Diffusion Approximation for a Metapopulation Model with Habitat Dynamics

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THE PROBLEM

- Develop a model for a population inhabiting a patchy, dynamic landscape and analyse the effects of habitat dynamics on population persistence.

MOTIVATION

- Understanding the dynamics of populations that inhabit patchy environments is a pivotal problem in ecology. This area is known as metapopulation ecology [1].
- Classical metapopulation ecology assumes a constant number of patches. However, in many cases the number of suitable patches changes as a result of patches being ephemeral or because they become temporarily unsuitable.
- Therefore, of primary importance in ecology are simple models for metapopulations in dynamic landscapes and simple formulae for the effects of these habitat dynamics on persistence.

THE MODEL

- The model we present for a metapopulation in a dynamic landscape is a continuous-time Markov chain. We will assume that $(X(t), t \geq 0)$ is a Markov chain with transition rates $Q = (q(i,j), i,j \in S)$, so that $q(i,j)$ represents the rate of transition from state i to state j, for $j \neq i$, and $q(i,i) = -q(i)$, where

$$q(i) := \sum_{j \neq i} q(i,j) \ (< \infty)$$

represents the total rate out of state i.

- Denoting by $m(t)$ and $n(t)$, respectively, the number of suitable patches and the number of occupied patches at time t, our process takes values in $S_M = \{(m,n) : 0 \leq n \leq m \leq M\}$ and has non-zero transition rates

$$q((m,n),(m+1,n)) = r(M-m)$$

corresponding to recovery of an unsuitable patch,

$$q((m,n),(m-1,n)) = s(m-n)$$

corresponding to disturbance of a suitable unoccupied patch,

$$q((m,n),(m-1,n-1)) = sn$$

corresponding to disturbance an occupied patch,

$$q((m,n),(m,n+1)) = c\frac{n}{M}(m-n)$$

corresponding to colonisation of a suitable unoccupied patch, and

$$q((m,n),(m,n-1)) = en$$

corresponding to a local population extinction.

- M is the total number of patches in the network.
- r is the per patch rate of recovery.
- s is the per patch rate of disturbance.
- c is the colonisation rate.
- e is the local population extinction rate.

METHOD

- How do we analyse our model to derive simple results?
- We use the remarkable work of Kurtz [2,3], which may be applied to any process with a particular type of rates, called density-dependent rates.

RESULTS

Deterministic Approximation

- As the number of patches M in our metapopulation becomes large the process $x_M(t) = (m(t)/M, n(t)/M)$ converges, uniformly in probability over finite time intervals, to the unique trajectory $x(t) = (u(t), v(t))$ of the deterministic model

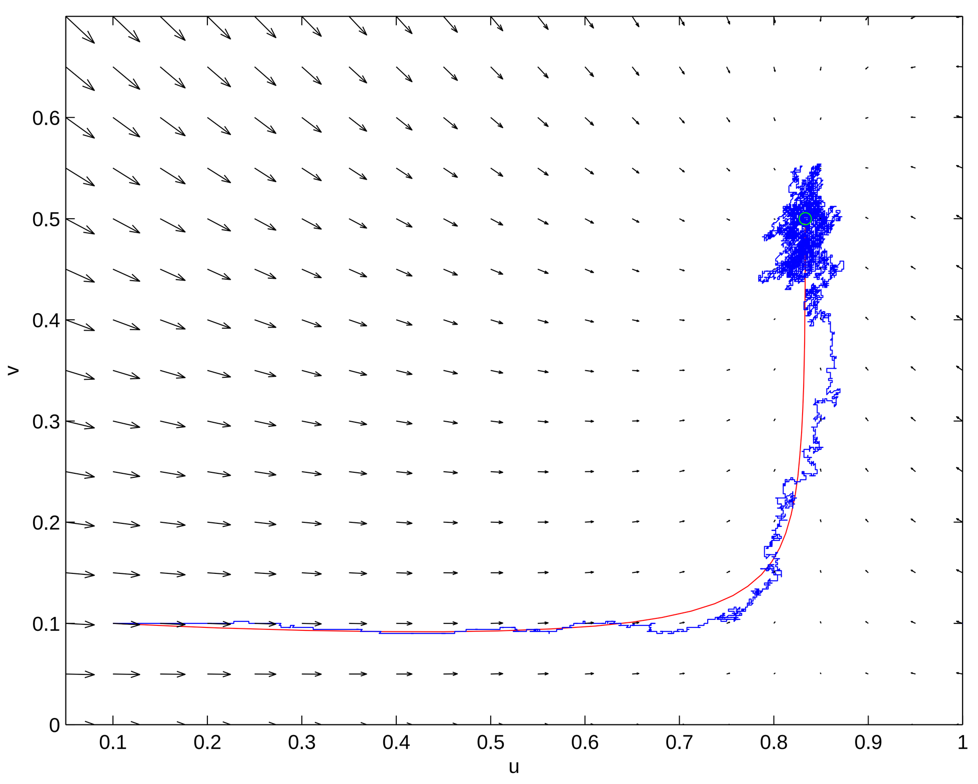
$$\frac{du}{dt} = r(1-u) - su \quad \text{and} \quad \frac{dv}{dt} = cv(u-v) - (e+s)v.$$

