Estimating Extinction Risk in Population Models

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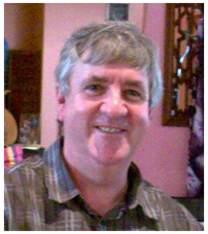


Mathematical modelling, stochastic process theory and applications: ecology, epidemiology, parasitology, telecommunications and chemical kinetics.

A current project: *Estimating extinction risk in population models*.

Ross McVinish

Lévy processes and stochastic processes displaying long memory, Bayesian nonparametrics, computation for Bayesian statistics and time series analysis.

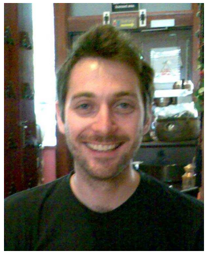
A current project: *Statistical inference for partially observed population processes*.

PhD Projects

Robert Cope (July 2009 –)

Animal Movement Between Populations Deduced from Family Trees

Daniel Pagendam (March 2007 –)



Experimental Design and Inference for Population Models

Nimmy Thaliath (February 2009 –)

Minimum Risk Optimal Portfolio Allocation: a Game Theoretic Approach

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.

A simple model

Suppose there are N patches. Let $n(t)$ be the number occupied at time t and suppose that $(n(t),\, t \geq 0)$ is a continuous-time Markov chain with transitions:

Event	Transition	Rate
Colonisation	$n \to n+1$	$\frac{c}{N} n(N-n)$
Local extinction	$n \to n-1$	en

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Colonisation	$n \to n+1$	$\frac{c}{N} n(N-n)$
Local extinction	$n \to n-1$	en

This is the *stochastic logistic (SL) model*, though it has many names, having been rediscovered several times since Feller* proposed it.

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

A simple model

It is a stochastic analogue the classical Verhulst* population model (here, for the *proportion* of occupied patches): $x_t' = cx_t(1 - x_t) - ex_t = cx_t\,(1 - \rho - x_t)$, where $\rho = e/c$, so that

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

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

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There are two equilibria: $x=0$ is stable if $c<e$, while $x = 1-\rho$ $(= 1-e/c)$ is stable if $c>e$.

