A Spatially Structured Metapopulation Model with Environmental Influence

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Metapopulations

- Populations that occupy geographically distinct locations.
- Individuals reside on patches and can migrate to other patches.
- When an individual migrates to an empty patch, they colonise it.
- Patches can become extinct when no individuals are left.
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Structured Metapopulation Models

Our Model

- Our model is an example of Kingman's [1] Markov population process.
- Define J to be the number of patches in the metapopulation and $n_i(t)$ as the number of individuals occupying patch i at time t.
- The Markov process $(n(t),\ t \geq 0)$ describing the state of the metapopulation takes values in $S_N = \{0, \ldots, N_1\} \times \cdots \times \{0, \ldots, N_J\}$.
- The only nonzero transition rates are given by

$$q(n, n + e_i) = n_i b_i \left(\frac{n_i}{N_i} \right),$$

$$q(n, n - e_i) = \phi_i n_i \lambda_{i0} + d_i n_i,$$

$$q(n, n - e_i + e_j) = \phi_i n_i \lambda_{ij} \frac{N_j - n_j}{N_j} \quad \text{for all } j \neq i.$$

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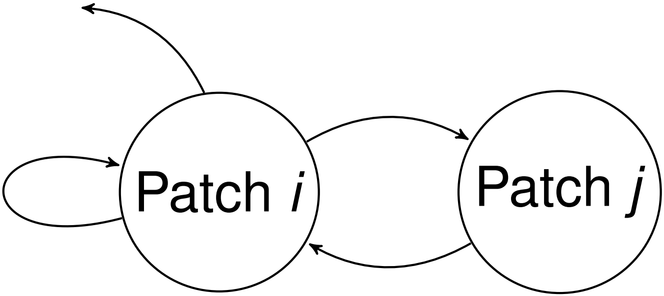
Diagram



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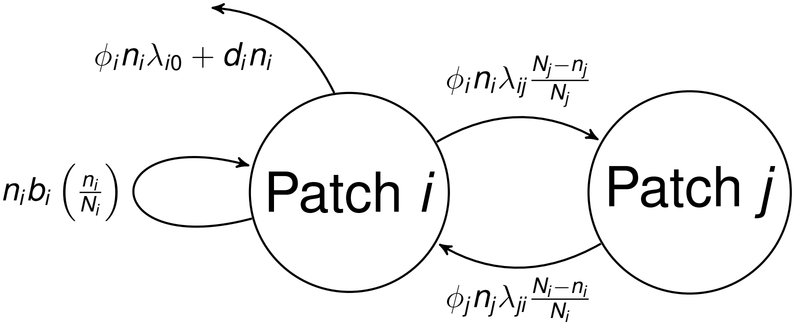
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Assumptions

We assume

(I) $\frac{N_i}{N} \to M_i$ as $N \to \infty$, where $N = \sum_j N_j$.

(II) The birth function b_i is

- Lipschitz,
- strictly decreasing on $[0, 1]$,
- $b_i(x) = 0$ for all $x \geq 1$ and
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Deterministic Limit

Theorem

If $\lim_{N\to\infty} n(0)/N = x_0$*, then, for every* $s > 0$ *and* $\delta > 0$*,*

$$\lim_{N\to\infty} \Pr\left(\sup_{t\le s}\left|\frac{n(t)}{N} - x(t,x_0)\right| > \delta\right) = 0.$$

