t(1 - x_t) - ex_t = cx_t(1 - \rho - x_t),$$

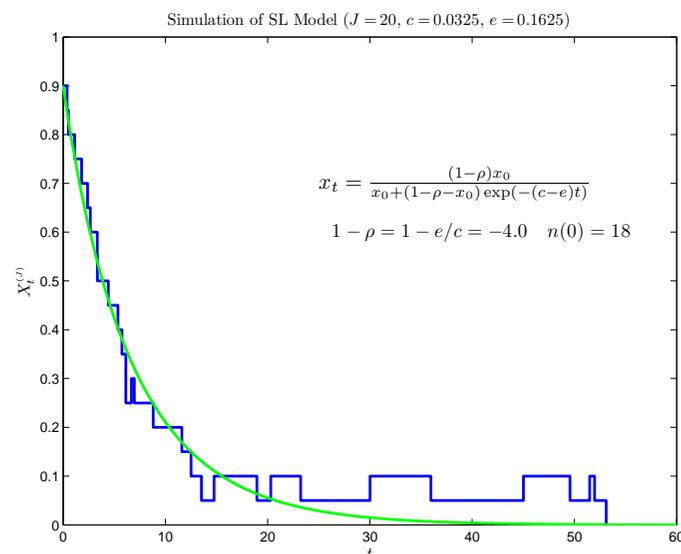
namely

$$x_t = \frac{(1 - \rho)x_0}{x_0 + (1 - \rho - x_0)e^{-(c-e)t}},$$

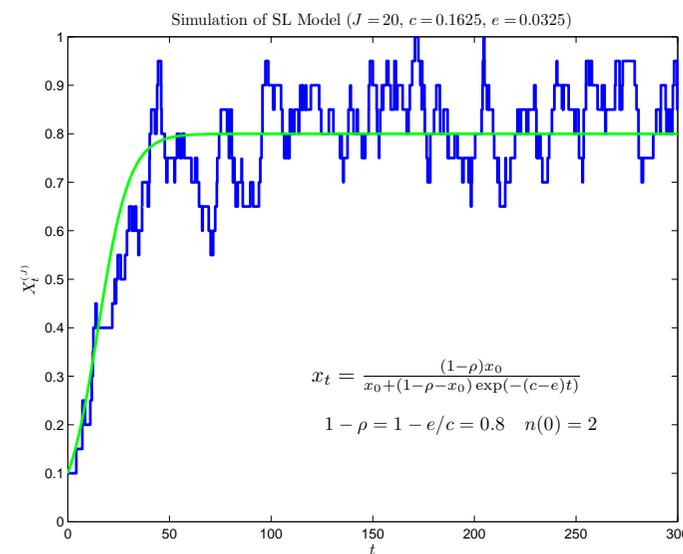
being the classical Verhulst* model.

*Verhulst, P.F. (1838) Notice sur la loi que la population suit dans son accroissement. Corr. Math. et Phys. X, 113–121.

The SL model ($c < e$) $x = 0$ stable

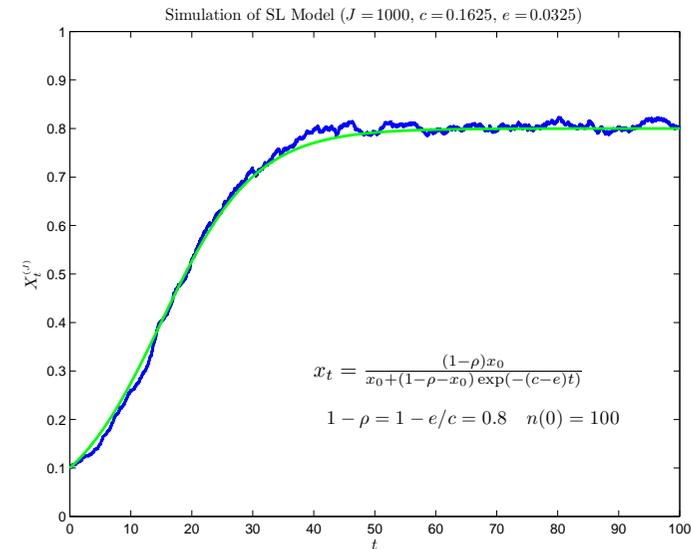


The SL model ($c > e$) $x = 1 - e/c$ stable



Theorem If $X_0^{(J)} \rightarrow x_0$ as $J \rightarrow \infty$, then the family of processes $(X_t^{(J)})$ converges *uniformly in probability on finite time intervals* to the deterministic trajectory (x_t) : for every $\epsilon > 0$,

$$\lim_{J \rightarrow \infty} \Pr \left(\sup_{s \leq t} |X_s^{(J)} - x_s| > \epsilon \right) = 0.$$



