

# Limit theorems for metapopulation processes subject to 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.

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  - Species utilising successional habitat depend on habitat dynamics;
  - Some species appear to have a negative impact on their local habitat.

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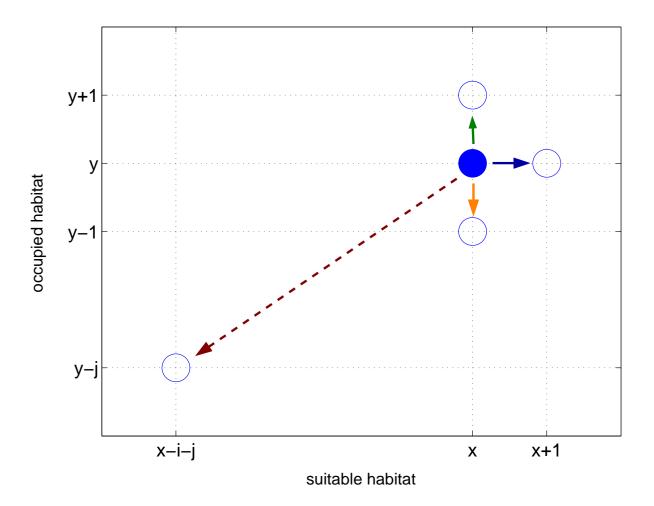
- *N* be the total number of habitat patches,
- $\mathbf{X} = [X \ Y]^T$  be the state of the metapopulation, where
  - *X* is the number of suitable patches;
  - *Y* is the number of occupied patches.

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#### The model of the half-hour...

# (Habitat dynamics driven by catastrophes.)

#### The model of the half-hour...



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• Each unsuitable patch recovers in IID time  $\sim Exp(r)$ 

• Each unsuitable patch recovers at rate *r* 

•  $(x, y) \rightarrow (x + 1, y)$  at rate r(N - x),

- $(x,y) \rightarrow (x+1,y)$  at rate r(N-x),
- Each occupied patch produces migrants at rate *c*, which may colonise empty, suitable patches

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- Each local population goes extinct at rate *e*

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$$(x, y) \rightarrow (x, y - 1)$$
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on  $S = \{(x, y) \mid x, y \in \mathbb{N}, 0 \le y \le x \le N\}.$ 

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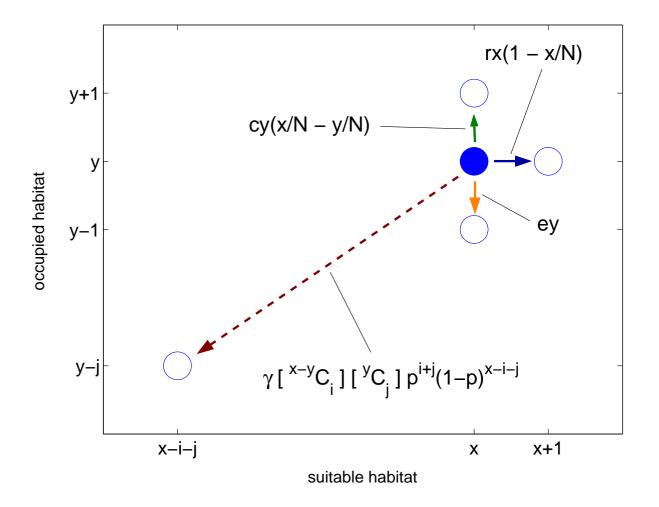
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$$(x,y) \to (x - (i+j), y - j)$$
 at rate  
 $\gamma \begin{pmatrix} x - y \\ i \end{pmatrix} \begin{pmatrix} y \\ j \end{pmatrix} p^{i+j} (1-p)^{x-i-j}.$ 

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#### The model again...



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### **Finite State-space Processes**

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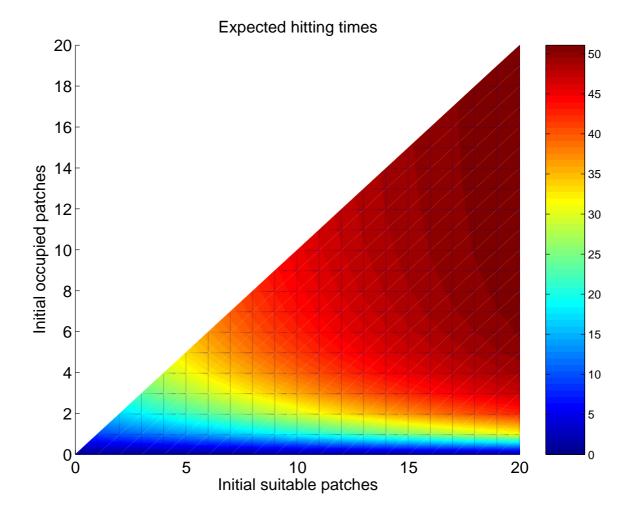
If N is small, (e.g.) expected extinction times are easy to calculate.