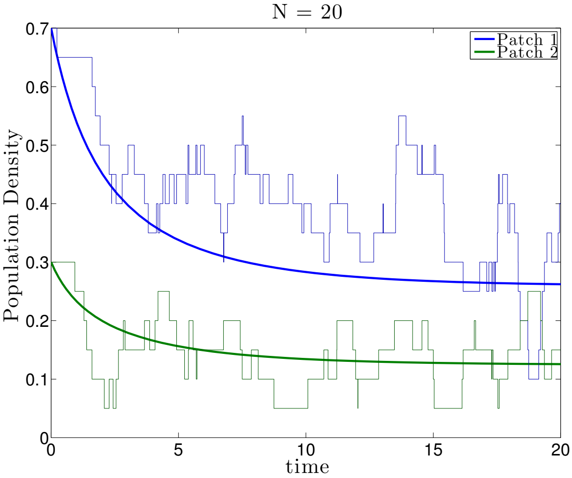
where $x(t, x_0)$ *is the solution to*

$$\frac{dx(t)}{dt} = F(x), \quad x(0) = x_0,$$

with

$$\begin{aligned} F_i(x) = &\left(b_i\left(\frac{x_i}{M_i}\right) - d_i - \phi_i\right)x_i \\ &+ \sum_{j\neq i}\left(\phi_j x_j \lambda_{ji} + \left(\phi_i x_i \lambda_{ij}\frac{x_j}{M_j} - \phi_j x_j \lambda_{ji}\frac{x_i}{M_i}\right)\right), \end{aligned}$$

Stochastic to Deterministic



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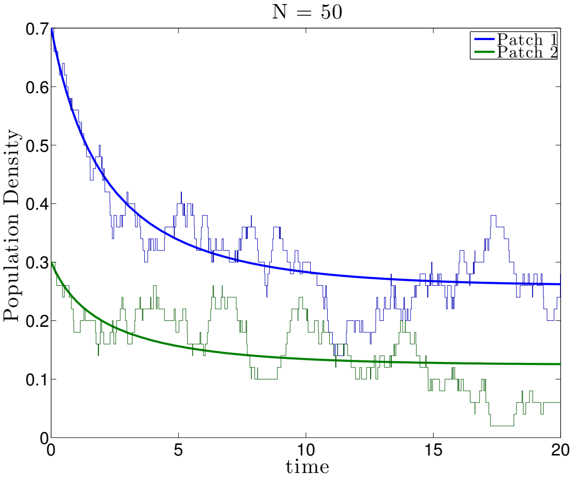

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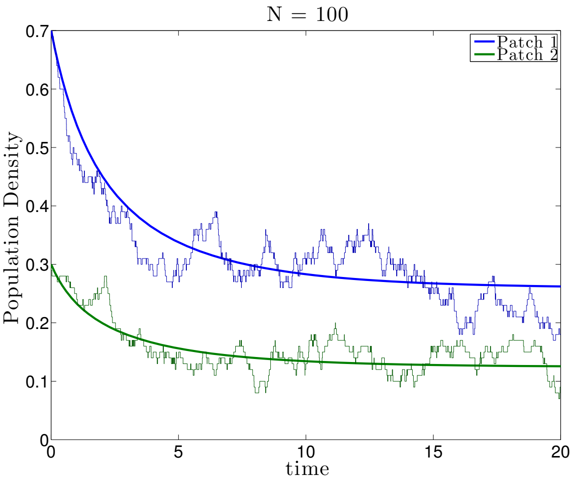

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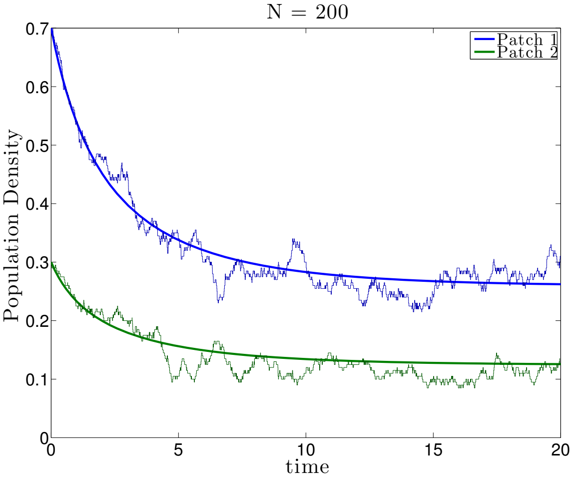