Accounting for life cycle

Many species have life cycles (often annual) that consist of distinct phases, and the propensity for colonization and local extinction is different in each phase. 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



Butterfly life cycle

Egg $\simeq 4$ days



Larva (caterpillar) $\simeq 14$ days



Pupa (chrysalis) $\simeq 7$ days



Adult (butterfly) $\simeq 14$ days



Colonization is restricted to the adult phase, and there is a greater propensity for local extinction in the non-adult phases.

We will assume that that colonization (C) and extinction (E) occur in separate distinct phases.

There are several ways to model this:

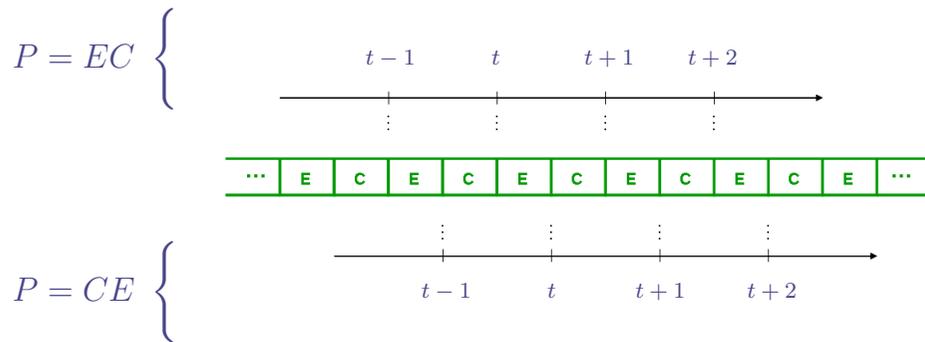
- A quasi-birth-death process with two phases
- A non-homogeneous continuous-time Markov chain (cycle between two sets of transition rates)
- A discrete-time Markov chain ✓

Recall that there are J patches and that n_t is the number of occupied patches at time t . We suppose that $(n_t, t = 0, 1, \dots)$ is a discrete-time Markov chain taking values in $S = \{0, 1, \dots, J\}$ with a 1-step transition matrix $P = (p_{ij})$ constructed as follows.

The extinction and colonization phases are governed by their own transition matrices, $E = (e_{ij})$ and $C = (c_{ij})$.

We let $P = EC$ if the census is taken after the colonization phase or $P = CE$ if the census is taken after the extinction phase.

EC versus CE



Extinction phase

Suppose that local extinction occurs *at any given patch* with probability e ($0 < e < 1$), independently of other occupied patches. So, the number of extinctions when there are i patches occupied has a binomial $Bin(i, e)$ distribution, and therefore

$$e_{i,i-k} = \binom{i}{k} e^k (1-e)^{i-k} \quad (k = 0, 1, \dots, i).$$

We also have $e_{ij} = 0$ if $j > i$.

Colonization phase

Suppose that colonization occurs according to the following mechanism.

If there are i occupied patches, then each unoccupied patch is colonized with probability $c_i = (i/J)c$, where $c \in (0, 1]$ is a **fixed maximum colonization potential**, the (hypothetical) probability that a single unoccupied patch is colonized by the fully occupied network.

So, the unoccupied patches are colonized independently with the same probability, this probability being **proportional to** the number of patches with the potential to colonize.

Colonization phase

Therefore, the number of colonizations when there are i patches occupied has a binomial $Bin(J - i, c_i)$ distribution, and so

$$c_{i,i+k} = \binom{J-i}{k} c_i^k (1 - c_i)^{J-i-k}, \quad (k = 0, 1, \dots, J - i),$$

In particular, $c_{0j} = \delta_{0j}$. We also have $c_{ij} = 0$, for $j < i$.

Notice that 0 is an absorbing state and $C = \{1, \dots, J\}$ is a communicating class.

There are other sensible choices for c_i : for example $c_i = c(1 - (1 - c_1/c)^i)$ or $c_i = 1 - \exp(-i\beta/J)$.