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#### **Extinction Times**



### **Extinction Times**



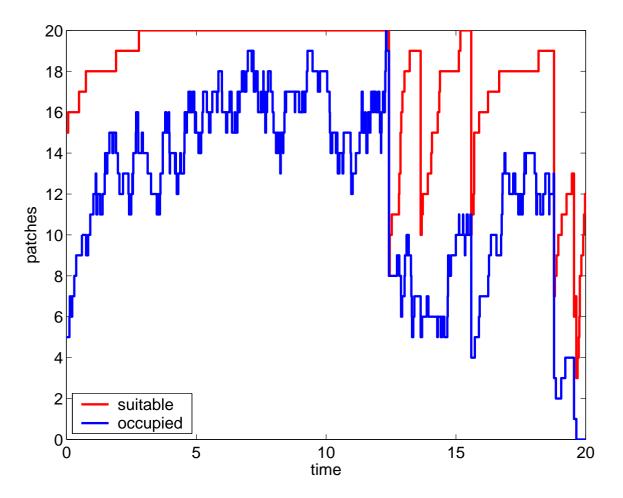
Direct computation of hitting times, etc., becomes infeasible as N gets large:  $\#S = \frac{1}{2}(N+1)(N+2).$  Direct computation of hitting times, etc., becomes infeasible as N gets large:  $\#S = \frac{1}{2}(N+1)(N+2).$ 

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

### **Simulations**

# Simulations can inform our intuition about the behaviour of a process, and suggest possible approximations.

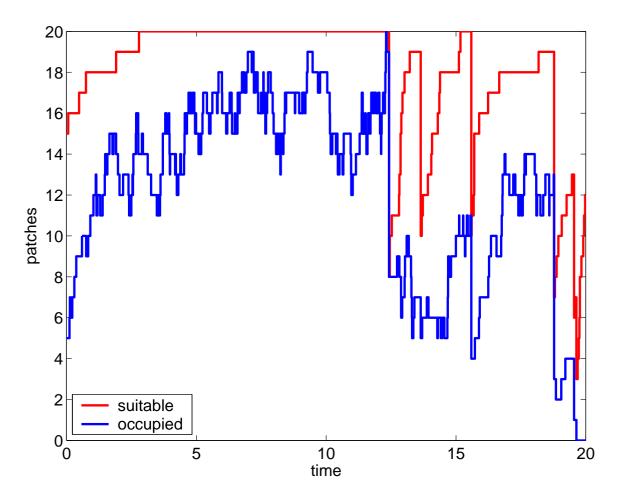
#### **Simulations**



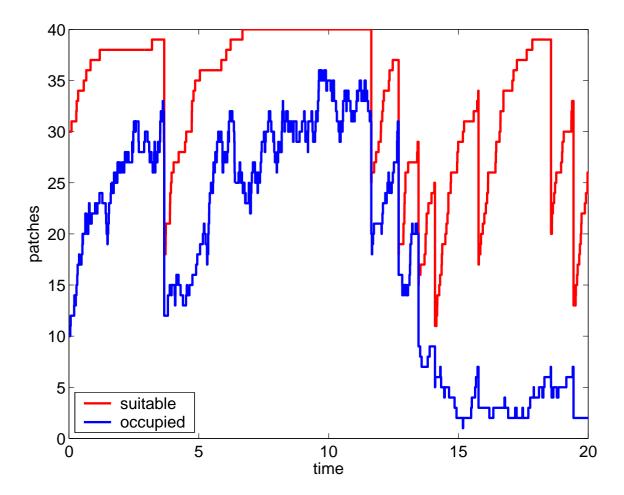
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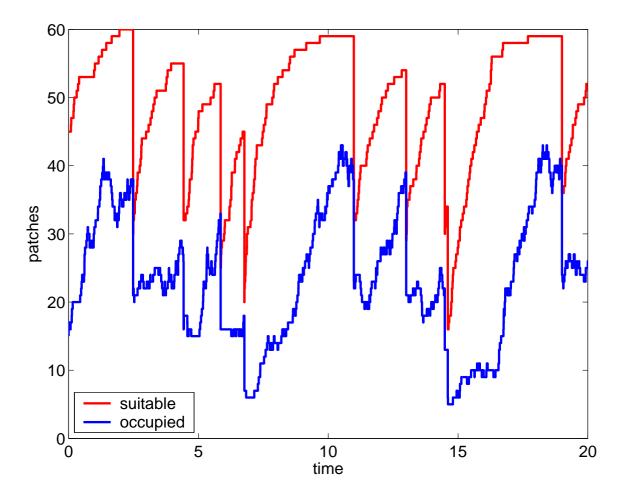


#### (How does the process change as *N* increases?)



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# As N increases, the process begins to look more deterministic.