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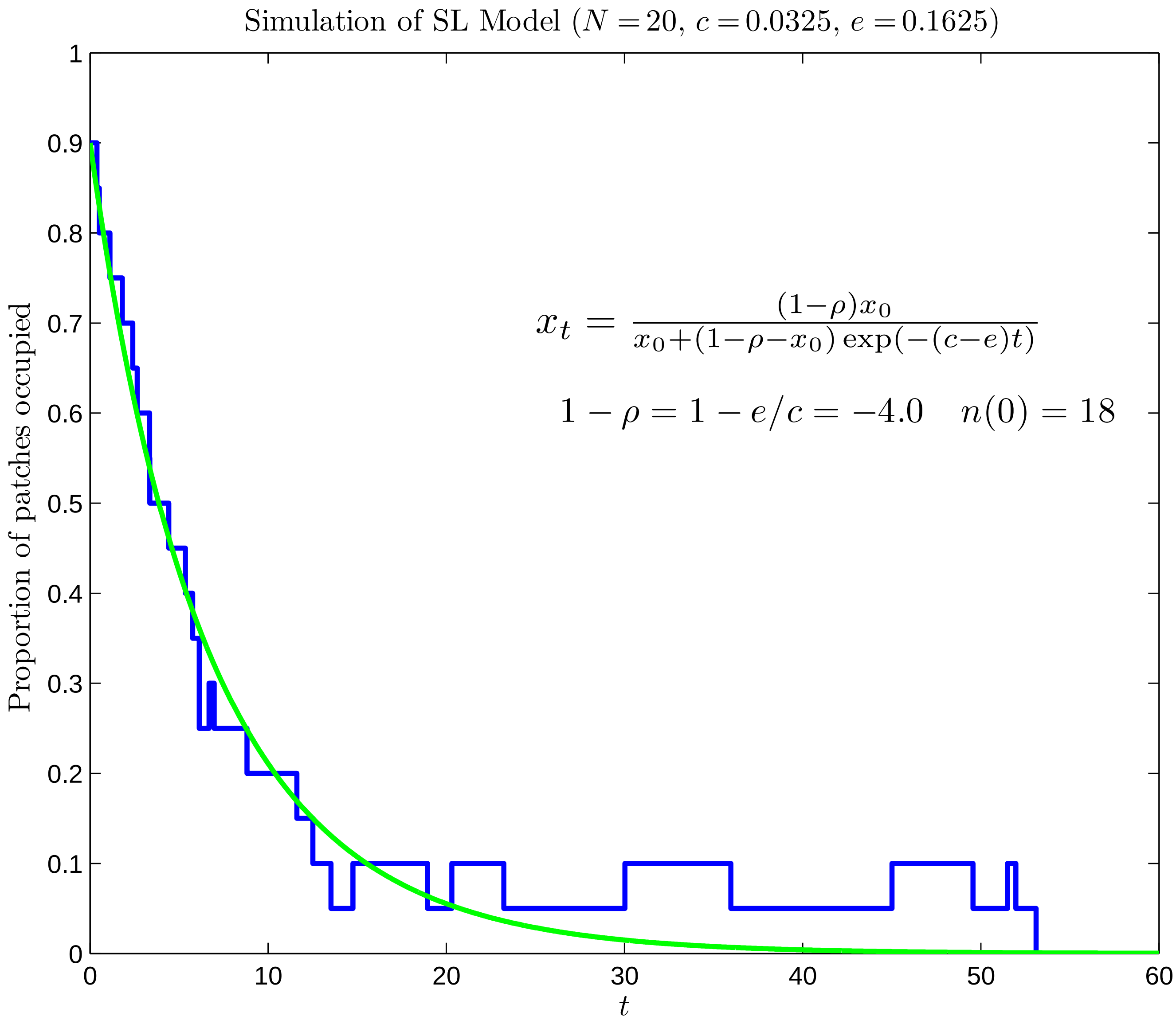
