Extinction in metapopulations with environmental stochasticity driven by catastrophes

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Background and Summary

- 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.

Demographic Events

Paired metapopulation-habitat states make the following ‘demographic’ transitions:

$$\begin{aligned}
(x,y) &\to (x+1,y) && \text{at rate} && r\,(N-x)\,, \\
(x,y) &\to (x,y+1) && \text{at rate} && cy\left(\frac{x}{N}-\frac{y}{N}\right), \\
(x,y) &\to (x,y-1) && \text{at rate} && ey,
\end{aligned}$$

on $S = \{(x,y) \mid x,y \in \mathbb{N}, 0 \le y \le x \le N\}$.

Catastrophic Events

Catastrophic jumps occur at a constant rate, γ, affecting each habitat patch independently:

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

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

- p is the probability that each patch is rendered unsuitable by a catastrophe.

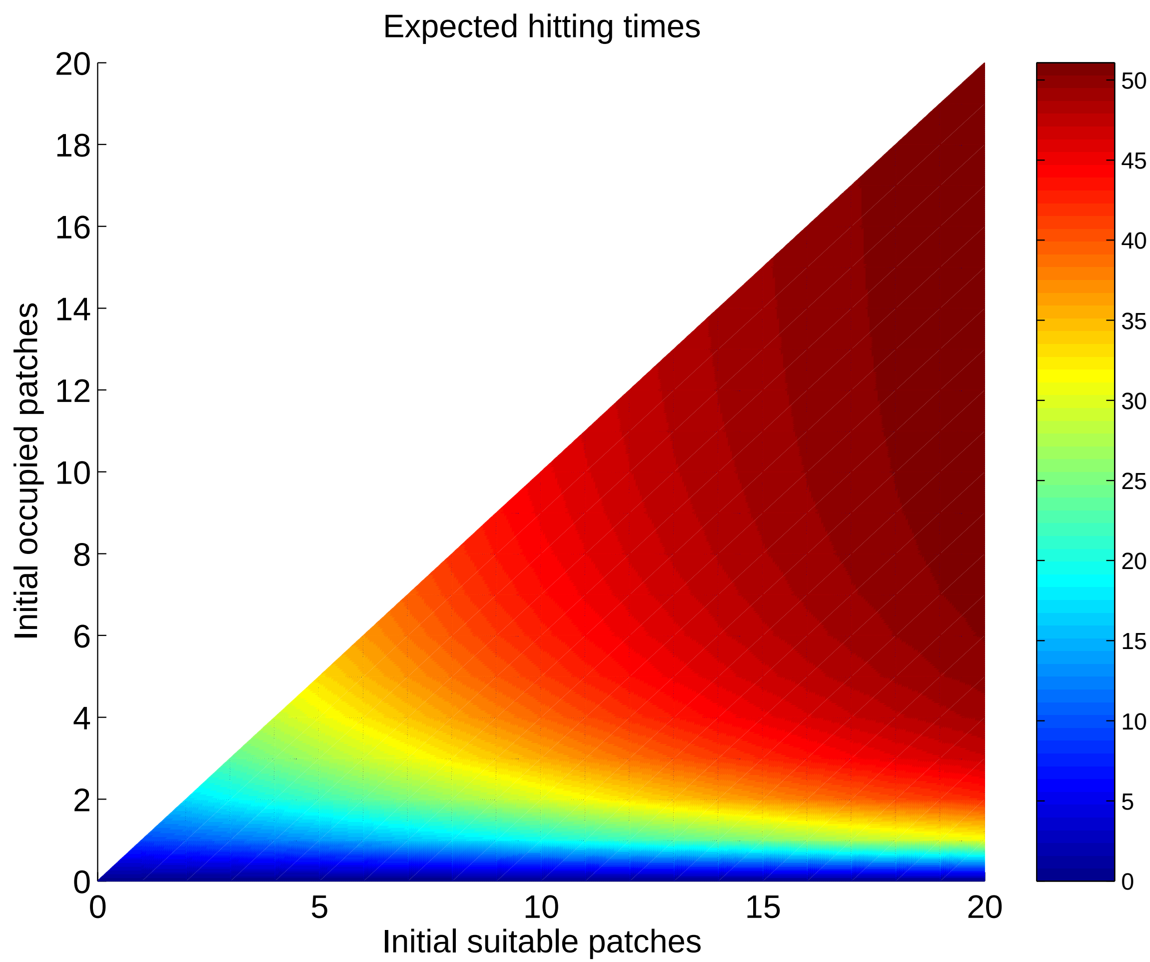
Finite State-space Processes

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

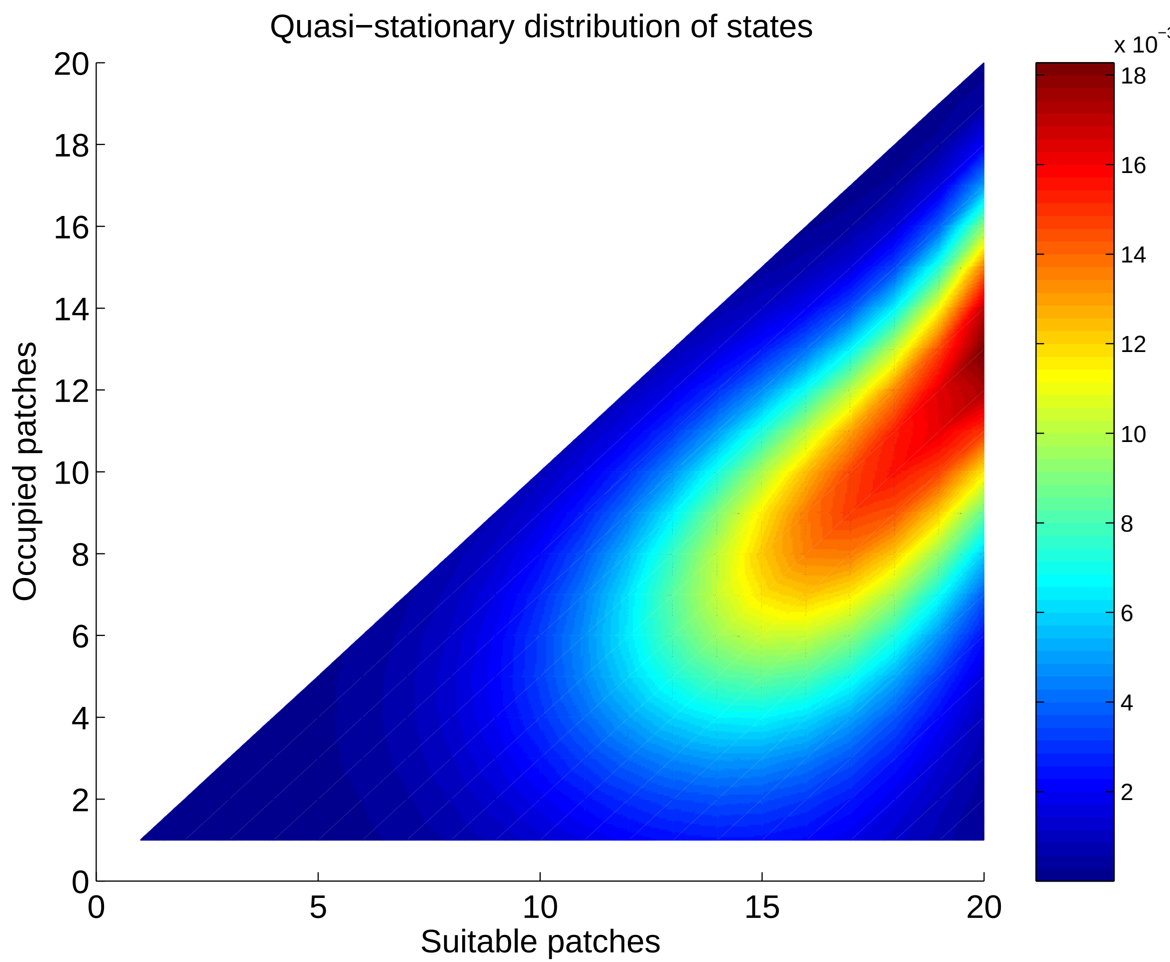
- Extinction (first passage) times are almost surely finite!
- Quasi-stationary distributions exist!

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

Extinction Times



Quasi-stationary distributions



A Deterministic Limit

- Assume for the moment that there are no catastrophes.