Evaluation of P

We can evaluate P elementwise as follows. If $P = EC$, then $p_{0j} = \delta_{0j}$, $p_{i0} = e^i$, $i \geq 1$, and, for $i, j \geq 1$,

$$p_{ij} = \sum_{k=1}^{\min\{i,j\}} \binom{i}{k} (1-e)^k e^{i-k} \binom{J-k}{j-k} c_k^{j-k} (1-c_k)^{J-j}.$$

If $P = CE$, then $p_{0j} = \delta_{0j}$, and, for $i \geq 1$ and $j \geq 0$,

$$p_{ij} = \sum_{k=\max\{i,j\}}^J \binom{J-i}{k-i} c_i^{k-i} (1-c_i)^{J-k} \binom{k}{k-j} e^{k-j} (1-e)^j.$$

In particular, for $i \geq 1$, $p_{i0} = e^i (1 - c_i (1 - e))^{J-i}$.

Equivalent independent phases

For the CE -model,

$$\mathbf{E}(z^{n_{t+1}} | n_t = i) = (e + (1-e)z)^i (1 - (1-e)c_i(1-z))^{J-i}.$$

Thus, given $n_t = i$, n_{t+1} has the **same distribution** as $B_1 + B_2$, where B_1 and B_2 are two **independent** random variables with $B_1 \sim Bin(i, 1 - e)$ and $B_2 \sim Bin(J - i, (1 - e)c_i)$.

It is as if each of the i occupied patches remains occupied with probability $1 - e$ and each of the $J - i$ unoccupied patches becomes occupied with probability $(1 - e)c_i$, all J patches being affected independently.

For the *EC*-model, the best we can do is

$$\mathbf{E}(z^{n_{t+1}} | n_t = i) = \mathbf{E} \left\{ z^B (1 - c_B(1 - z))^{J-B} \right\},$$

where $B \sim \text{Bin}(i, 1 - e)$.

However, note the large- J asymptotics when $c_i = ic/J$.

Write $p_i^{(J)}(z) = \mathbf{E}(z^{n_{t+1}} | n_t = i)$.

For the *CE*-model,

$$\lim_{J \rightarrow \infty} p_i^{(J)}(z) = [e + (1 - e)z \exp(-c(1 - e)(1 - z))]^i.$$

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Branching!

Now $S = \{0, 1, \dots\}$.

The number of extinctions when there are i patches occupied follows the *Bin*(i, e) law (as before), but in the colonization phase the number of colonizations when there are i patches occupied follows a *Poisson*(ic) law (previously a binomial *Bin*($J - i, ic/J$) law).

The effect is ...

Theorem Both infinite patch models are Galton-Watson branching processes.

The occupied patches independently produce “offspring” according to the following distributions.

For the *EC*-model, $p_{10} = e$ and

$$p_{1j} = (1 - e) \exp(-c) \frac{c^{j-1}}{(j-1)!} \quad (j \geq 1),$$

the interpretation being that each individual “dies” with probability e or otherwise is *joined by* a random number of new offspring that follows a *Poisson*(c) law.

For the *CE*-model, $p_{10} = e \exp(-c(1 - e))$ and

$$p_{1j} = (1 - e) \exp(-c(1 - e)) \frac{(c(1 - e))^{j-1}}{(j-1)!} + e \exp(-c(1 - e)) \frac{(c(1 - e))^j}{j!} \quad (j \geq 1).$$

The individual survives with probability $1 - e$ or dies with probability e , and there is a random number of *new* offspring that follows a *Poisson*($c(1 - e)$) law.

We can now invoke the encyclopaedic theory of branching processes.

Infinitely many patches

For both the *EC* and *CE* models, the mean number of offspring μ is given by $\mu = (1 + c)(1 - e)$. The corresponding variance σ^2 is:

For the *EC*-model $\sigma^2 = (1 - e)((1 + c)^2 e + c)$.

For the *CE*-model $\sigma^2 = (e + c)(1 - e)$.

Notice that $\sigma_{EC}^2 - \sigma_{CE}^2 = c(2 + c)e(1 - e) > 0$.

Recall that, given $n_0 = i$, $\mathbf{E}(n_t) = i\mu^t$ and

$$\text{Var}(n_t) = \begin{cases} i\sigma^2 t & \text{if } \mu = 1 \quad (e = c/(1 + c)) \\ i\sigma^2(\mu^t - 1)\mu^{t-1}/(\mu - 1) & \text{if } \mu \neq 1 \quad (e \neq c/(1 + c)). \end{cases}$$

Infinitely many patches - total extinction

Theorem For both models extinction occurs with probability 1 if and only if $e \geq c/(1 + c)$; otherwise the extinction probability η is the unique solution to $s = p(s)$ on the interval $(0, 1)$, where:

EC-model: $p(s) = e + (1 - e)s \exp(-c(1 - s))$

CE-model: $p(s) = (e + (1 - e)s) \exp(-c(1 - e)(1 - s))$

And much more . . .