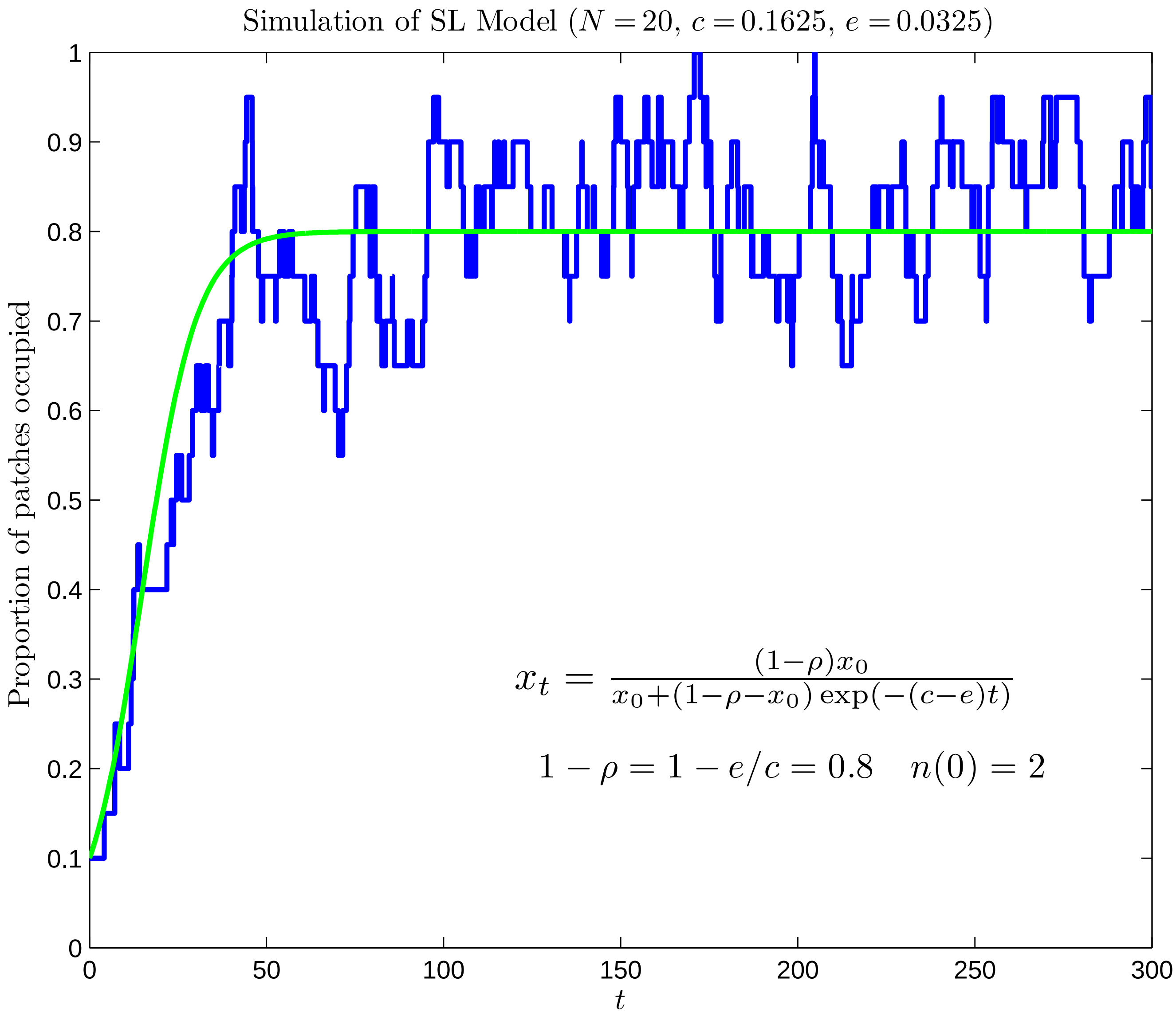
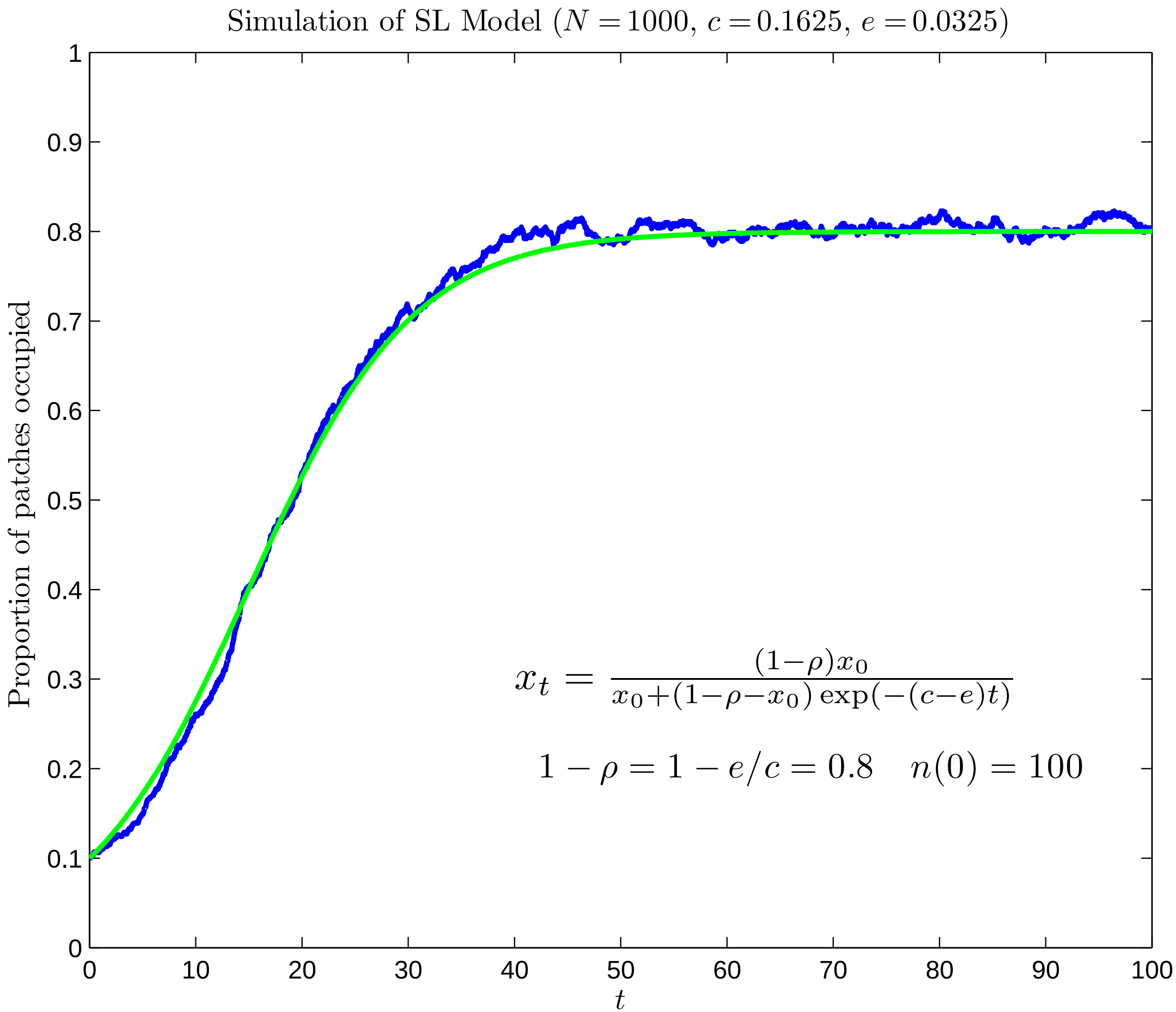
The SL model ($c < e$) $x = 0$ stable



