Extinction in metapopulations with environmental stochasticity driven by catastrophes

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A metapopulation model

look left
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Cast of ‘characters’

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- $X = [X \ Y]^T$. The state of the metapopulation:
  - $X$ is the number of suitable patches;
  - $Y$ is the number of occupied patches.
- $r, c, e, \gamma, p$. Rates and other parameters.
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- Each unsuitable patch recovers in IID time $\sim \text{Exp}(r)$
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- Each occupied patch produces migrants at rate \(c\), which may colonise empty, suitable patches
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- $(x, y) \rightarrow (x + 1, y)$ at rate $r \left( N - x \right)$,
- $(x, y) \rightarrow (x, y + 1)$ at rate $cy \left( \frac{x}{N} - \frac{y}{N} \right)$,
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- Each local population goes extinct at rate \(e\)
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- \((x, y) \rightarrow (x, y - 1)\) at rate \(ey\).
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- \((x, y) \rightarrow (x, y - 1)\) at rate \(e_y\).

on \(S = \{(x, y) \mid x, y \in \mathbb{N}, 0 \leq y \leq x \leq N\}\).
Catastrophic Events

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$$(x, y) \rightarrow (x - (i + j), y - j) \quad \text{at rate}$$

$$\gamma \binom{x - y}{i} \binom{y}{j} p^{i+j} (1 - p)^{x-i-j}.$$

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Finite State-space Processes

When $\mathcal{N}$ is finite, we can hope to evaluate measures of interest directly.

- Extinction times (a.k.a. first passage or 'hitting' times) are almost surely finite!
- Quasi-stationary distributions exist! (limiting distribution conditional on non-extinction)
Finite State-space Processes

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If these are easy to calculate (or approximate), we can use them to analyse the system.
\( Q_C \tau = -1 \)

(Generally, take the minimal, non-negative solution.)
Extinction Times

Initial suitable patches vs. Initial occupied patches

Expected hitting times

Color scale:
- 0 - 5
- 5 - 10
- 10 - 15
- 15 - 20
- 20 - 25
- 25 - 30
- 30 - 35
- 35 - 40
- 40 - 45
- 45 - 50

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Quasi-stationary distributions

\[ Q_C m = -\lambda m \]

(\(\lambda\) is the eigenvalue with max. real part.)
Quasi-stationary distributions

Quasi-stationary distribution of states

Occupied patches

Suitable patches

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Difficulties as $N \uparrow$

Direct computation of hitting times, etc., becomes infeasible as $N$ gets large:

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Direct computation of hitting times, etc., becomes infeasible as $N$ gets large:

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- To make progress, we need good approximations: e.g. stochastic differential equations for the limit as $N \to \infty$?
A Deterministic Limit

- A little *ad hoc*ery: assume for the moment that there are no catastrophes.
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Let $X(0) = X(s, 0)$. It is possible to show that $X(s, t)/N \to U(s, t)$, satisfying the system of ODEs...

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A Deterministic Limit

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$$a(U) = \begin{bmatrix} \frac{\partial u}{\partial t} \\ \frac{\partial v}{\partial t} \end{bmatrix} = \begin{bmatrix} r(1 - u) \\ cv(u - v) - ev \end{bmatrix},$$

with initial conditions $U(s, 0) = \lim_{N \rightarrow \infty} X(s, 0)/N$. (Kurtz, 1970)
Catastrophes in the Limit

Treating catastrophes as a separate component...

- The arrival rate of catastrophes is unaffected by scaling.
- As $N \rightarrow \infty$, if $T_1$ is a catastrophe time,

$$\frac{X(s, T_1)}{N} \xrightarrow{P} (1 - p) U(s, T_1 -).$$
A Stochastic Integral Equation

The limiting, scaled process:

\[ dU(s, t) = a(U(s, t))dt + \int_M c(U(s, t), m) P[dm, dt; \gamma] \]

- \( c(U, dm) \) describes effect of catastrophes
- Poisson random measure \( P \) describes arrival of catastrophes and their magnitudes, \( m \).
- Generalised Itô fomula gives first passage times. (Gihman & Skorohod, 1972)
First passage times, $\tau_G(U_0)$, into a closed set $S \setminus G$ (i.e. out of $G$), starting from $U_0$, are a twice continuously differentiable solution, $g(U)$, to

\[
(Lg)(U) = -1, \quad U \in G
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g(U) = 0, \quad U \notin G,
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$$\begin{align*}
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\end{align*}$$

- In the present case, $(Lh)(U)$ is given by

$$\begin{align*}
(Lh)(U) &= \nabla h(U) \cdot a(U) - \gamma h(U) + \gamma h((1-p)U).
\end{align*}$$
Slightly different conditions:

- $g(U)$ should be \textit{continuous} along all trajectories $U(s, t)$, and piecewise smooth along other smooth paths.