- It is possible to show that $\mathbf{X}(s,t)/N \to \mathbf{U}(s,t)$, which satisfies a system of ODEs:

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

with initial conditions $\mathbf{U}(s,0) = \lim_{N\to\infty} X(s,0)/N$. (Kurtz, 1970)

Catastrophes in the Limit

- 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,

$$\frac{\mathbf{X}(s, T_1)}{N} \xrightarrow{P} (1-p)\mathbf{U}(s, T_1-).$$

A Stochastic Integral Equation

The limiting, scaled process:

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

- $\mathbf{c}(\mathbf{U},d\mathbf{m})$ describes effect of catastrophes
- Poisson random measure $\mathcal{P}$ describes arrival of catastrophes and their magnitudes, $\mathbf{m}$.
- Generalised Itô fomula gives first passage times. (Gihman & Skorohod, 1972)

First Passage Times

First passage times, $\tau_G\big(\mathrm{U}_0\big)$, into a closed set $S\backslash G$ (i.e. out of G), starting from U_0, are a twice continuously differentiable solution, $g(\mathbf{U})$, to

$$(Lg)(\mathbf{U}) = -1, \mathbf{U} \in G$$
$$g(\mathbf{U}) = 0, \mathbf{U} \notin G,$$

- In the present case, $(Lh)(\mathbf{U})$ is given by

$$(Lh)(\mathbf{U}) = \nabla h(\mathbf{U})\cdot\mathbf{a}(\mathbf{U}) - \gamma h(\mathbf{U}) + \gamma h\big((1-p)\mathbf{U}\big).$$

Solving First Passage Times

Slightly different conditions:

- $g(\mathbf{U})$ 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.