- The expected time to extinction.
- Yaglom’s theorem on limiting-conditional (quasi-stationary) distributions.

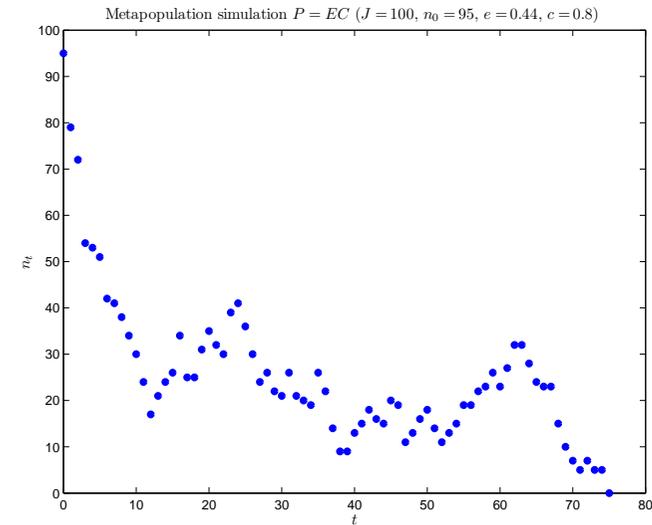
Recall that ...

In the extinction phase the number of extinctions when there are i patches occupied follows a $Bin(i, e)$ law.

In the colonization phase the number of colonizations when there are i patches occupied follows a binomial $Bin(J - i, c_i)$ law, where $c_i = ic/J$.

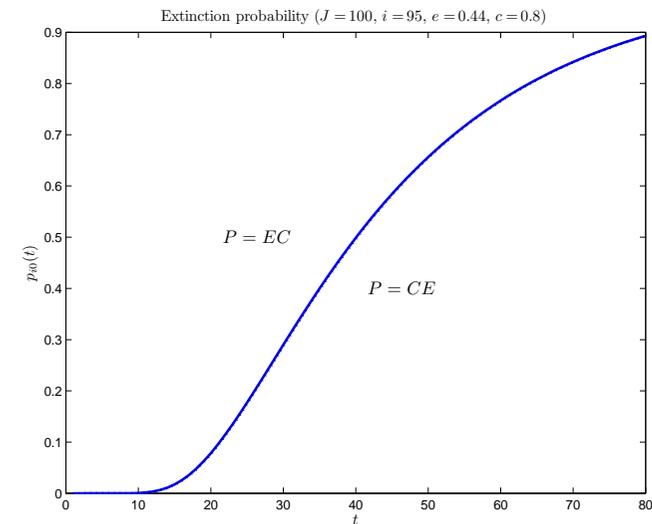
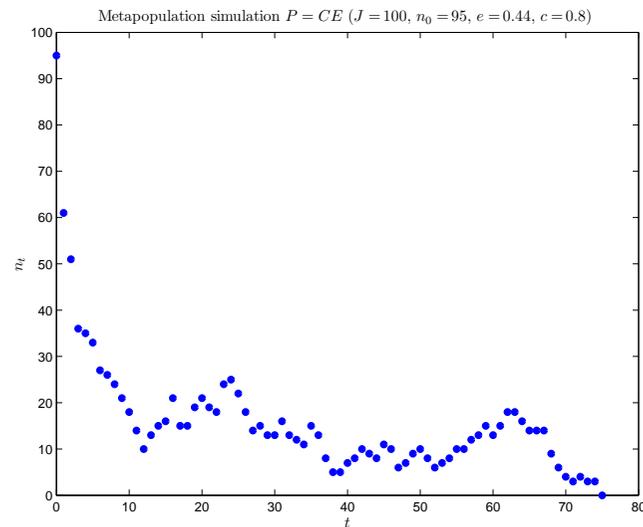
Exact analytical results are difficult to come by—later we study deterministic and Gaussian approximations.

Numerical procedures are routine.