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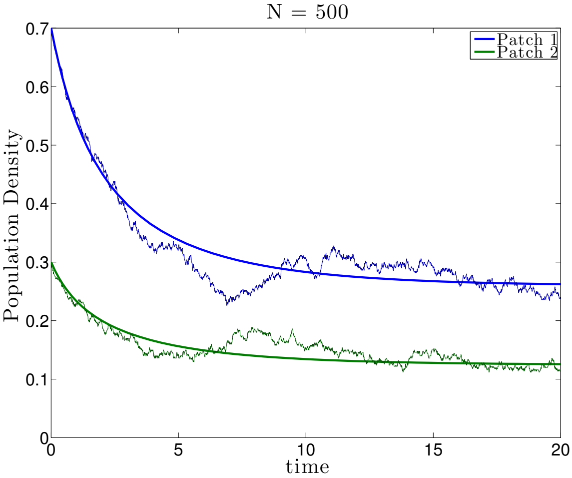

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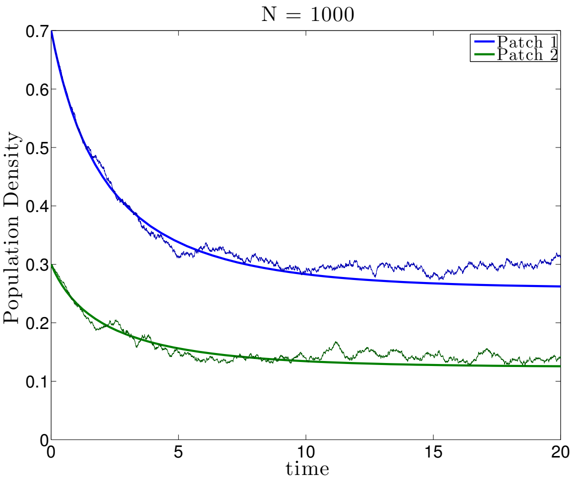

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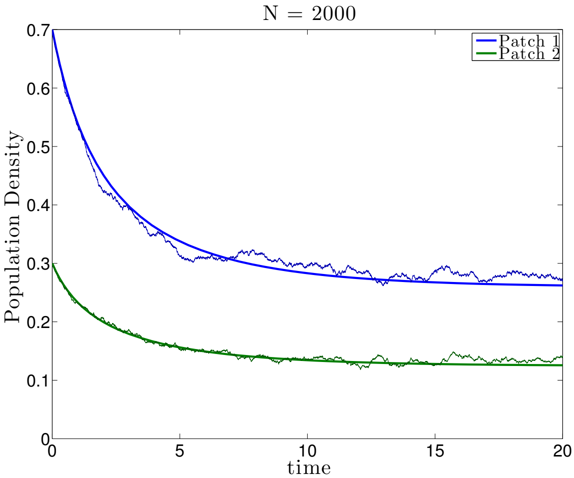

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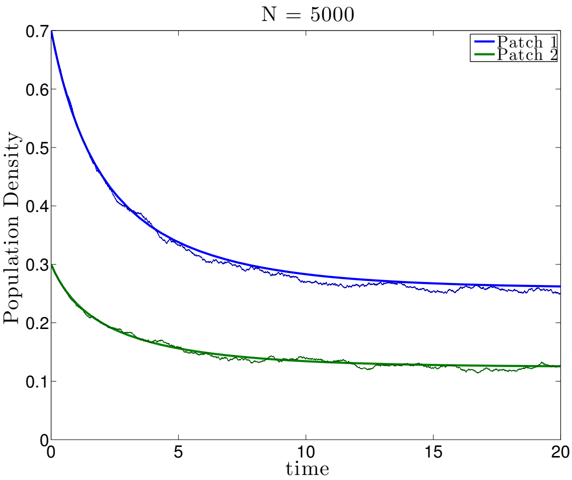

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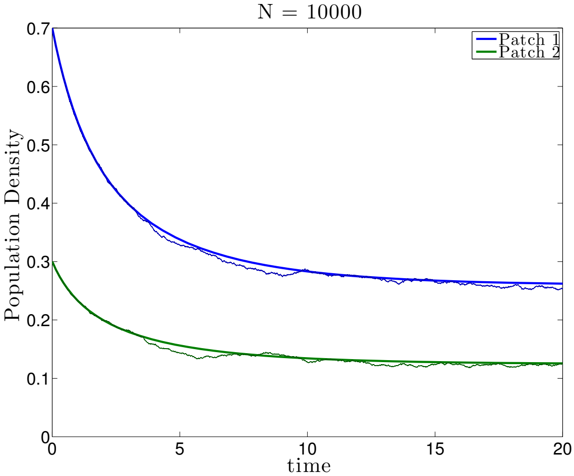