Solving First Passage Times

The solution has the form

$$e^{-\gamma t} g\big(\mathbf{U}(s,t)\big) = -\int_0^t \gamma e^{-\gamma r} g\big((1-p)\mathbf{U}(s,r)\big)\,dr$$
$$-\gamma^{-1}\left[1-e^{-\gamma t}\right] + C_1(s),$$

but we want a bounded solution, so set

$$C_1(s) = \int_0^\infty \gamma e^{-\gamma r} g\big((1-p)\mathbf{U}(s,r)\big)\,dr + \gamma^{-1}.$$

Solving First Passage Times

Hence (along trajectories that remain within G)

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

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

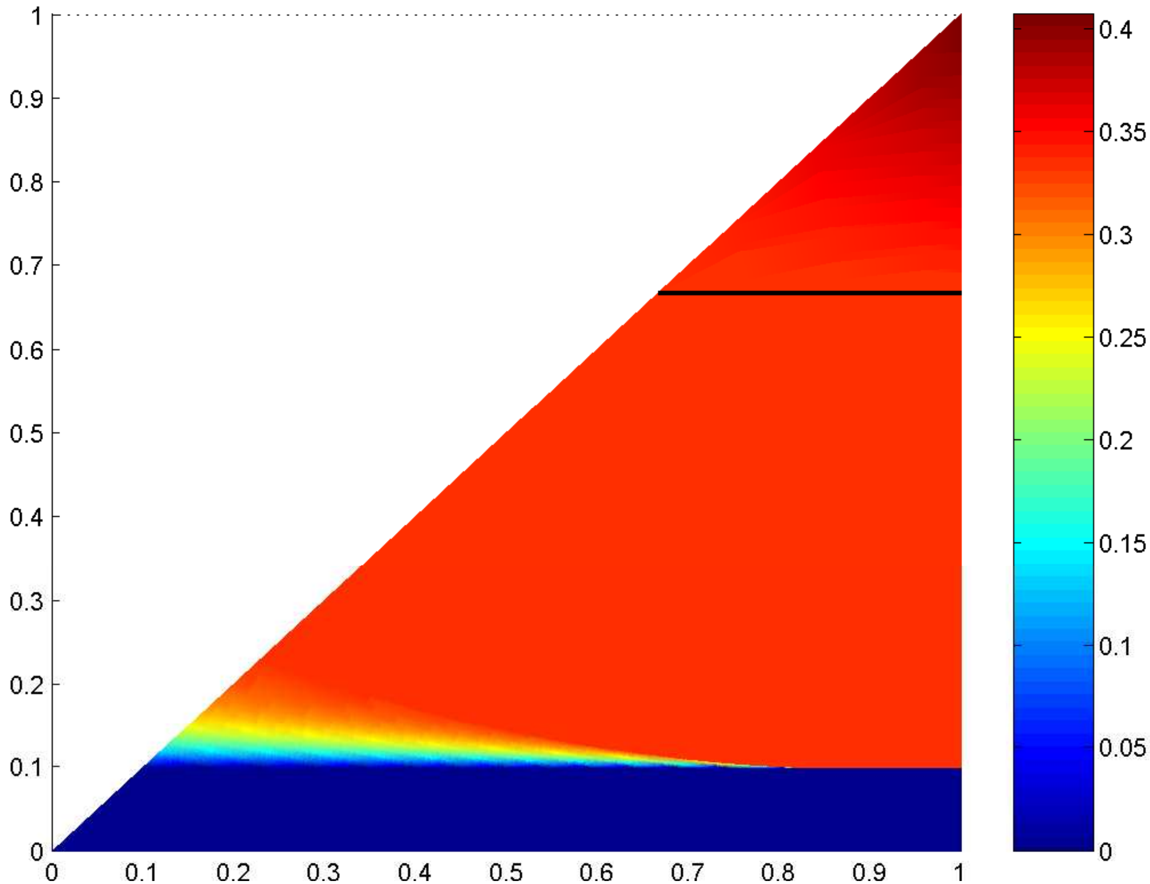
- if $G = G_1$, $g(\mathbf{U}) = \gamma^{-1}$ for all $\mathbf{U}$ on trajectories remaining in G;
- if $\mathbf{U}_\infty = \lim_{t\to\infty} \mathbf{U}(s,t)$ is in G, then $g(s,\infty-) = \gamma^{-1} + g\big((1-p)\mathbf{U}_\infty\big)$.

Solutions: A Special Case

If the fixed point is on the first ‘step’,

- $g\big(\mathbf{U}(s,t)\big) = \gamma^{-1}$, 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



Solutions: General Case

The general case is a little more difficult.

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

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

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

$$f\big(\mathbf{U}(s,t)\big) \geq \frac{1}{\gamma} + e^{\gamma t} \int_t^{\infty} \gamma e^{-\gamma r} f\left((1-p)\mathbf{U}(s,r)\right) dr.$$

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

$$(Lh)(\mathbf{U}) \leq -1, \mathbf{U} \in G$$
$$h(\mathbf{U}) \geq 0, \mathbf{U} \notin G,$$

$\equiv$ 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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