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



The SL model ($c > e$) N large



Spatially realistic models

The state of our Markov chain is now $\boldsymbol{n} = (n_1, \ldots, n_N)$, where $n_i = 1$ if patch i is occupied and $n_i = 0$ if unoccupied. The transitions rates are:

Event	Transition	Rate
Colonisation	$\boldsymbol{n} \to \boldsymbol{n} + \boldsymbol{1}_i$	$(1 - n_i) \sum_{j \neq i} n_j \lambda_{ji}$
Local extinction	$\boldsymbol{n} \to \boldsymbol{n} - \boldsymbol{1}_i$	$n_i \lambda_{i0}$

Here $\boldsymbol{1}_i$ is the unit vector with a 1 as its i-th entry, λ_{ji} is the propagation rate from patch j to patch i and λ_{i0} is the local extinction rate.

Spatially realistic models

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Local extinction	$\boldsymbol{n} \to \boldsymbol{n} - \mathbf{1}_i$	$n_i \lambda_{i0}$

For example, $\lambda_{ij} = g e^{-\beta \sqrt{d_{ij}}}$, where g is the base propagation rate, β is the exponential dispersion parameter and d_{ij} is the distance between patches i and j, and, $\lambda_{i0} = \kappa / A_i$, where A_i is the area of patch i; the rate of colonisation decreases with distance between patches, and the rate of local extinction decreases with patch area.

Persistence times

How do we evaluate the expected time to (total) extinction?

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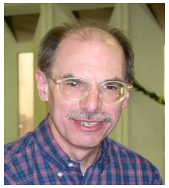
Mangel and Tier's* Fact 2: "There is a simple and direct method for the computation of persistence times that virtually all biologists can use".

*Mangel, M. and Tier, C. (1994) Four facts every conservation biologist should know about persistence. Ecology 75, 607–614.



Persistence times - my take on it

Theorem For a Markov chain with transition rates $Q = (q(m,n), m, n \in S)$, whose state space S (possibly infinite) includes a subset E which is reached with probability 1, the expected time τ_i it takes to reach E starting in state i is the minimal non-negative solution to $\sum_{i \in S} q(i,j)\tau_j + 1 = 0$, $i \notin E$, with $\tau_i = 0$ for $i \in E$.

For birth-death processes

For birth-death processes (such as the SL model) with birth rates (a_n) and death rates (b_n), the expected time $\tau_i(N)$ it takes to reach (the extinction state) 0 starting in state i is given by

$$\tau_i(N) = \sum_{j=1}^{i} \frac{1}{b_j \pi_j} \sum_{k=j}^{N} \pi_k, \quad \text{with } \tau_0(N) = 0,$$

where the "potential coefficients" (π_j) are given by $\pi_1 = 1$ and $\pi_j = \prod_{k=2}^{j} (a_{k-1}/b_k)$ for $j \geq 2$.

(This formula is valid in the infinite state-space case, replacing N by ∞.)

For the SL model

For the SL model, the expected time to total extinction starting with i patches occupied is given by

$$\tau_i(N) = \frac{1}{e} \sum_{j=1}^{i} \sum_{k=0}^{N-j} \frac{1}{j+k} \prod_{l=0}^{k-1} \left(\frac{N-j-l}{N\rho} \right).$$

(Recall that $\rho = e/c$, where c is the colonisation rate and e is the local extinction rate.)

Whilst this admits further simplification, the form given reflects the algorithm one might use to evaluate $\tau_i(N)$, the product being evaluated recursively, and the sums evaluated in such a way as to minimize round-off error.