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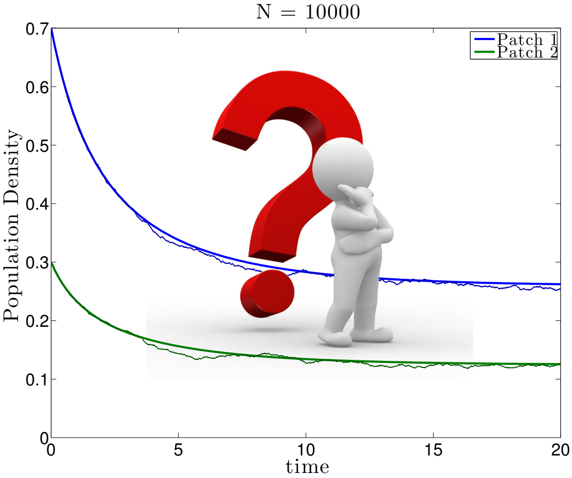

Extinction

(A) For all i and j, $\lambda_{ij} = 0$ implies $\lambda_{ji} = 0$.

(B) For all i and j, there is a finite sequence (a_k) such that $\lambda_{ia_1}\lambda_{a_1a_2}\dots\lambda_{a_mj} \neq 0$.

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Theorem

Assume (A) and (B) hold. If there exists a $y \in \mathbb{R}_+^J \backslash \{\mathbf{0}\}$ such that

$$(b_i(0) - d_i - \phi_i)\, y_i + \phi_i \sum_{j \neq i}^{J} \lambda_{ij} y_j \leq \mathbf{0}, \quad \text{for all } i, \tag{1}$$

with an inequality for at least one i, the fixed point $\mathbf{0}$ is asymptotically stable. If there is no $y \in \mathbb{R}_+^J \backslash \{\mathbf{0}\}$ satisfying (1), then $\mathbf{0}$ is unstable.

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But what happens if it is unstable?

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then there exists at least one non-zero fixed point x^* and, for all x_0 such that $\mathbf{0} < x_0 \leq x^*$, $x(t, x_0) \to x^*$.

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As long as the population is not extinct to begin with, it will persist. This theorem implies that the metapopulation will eventually be equal to or larger than x^*.

A Sufficient Condition

- We have determined a *sufficient* condition for survival.
- However, if **0** is stable, will the population necessarily go extinct?
- We introduce the following assumption

  (C) The parameters ϕ_i, λ_{ij} and M_i satisfy $\phi_i \lambda_{ij} M_i = \phi_j \lambda_{ji} M_j$ for all i, j.

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Assume (A)–(C) hold. If $\mathbf{0}$ *is stable, then* $x(t, x_0) \to \mathbf{0}$ *for all* x_0.

The metapopulation will go extinct, regardless of its initial size.

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Assume (A)–(C) hold. If $\mathbf{0}$ *is unstable, then there is a unique non-zero fixed point* x^* *and* $x(t, x_0) \to x^*$ *for all* $x_0 \neq \mathbf{0}$.

The metapopulation will persist at the level x^* provided it is not initially extinct.