In order to get a limit to the process, we need to scale it. If  $\mathbf{X}(t) = [X(t) \ Y(t)]^T$  is our unscaled process, scale first by 1/N.

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It is possible to show that as  $N \to \infty$ ,  $(N^{-1}\mathbf{X}_N - \hat{\mathbf{X}}_N) \Rightarrow \mathbf{0}$  (assuming  $N^{-1}\mathbf{X}_N(0) = \hat{\mathbf{X}}_N(0)$ ). In order to get a limit to the process, we need to scale it. If  $\mathbf{X}(t) = [X(t) \ Y(t)]^T$  is our unscaled process, scale first by 1/N.

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 \$\hfrac{X}{N}\$ is deterministic between catastrophes of fixed size, and these catastrophes occur at the same time as catastrophes in \$\mathbf{X}\_N\$.

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 $G_{\hat{\mathbf{X}}}f(x,y) = r(1-x)f_x(x,y)$  $+ [cy(x-y) - ey]f_y(x,y)$  $+ \gamma [f(x-px,y-py) - f(x,y)].$ 

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$$G_{\hat{\mathbf{X}}}f(x,y) = r(1-x)f_x(x,y) + [cy(x-y) - ey]f_y(x,y) + \gamma [f(x-px,y-py) - f(x,y)].$$

(The generator tells us how the distribution of  $\hat{\mathbf{X}}$  changes over time.)

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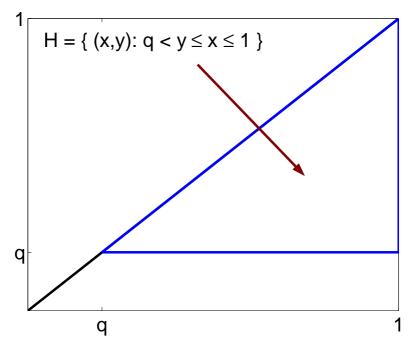
There's a lot we can do with this simple scaling.

A solution h(x, y) to the system of equations

$$G_{\hat{\mathbf{X}}}h(x,y) = -1, \quad (x,y) \in H \subset [0,1]^2,$$
$$h(x,y) = 0, \quad (x,y) \notin H,$$

gives the expected time to depart the set H (Gihman & Skorohod, 1972).

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Fortunately, it is relatively easy to show that in this case, a solution h(x, y) exists, but...

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- The solution can be tough to evaluate (numerically)!
- The existence of a solution is not proven for other (even closely related) models.

Density dependent processes (as  $X_N$  would be, if not for the catastrophes) are well known to converge to Gaussian diffusion processes when appropriately scaled and normalised.

Let  $Z_N(t) = \sqrt{N} (N^{-1}X_N(t) - \hat{\mathbf{X}}_N(t))$ . Then it is possible to show that

$$egin{bmatrix} \mathbf{Z}_N \ \mathbf{\hat{X}}_N \end{bmatrix} \Rightarrow egin{bmatrix} \mathbf{Z} \ \mathbf{\hat{X}} \end{bmatrix}$$

What is Z? From the theory of density dependent processes we might expect a diffusion process with drift, plus catastrophes, and that is exactly what we get.

It is again possible to write down the generator...

Generator  $Gf(z_1, z_2, x_1, x_2)$  of  $\begin{bmatrix} \mathbf{Z}^T & \hat{\mathbf{X}}^T \end{bmatrix}^T$  has components:

• Drift components derived from

$$\begin{bmatrix} \frac{\partial F_i}{\partial z_j} \end{bmatrix} = \begin{bmatrix} -r & 0\\ cz_2 & cz_1 - 2cz_2 - e \end{bmatrix}$$

- Diffusion components  $\frac{1}{2}r(1-z_1)f_{z_1z_1}$  and  $\frac{1}{2}[cz_2(z_1-z_2)+ez_2]f_{z_2z_2}$ .
- Catastrophe component obtained by  $E[f(Z_1 + U_1, Z_2 + U_2, \cdot) f(Z_1, Z_2, \cdot)]$ , where  $(U_1, U_2)$  is bivariate normal.

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...and we could approximate  $\mathbf{X}_N$  by  $\mathbf{\hat{X}} + N^{-1/2}\mathbf{Z}$ .

#### **Future directions**

- Extension of this approach to general density dependent processes subject to a wider class of catastrophes.
- Investigation of the accuracy of the approximations and their properties (e.g. hitting times).
- When do features of small-N processes remain in large-N approximations?



#### Phil Pollett and Hugh Possingham (advisors), Andrew Barbour and Chris Wilcox.



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