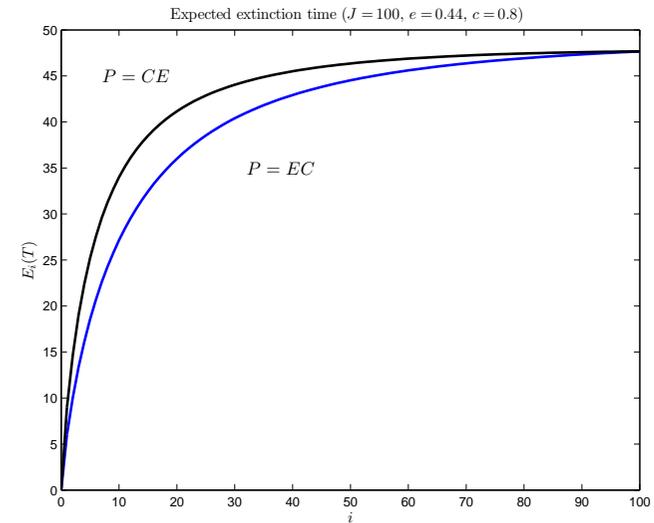
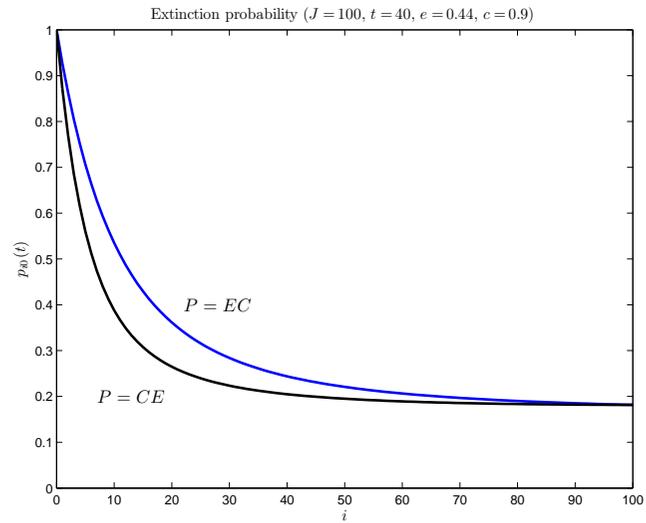
Simulation: $P = CE$

Extinction probability: vary t



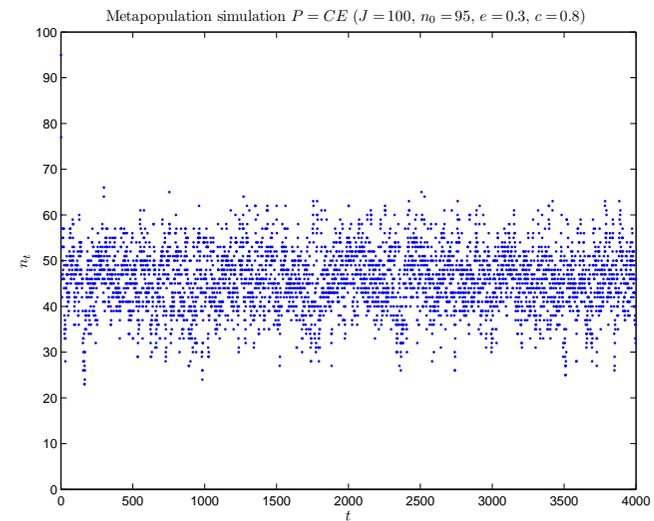
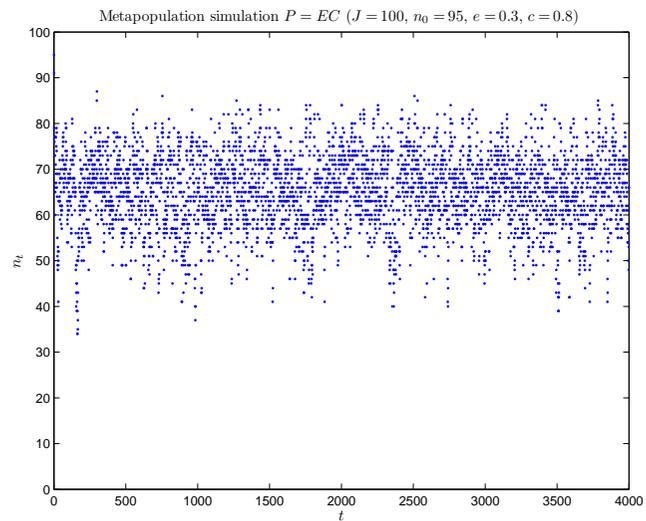
Extinction probability: vary n_0

Expected extinction time: vary n_0



Simulation: $P = EC$

Simulation: $P = CE$



We can model this behaviour using a *limiting conditional distribution (lcd)* $(m_j, j = 1, \dots, J)$; often called a *quasi-stationary distribution (qsd)**