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Other Behaviour

- Under assumption (C), the picture is complete.
- But is the picture the same when (C) doesn't hold?
- Is the persistence of the population purely dependent on the whether the extinction condition is satisfied?
- The Allee effect is when the initial population size determines whether the population will go extinct or persist.
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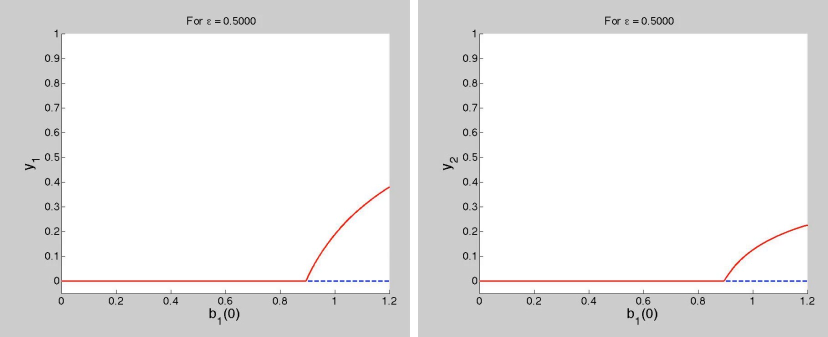
Demonstrating the Allee Effect



Demonstrating the Allee Effect

Influence due to the Environment

- Previously, we assumed that the birth, death and migration rates were constant with respect to time.
- However, is this a reasonable assumption? Is it reasonable over a long period of time?
- What happens if the environment changes?
    - Breeding seasons,
    - Migration paths cut,
    - Catastrophes,
    - And various others.
- Some influences are deterministic and can be accounted for with a similar functional law of large numbers.
- But others are stochastic.

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Model

- To account for this, we let our parameters depend on a variable that models the environment.
- Define $C(t)$ to be the configuration we are in at time t and assume there are only K configurations.
- As before, $n_i(t)$ is the number of individuals on patch i. The process $(C(t), n(t))$ has state space $\{1, \ldots, K\} \times S_N$ and the following transition rates:

$$q\left((C,n),(C,n)+(0,e_i)\right) = b_i^{(C)} \frac{n_i}{N_i}(N_i - n_i),$$

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$$q\left((C,n),(C,n)+(0,e_i)\right) = b_i^{(C)} \frac{n_i}{N_i}(N_i - n_i),$$

$$q\left((C,n),(C,n)+(0,-e_i)\right) = \phi_i^{(C)} n_i \lambda_{i0}^{(C)} + d_i^{(C)} n_i,$$

$$q\left((C,n),(C,n)+(0,-e_i+e_j)\right) = \phi_i^{(C)} n_i \lambda_{ij}^{(C)} \frac{N_j - n_j}{N_j} \qquad \forall\, j \neq i,$$

$$q\left((C,n),(C,n)+(I_i,\mathbf{0})\right) = g_i\left(C, n/N\right), \text{ for } i = 1, \ldots, k.$$

- We can use the results of Franz et al (2012) to approximate the trajectory of $Y_N(t) := (C(t), n(t)/N)$.

Piecewise-Deterministic Trajectory

Theorem

Assume g is smooth. Then if, $\lim_{N\to\infty} Y_N(0) \to y_0$*, then a.s.* $Y_N(t) \to Y(t)$*, in Skorokhod topology, where* $Y(t)$ *is given by*

$$Y(t) = y_0 + \sum_{i=1}^{K} (l_i, \mathbf{0}^T)\, \Pi_i \left(\int_0^t g_i\,(Y(s))\, ds \right) + \int_0^t V(Y(s))ds, \qquad (2)$$

$\Pi_i(\cdot)$ *are Poisson processes with unit rates and* V *has elements*

$$V_1(c,x) = 0,$$

$$V_{1+i}(c,x) = F_i^{(c)}(x) = \left(b_i^{(c)} - d_i^{(c)} - \phi_i^{(c)}\right) x_i - \frac{b_i^{(c)}}{M_i} x_i^2 + \sum_{j\neq i} \left(\phi_j^{(c)} x_j \lambda_{ji} + \left(\phi_i^{(c)} x_i \lambda_{ij}^{(c)} \frac{x_j}{M_j} - \phi_j^{(c)} x_j \lambda_{ji}^{(c)} \frac{x_i}{M_i} \right) \right).$$

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Equilibrium Behaviour

- As the environment changes, what happens to the metapopulation as t gets large?
- The metapopulation size is deterministic until a configuration transition.
- Let τ_i be the time between the $(i-1)$th and ith jump between configurations (noting that $\tau_0 = 0$), $N(t)$ be the number of jumps at time t and $J_c = \nabla F^{(c)}(0)$. Then

$$x(t) = \exp\left(J_{C(t)}\left(t - \sum_{i=1}^{N(t)} \tau_i\right)\right) x\left(\tau_{N(t)}\right)$$
$$- \int_{\tau_{N(t)}}^{t} \exp\left(J_{C(t)}\left(t-s\right)\right) \tilde{F}^{(C(s))}(x(s))ds.$$

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where $N_i(t)$ is the number of visits for configuration i at time t.