For the SL model

This is far from being an explicit formula.

$$\tau_i(N) = \frac{1}{e} \sum_{j=1}^{i} \sum_{k=0}^{N-j} \frac{1}{j+k} \prod_{l=0}^{k-1} \left(\frac{N-j-l}{N\rho} \right).$$

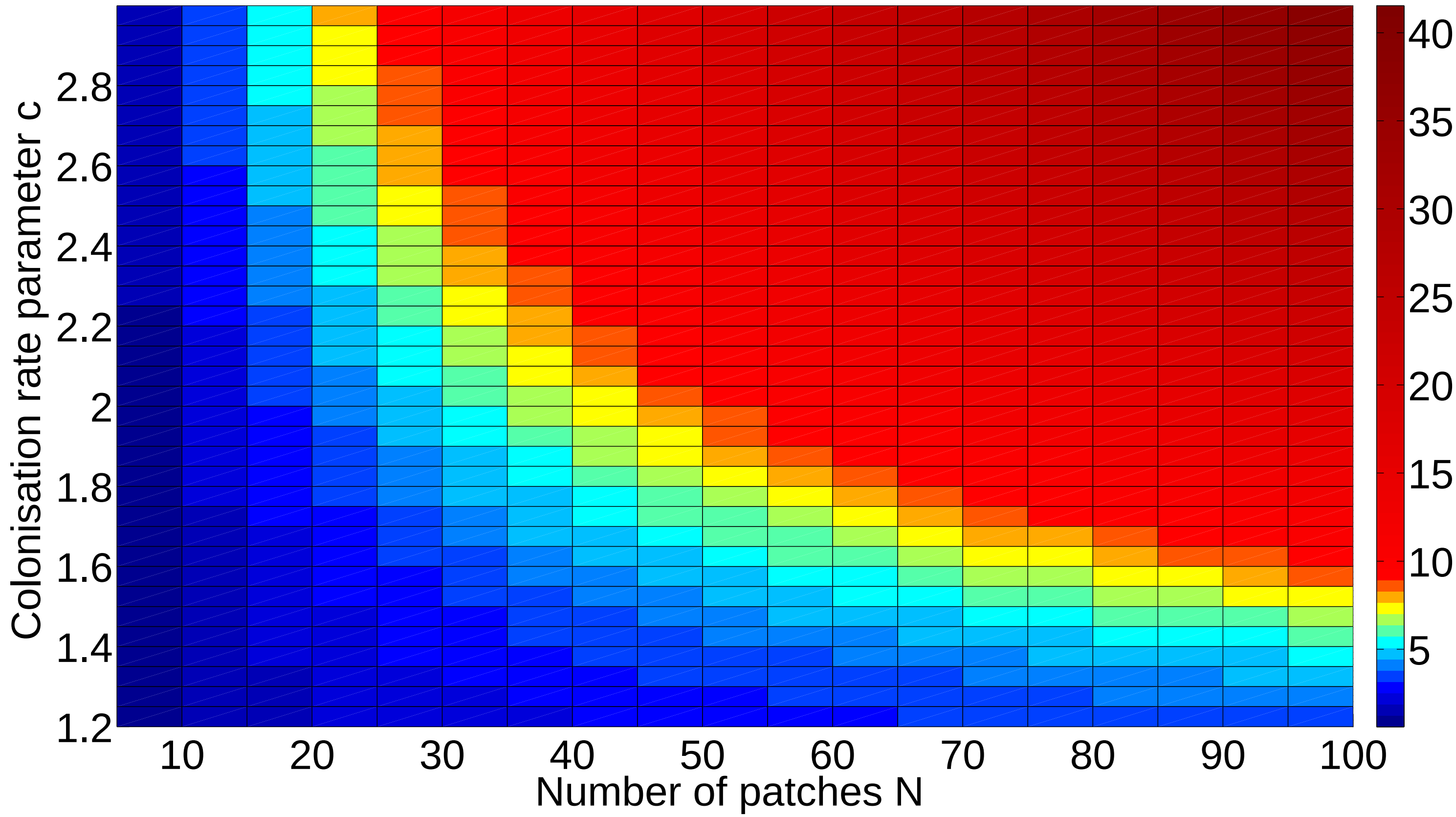
For the SL model ($\rho < 1$)

Note. $a_N \sim b_N$ here means $a_N/b_N \to 1$ as $N \to \infty$.