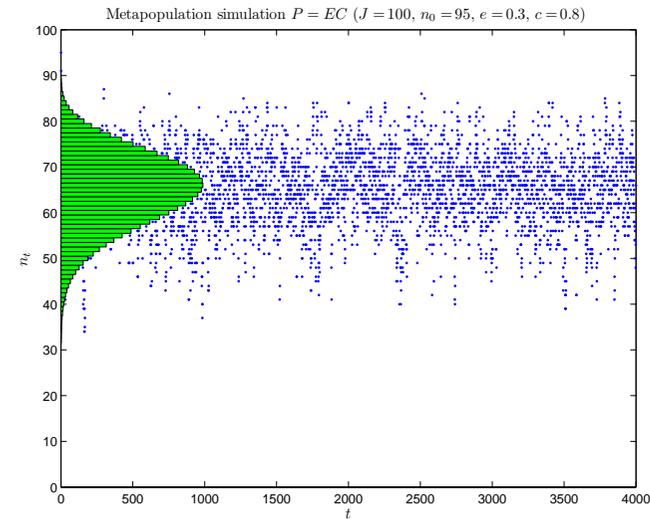
lcd:

$$\lim_{t \rightarrow \infty} \Pr(n_t = j | n_t \neq 0) = m_j.$$

qsd:

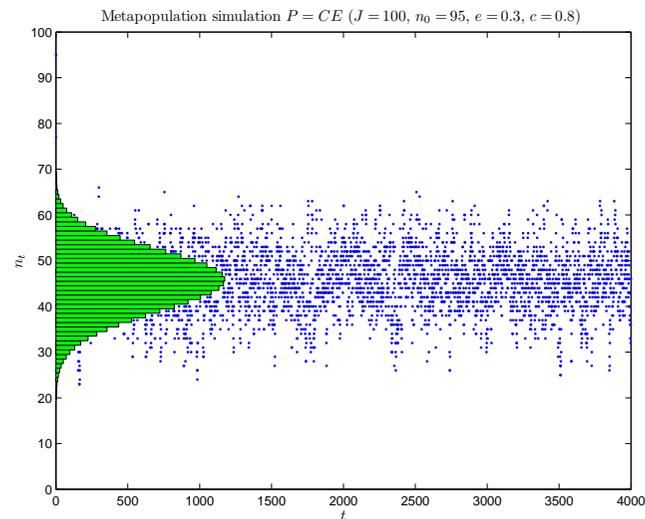
$$\Pr(n_0 = j) = m_j \implies \Pr(n_t = j | n_t \neq 0) = m_j \quad (\forall t > 0).$$

*In the infinite state space setting, the distinction between lcd and qsd is both subtle and interesting.



Simulation and qsd: $P = CE$

J-patch Mainland-Island models



In the extinction phase the number of extinctions when there are i patches occupied follows a $Bin(i, e)$ law.

In the colonization phase the number of colonizations when there are i patches occupied follows a binomial $Bin(J - i, c)$ law.

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This greatly simplifies the analysis!

The behaviour of both models can be summarized in terms of a single pair of parameters (p, q) :

$$EC\text{-model: } p = 1 - e(1 - c) \text{ and } q = c$$

$$CE\text{-model: } p = 1 - e \text{ and } q = (1 - e)c$$

Proposition Given $n_t = i$, n_{t+1} has the same distribution as $B_1 + B_2$, where B_1 and B_2 are two *independent* random variables with $B_1 \sim Bin(i, p)$ and $B_2 \sim Bin(J - i, q)$.

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It is as if each of the i currently occupied patches remains occupied with probability p and each of the $J - i$ currently unoccupied patches become occupied with probability q (all patches being affected independently). *Thus the process has some of the character of an urn model.*

We can improve on this result ...

Reparameterize by setting $a = p - q = (1 - e)(1 - c)$, being the *same* for both models ($0 < a < 1$), and $q^* = q/(1 - a)$. Define sequences (p_t) and (q_t) by

$$q_t = q^*(1 - a^t) \quad \text{and} \quad p_t = q_t + a^t \quad (t \geq 0).$$

Theorem Given $n_0 = i$ patches occupied initially, the number n_t occupied at time t has the same distribution as $B_1 + B_2$, where B_1 and B_2 are *independent* random variables with $B_1 \sim \text{Bin}(i, p_t)$ and $B_2 \sim \text{Bin}(J - i, q_t)$. The limiting distribution of n_t is $\text{Bin}(J, q^*)$.