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- Define $\eta_i := \lim_{t\to\infty} N_i(t)/N(t) > 0$ and assume, for a given i that each τ_{ij} is i.i.d. Then $\frac{1}{n}\sum_{j=1}^{n}\tau_{ij} \to \mathbb{E}\tau_{ij} = \left(\sum_{j=1}^{k} g_j(i)\right)^{-1}$.

Theorem

Assume the metapopulation has K configurations and $\phi_i^{(c)}\lambda_{ij}^{(c)} = \rho_c\,\forall i,j$. Then for any $\varepsilon > 0$

$$\sum_{i=1}^{K} r_i\eta_i \left(\sum_{j=1}^{k} g_j(i)\right)^{-1} < 0 \quad\Longrightarrow\quad \lim_{t\to\infty}\mathbb{P}\left(|x(t)| > \varepsilon\right) \to 0.$$

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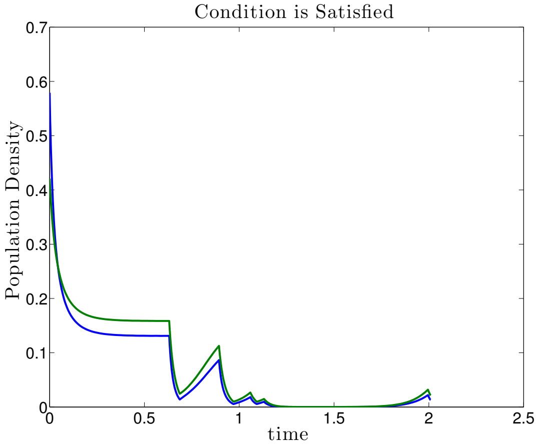
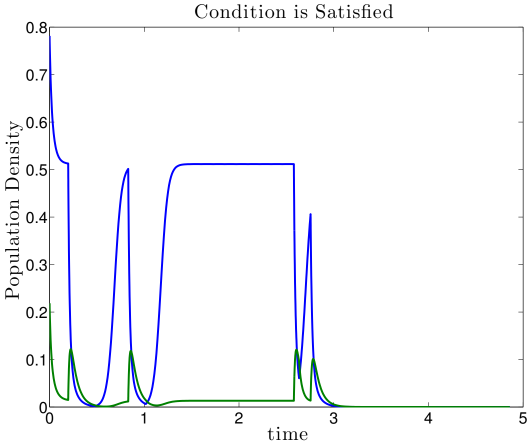
Examples



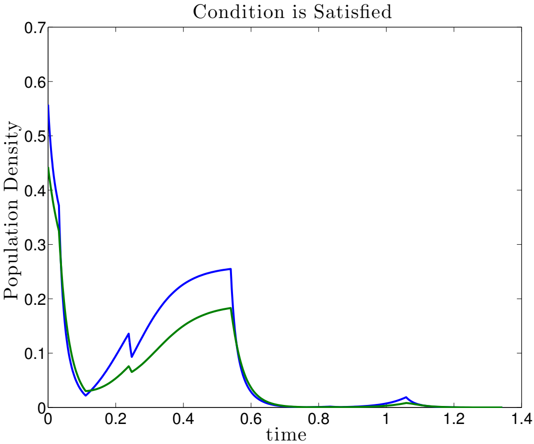
$$r_1 = 13.07,\ r_2 = -29.35,\ \mathbb{E}\tau_{1j} = 1/5,\ \mathbb{E}\tau_{2j} = 1/9$$