Theorem. If $\rho < 1$, then

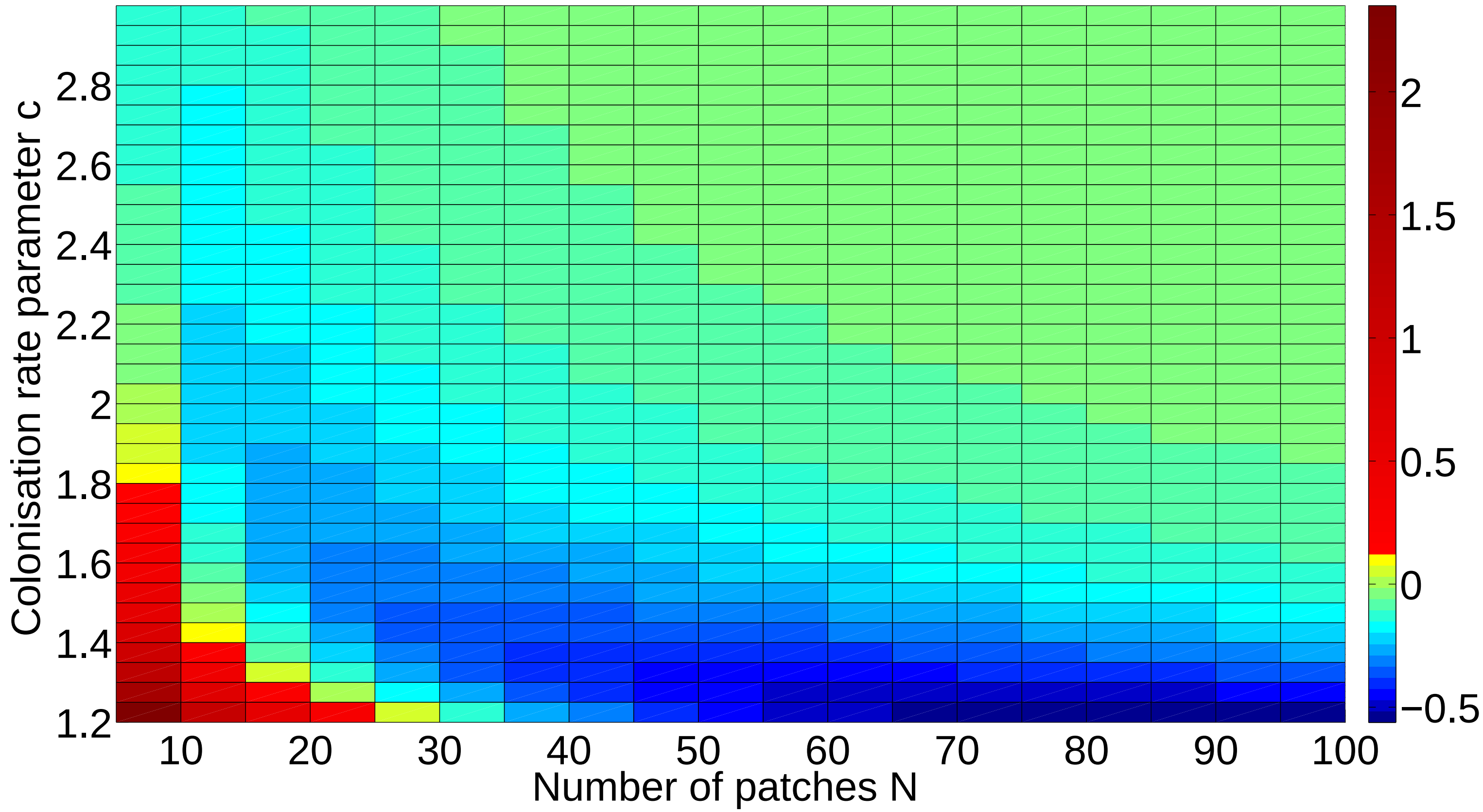
$$\tau_i(N) \sim \frac{1-\rho^i}{c(1-\rho)^2} \left(\frac{e^{-(1-\rho)}}{\rho} \right)^N \sqrt{\frac{2\pi}{N}} \quad \text{as } N \to \infty.$$

The approximation



Log_{10} of approximated expected time to extinction. The initial number of occupied patches is $n(0) = N/5$ and $e = 1$.

The approximation



Relative error in the approximation. The initial number of occupied patches is $n(0) = N/5$ and $e = 1$.

Bonus theorem: for the SL model ($\rho > 1$)

Theorem. If $\rho > 1$, then

$$\tau_1(N) \to \frac{1}{c} \log\left(\frac{\rho}{\rho - 1}\right)$$

and, for $i \geq 2$,

$$\tau_i(N) \to \frac{1}{c(\rho - 1)} \left\{ (\rho^i - 1) \log\left(\frac{\rho}{\rho - 1}\right) - \sum_{k=1}^{i-1} \frac{(\rho^{i-k} - 1)}{k} \right\}.$$