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It is as if each of the i initially occupied patches remains occupied with probability p_t and each of the $J - i$ initially unoccupied patches become occupied with probability q_t (all patches being affected independently). The limiting expected proportion occupied is q^* .

We have in particular that

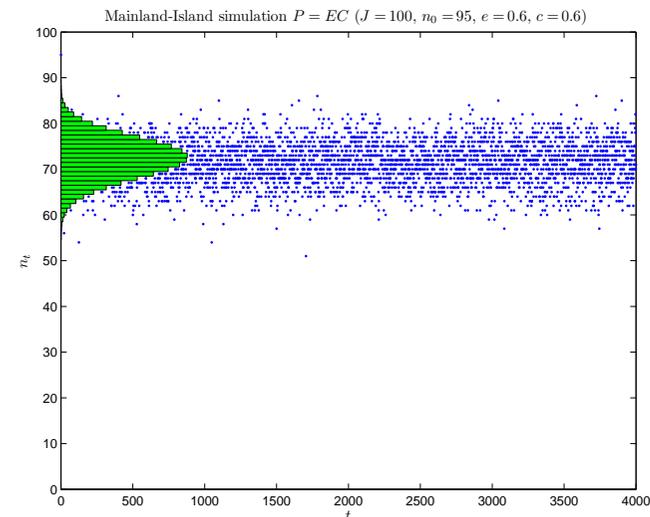
$$E(n_t | n_0 = i) = ip_t + (J - i)q_t = ia^t + Jq_t$$

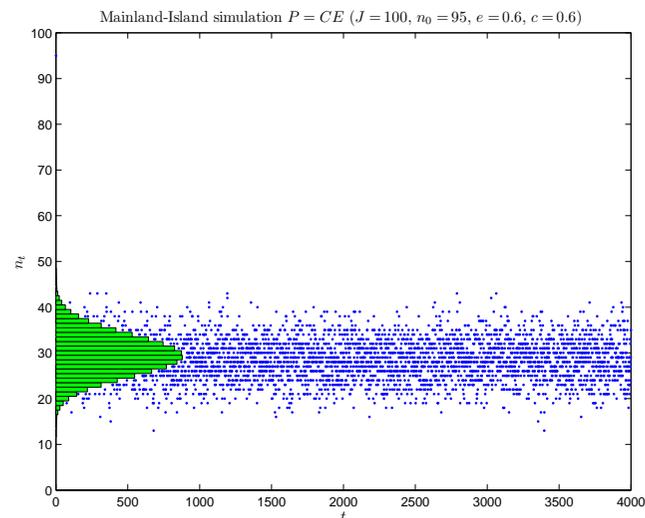
$$(\rightarrow Jq^* \text{ as } t \rightarrow \infty)$$

and

$$\begin{aligned} \text{Var}(n_t | n_0 = i) &= ip_t(1 - p_t) + (J - i)q_t(1 - q_t) \\ &= ia^t(1 - a^t)(1 - 2q^*) + Jq_t(1 - q_t) \end{aligned}$$

$$(\rightarrow Jq^*(1 - q^*) \text{ as } t \rightarrow \infty).$$





Now suppose that $c = d/J$ (imagine that a fixed external colonization potential d is distributed evenly among all J patches).

In the limit as $J \rightarrow \infty$, the number of unoccupied patches that are colonized has a Poisson distribution with mean d (all unoccupied patches being affected independently).

Thus, the analogous infinite-patch model has $c_{ij} = 0$ for $j < i$ and $c_{ij} = \exp(-d)d^{j-i}/(j-i)!$ ($j = i, i+1, \dots$).

Note that in contrast with our earlier infinite-state models, state 0 is *no longer absorbing*.

Infinite-patch Mainland-Island models

Let $m = d$ for the *EC*-model and $m = (1 - e)d$ for the *CE*-model.

Proposition Given $n_t = i$, n_{t+1} has the same distribution as $B + M$, where B and M are two *independent* random variables with $B \sim \text{Bin}(i, 1 - e)$ and $M \sim \text{Poisson}(m)$.

It is as if each of the i currently occupied patches remains occupied with probability $1 - e$ and a Poisson distributed number of unoccupied patches become occupied, the mean number being m (all patches being affected independently).