- $g(U)$ should be \textit{bounded} for all $U$. 
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- $g(\mathbf{U})$ should be *continuous* along all trajectories $\mathbf{U}(s, t)$, and piecewise smooth along other smooth paths.
- $g(\mathbf{U})$ should be *bounded* for all $\mathbf{U}$.

Solve in ‘steps’: $G_n$ is the region from which at least $n$ catastrophes are needed to leave $G$. 
The solution has the form

\[
e^{-\gamma t} g(U(s, t)) = -\int_0^t \gamma e^{-\gamma r} g((1 - p)U(s, r)) \, dr
- \gamma^{-1} [1 - e^{-\gamma t}] + C_1(s),
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but we want a bounded solution, so set

\[ C_1(s) = \int_0^\infty \gamma e^{-\gamma r} g((1 - p)U(s, r)) \, dr + \gamma^{-1}. \]
Hence (along trajectories that remain within $G$)

$$g(U(s, t)) = \frac{1}{\gamma} + e^{\gamma t} \int_{t}^{\infty} \gamma e^{-\gamma r} g((1 - p)U(s, r)) dr.$$
Hence (along trajectories that remain within \( G \))

\[
g(\mathbf{U}(s, t)) = \frac{1}{\gamma} + e^{\gamma t} \int_{t}^{\infty} \gamma e^{-\gamma r} g\left((1 - p)\mathbf{U}(s, r)\right) dr.
\]

Clearly, \( C_1(s) = g(s, 0) \). We can also confirm:
Solving First Passage Times

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- if $G = G_1$, $g(U) = \gamma^{-1}$ for all $U$ on trajectories remaining in $G$;
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- if $G = G_1$, $g(U) = \gamma^{-1}$ for all $U$ on trajectories remaining in $G$;
- if $U_\infty = \lim_{t \to \infty} U(s, t)$ is in $G$, then $g(s, \infty-) = \gamma^{-1} + g((1 - p)U_\infty)$. 
Solutions: A Special Case

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\[ g(U(s, t)) = \gamma^{-1}, \text{ for all trajectories not leaving } G_1 \text{ in finite time}, \]
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If the fixed point is on the first ‘step’,

- \( g(U(s, t)) = \gamma^{-1} \), for all trajectories not leaving \( G_1 \) in finite time,

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- solutions for trajectories heading out of \( G \) using the deterministic hitting time and a truncated exponential law, and

- a system of DEs \([\partial u/\partial t, \partial v/\partial t, \partial g/\partial t]\) gives first passage times for trajectories starting on higher steps.
The general case is a little more difficult.

- Recall that

\[
g(U(s,t)) = \frac{1}{\gamma} + e^{\gamma t} \int_t^\infty \gamma e^{-\gamma r} g((1 - p)U(s,r)) \, dr.
\]
The general case is a little more difficult.

- Define a mapping \( K : H \to H \),

\[
K(f(s,t)) := \frac{1}{\gamma} + e^{\gamma t} \int_t^\infty \gamma e^{-\gamma r} f ((1 - p)U(s,r)) \, dr,
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$$K(f(s,t)) := \frac{1}{\gamma} + e^{\gamma t} \int_t^\infty \gamma e^{-\gamma r} f((1 - p)U(s,r)) \, dr,$$

with $H$ being the set of bounded functions $f : G \to \mathbb{R}_+$ under the condition

$$f(U(s,t)) \geq \frac{1}{\gamma} + e^{\gamma t} \int_t^\infty \gamma e^{-\gamma r} f((1 - p)U(s,r)) \, dr.$$
Solutions: General Case

- $f \geq K(f)$, $f \in H$, so we might hope that the iterative application of $K$ would lead to a fixed point, but...
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- \( f \geq K(f), \ f \in H \), so we might hope that the iterative application of \( K \) would lead to a fixed point, but...

- \( H \neq \emptyset \) is equivalent to the existence of a solution, \( h \), to

\[
(Lh)(U) \leq -1, \ U \in G
\]

\[
h(U) \geq 0, \ U \notin G,
\]

\( \equiv \) to a condition from Gihman & Skorohod for the existence of a solution \( \tau_G \leq h \).
• Is $H$ empty? No! Hanson & Tuckwell (1981) analyse a similar 1D model for $u(s,t)$. 
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- In our 2D model, $u$ does not depend on $v$, so:
  1. take $G' \supset G$ so that the first passage out of $G''$ only depends on $u$;
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(i) take $G' \supset G$ so that the first passage out of $G'$ only depends on $u$;

(ii) find $h(u) = \tau_{G'}(u)$ (using H & T);

(iii) then $h(u)$ satisfies the inequality condition for all $v$ such that $(u,v) \in S$. 
Thanks

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