Extinction in metapopulations with environmental stochasticity driven by catastrophes

Ben Cairns

bjc@maths.uq.edu.au

ARC Centre of Excellence for Mathematics and Statistics of Complex Systems.
Department of Mathematics, The University of Queensland.
Metapopulations are ‘populations of populations’, existing in a system of habitat patches:

- Example 1: ... on ‘islands’.
- Example 2: ... in successional habitat.

Environmental events may reduce available habitat, which then gradually recovers.

We will discuss a 2-D Markov chain model for a metapopulation, incorporating stochastic habitat dynamics driven by catastrophes.
Paired metapopulation-habitat states make the following ‘demographic’ transitions:

\[(x, y) \rightarrow (x + 1, y) \quad \text{at rate} \quad r \left( N - x \right), \]

\[(x, y) \rightarrow (x, y + 1) \quad \text{at rate} \quad cy \left( \frac{x}{N} - \frac{y}{N} \right), \]

\[(x, y) \rightarrow (x, y - 1) \quad \text{at rate} \quad ey, \]

on \( S = \{(x, y) \mid x, y \in \mathbb{N}, 0 \leq y \leq x \leq N\} \).
Catastrophic jumps occur at a constant rate, \( \gamma \), affecting each habitat patch independently:

\[
(x, y) \rightarrow (x - (i + j), y - j)
\]

at rate

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

- \( p \) is the probability that each patch is rendered unsuitable by a catastrophe.
Finite State-space Processes

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

- Extinction (first passage) times are almost surely finite!
- Quasi-stationary distributions exist!

If these are easy to calculate (or approximate, e.g. matrix-analytic methods), we can use them to assess the characteristics of the system.
Quasi-stationary distributions

Quasi-stationary distribution of states

Occupied patches

Suitable patches

x $10^{-3}$

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Assume for the moment that there are no catastrophes.

It is possible to show that \( \frac{X(s, t)}{N} \to U(s, t) \), which satisfies a system of ODEs:

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

with initial conditions

\[ U(s, 0) = \lim_{N \to \infty} \frac{X(s, 0)}{N}. \] (Kurtz, 1970)
• Treat catastrophes as a separate component.
• The arrival rate of catastrophes is unaffected by scaling.
• As $N \to \infty$, if $T_1$ is a catastrophe time,

$$\frac{X(s, T_1)}{N} \xrightarrow{P} (1 - p)U(s, T_1 - ).$$
The limiting, scaled process:

\[ dU(s, t) = a(U(s, t))dt + \int_{\mathcal{M}} c(U(s, t), m) \mathcal{P}[dm, dt; \gamma] \]

- \( c(U, dm) \) describes effect of catastrophes
- Poisson random measure \( \mathcal{P} \) 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

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

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

$$
(Lh)(U) = \nabla h(U) \cdot a(U) - \gamma h(U) + \gamma h((1-p)U).
$$
Slightly different conditions:

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

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

\[ e^{-\gamma t} g(U(s, t)) = - \int_0^t \gamma e^{-\gamma r} g((1 - p)U(s, r)) \, dr \]

\[ - \gamma^{-1} [1 - e^{-\gamma t}] + C_1(s), \]

but we want a bounded solution, so set

\[ C_1(s) = \int_0^\infty \gamma e^{-\gamma r} g((1 - p)U(s, r)) \, dr + \gamma^{-1}. \]
Solving First Passage Times

Hence (along trajectories that remain within $G$)

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

Clearly, $C_1(s) = g(s, 0)$. We can also confirm:

- 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 $g(s, \infty^-) = \gamma^{-1} + g((1 - p)U_\infty)$. 
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,

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

- the 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.
Solutions: A Special Case
The general case is a little more difficult.

- Define a mapping $K : H \rightarrow H$,

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

with $H$ being the set of bounded functions $f : G \rightarrow \mathbb{R}_+$ 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...

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

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

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

\[
\equiv \text{to a condition from Gihman & Skorohod for the existence of a solution } \tau_G \leq h.
\]
Solutions: General Case

- Is $H$ empty? No! Hanson & Tuckwell (1981) analyse a similar 1D model for $u(s, t)$.

- In our 2D model, $u$ does not depend on $v$, so:
  (i) take $G' \supset G$ so that the first passage out of $G'$ only depends on $u$;
  (ii) find $h(u) = \tau_{G'}(u)$;
  (iii) then $h(u)$ satisfies the inequality condition for all $v$ such that $(u, v) \in S$. 

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