Infinite-patch Mainland-Island models

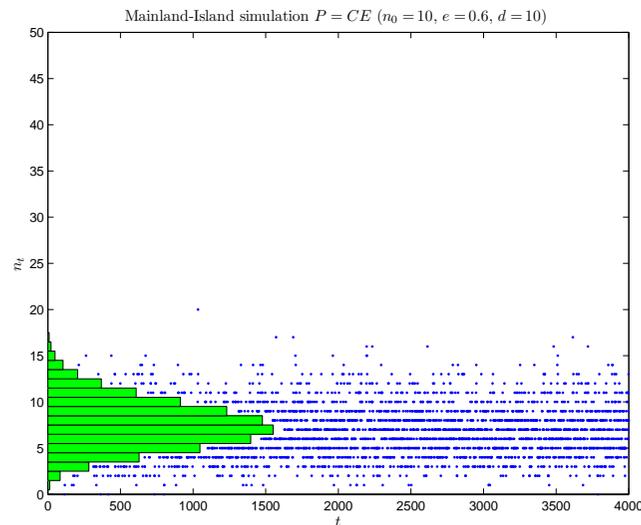
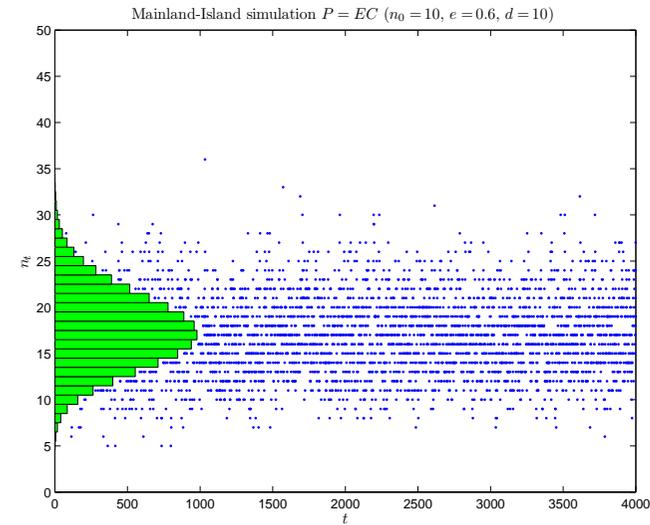
Indeed we observe that ...

Proposition The process (n_t) is a Galton-Watson process with immigration: each occupied patch has a Bernoulli $\text{Bin}(1, 1 - e)$ distributed number of offspring and in each generation there is a $\text{Poisson}(m)$ number of immigrants. The mean number of offspring is $1 - e$ (< 1) and the mean number of immigrants is m ($< \infty$).

Again we can invoke general theory.

Theorem For the infinite-patch model with parameters e and m , given $n_0 = i$ patches occupied initially, the number n_t occupied at time t has the same distribution as $B_t + M_t$, where B_t and M_t are two *independent* random variables with $B_t \sim \text{Bin}(i, (1 - e)^t)$ and $M_t \sim \text{Poisson}(m_t)$, where $m_t = (m/e)(1 - (1 - e)^t)$. The limiting distribution of n_t is $\text{Poisson}(m/e)$.

It is as if each of the i initially occupied patches remains occupied with probability $(1 - e)^t$ and a Poisson distributed number unoccupied patches become occupied, the mean number being m_t (all patches affected independently).



A measure of persistence for the Mainland-Island models is the expected time to *first* total extinction of the *island network*.

Theorem For the J -patch Mainland-Island model with parameters p and q , given $n_0 = i$ patches occupied initially, the expected time to first enter state 0 is given by

$$\begin{aligned} \mu_{i0} &= \sum_{k=1}^J \binom{J}{k} \frac{b^k}{1-a^k} - \sum_{j=0}^i \binom{i}{j} (-1)^j \sum_{k=0}^{J-i} \binom{J-i}{k} \frac{b^k (1 - \delta_{j0} \delta_{k0})}{1-a^{j+k}} \\ &= \sum_{n=0}^{\infty} \left[(1+ba^n)^J - (1-a^n)^i (1+ba^n)^{J-i} \right], \end{aligned}$$

where $a = p - q$ and $b = q/(1-p)$.

Theorem For the infinite-patch Mainland-Island model with parameters e and m , given $n_0 = i$ patches occupied initially, the expected time to first enter state 0 is always *finite* and is given by

$$\begin{aligned} \mu_{i0} &= \sum_{j=1}^i \binom{i}{j} (-1)^{j+1} \sum_{n=0}^{\infty} (1-e)^{jn} \exp\left(\frac{m}{e}(1-e)^n\right) \\ &= \sum_{n=0}^{\infty} [1 - (1 - (1-e)^n)^i] \exp\left(\frac{m}{e}(1-e)^n\right). \end{aligned}$$