Examples



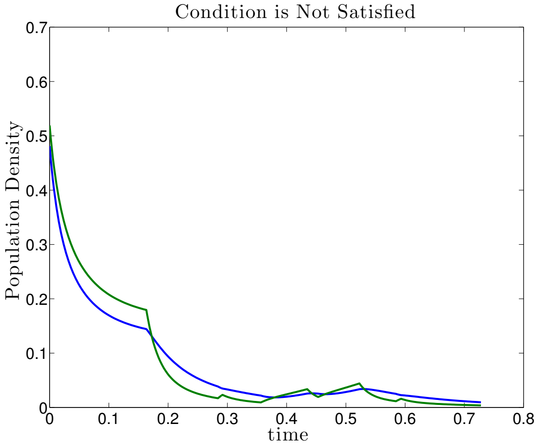
$$r_1 = 27.01,\ r_2 = -14.11,\ \mathbb{E}\tau_{1j} = 1/4,\ \mathbb{E}\tau_{2j} = 1/2$$

Examples



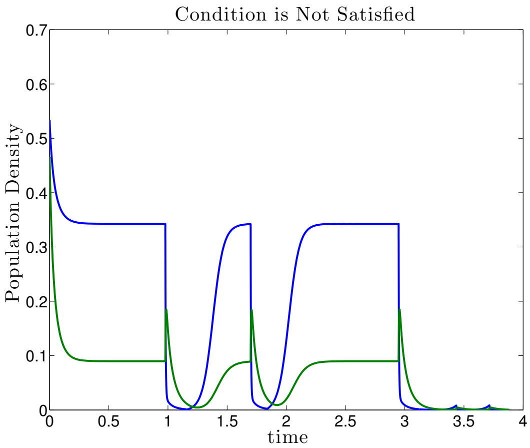
$$r_1 = 16.83,\ r_2 = -25.70,\ \mathbb{E}\tau_{1j} = 1/11,\ \mathbb{E}\tau_{2j} = 1/8$$

Examples



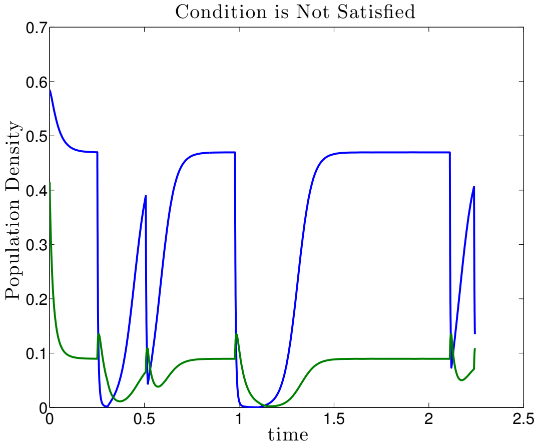
$$r_1 = 10.63,\ r_2 = -5.60,\ \mathbb{E}\tau_{1j} = 1/5,\ \mathbb{E}\tau_{2j} = 1/10$$

Examples



$$r_1 = 23.10,\ r_2 = -13.74,\ \mathbb{E}\tau_{1j} = 1,\ \mathbb{E}\tau_{2j} = 1/8$$

Examples



$$r_1 = 27.06,\ r_2 = -22.60,\ \mathbb{E}\tau_{1j} = 1,\ \mathbb{E}\tau_{2j} = 1/5$$

Summary

I have:

- Derived a metapopulation model that is structured spatially and accounts for with-in patch dynamics.
- Approximated the stochastic metapopulation by a dynamical system, and determined conditions for extinction and persistence.
- Introduced stochastic environmental influence.
- Approximated the stochastic environmental influence by a piecewise deterministic Markov process (PDMP).
- Determined conditions for extinction under a strict symmetry condition.

Future Work

In the future, I plan to:

- Determine explicitly when the Allee effect occurs for an arbitrarily sized metapopulation.
- Weaken the symmetry assumptions for the original process and the PDMP.
- Determine when the PDMP will persist.

Acknowledgments

- The ARC Centre of Excellence for MASCOS
- My supervisors & fellow postgraduate students

Questions?

AUSTRALIAN RESEARCH COUNCIL
Centre of Excellence for Mathematics
and Statistics of Complex Systems

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