- This model has equilibrium points at

$$x^*_{trivial} = \left(\frac{r}{r+s}, 0\right) \text{ and } x^* = \left(\frac{r}{r+s}, \frac{r}{r+s} - \frac{e+s}{c}\right).$$

- It also provides us with a simple condition for persistence of the species in the deterministic case

$$\frac{r}{r+s} > \frac{e+s}{c}.$$



Simulation with $r = 0.5$, $s = 0.1$, $c = 0.6$, $e = 0.1$, $M = 500$, for $10,000$ transitions, deterministic trajectory and gradient field.

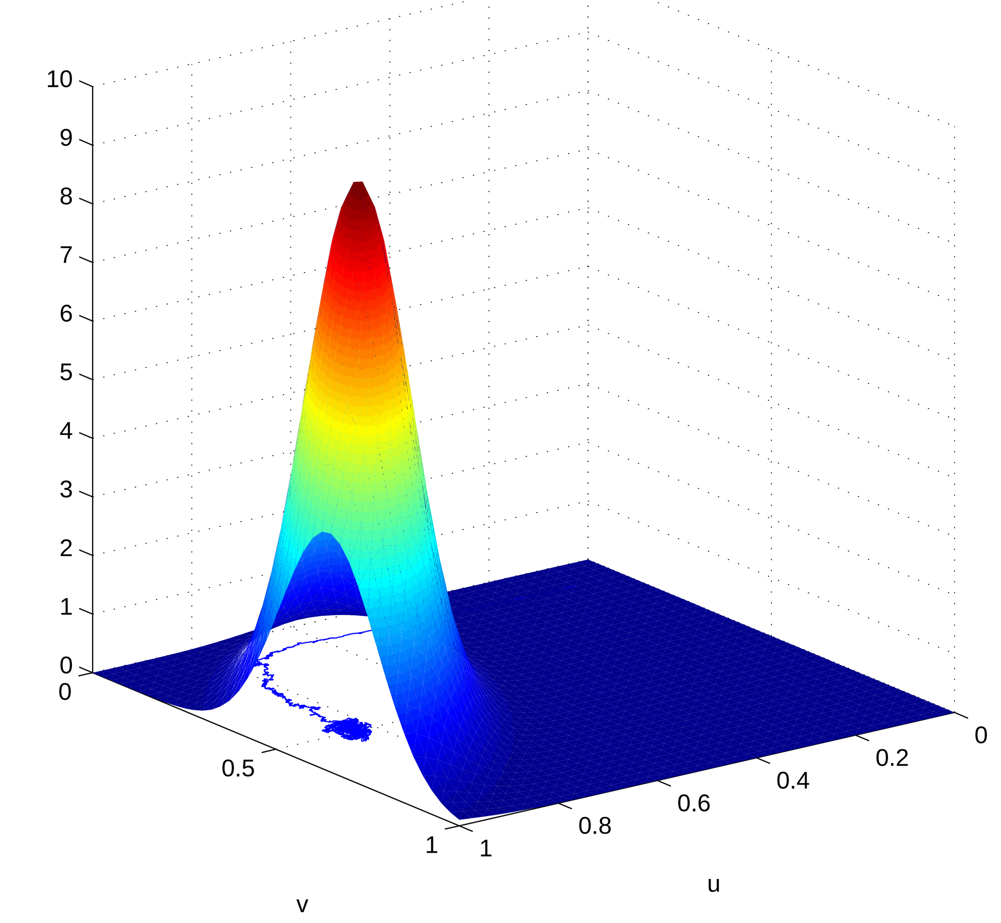
Diffusion Approximation

- Populations are not deterministic and thus it is important to model the variation in the population, in particular, fluctuations about the quasi-stationary point.
- Provided $\lim_{M \to \infty} \sqrt{M}\,(x_M(0) - x^*) = z$, the family $\{Z_M(\cdot)\}$, defined by

$$Z_M(t) = \sqrt{M}\,(x_M(t) - x^*), \quad 0 \leq t \leq \tau,$$

converges weakly in $D[0,\tau]$ (the space of right-continuous, left-hand limit functions on $[0,\tau]$) to an Ornstein-Uhlenbeck process $Z(\cdot)$, with initial value $Z(0) = z$, and with explicit expressions for the local drift matrix and the local covariance matrix.

- In particular, the fluctuations can be accurately described by a bivariate normal approximation, with explicit expressions for the mean and covariance matrix.



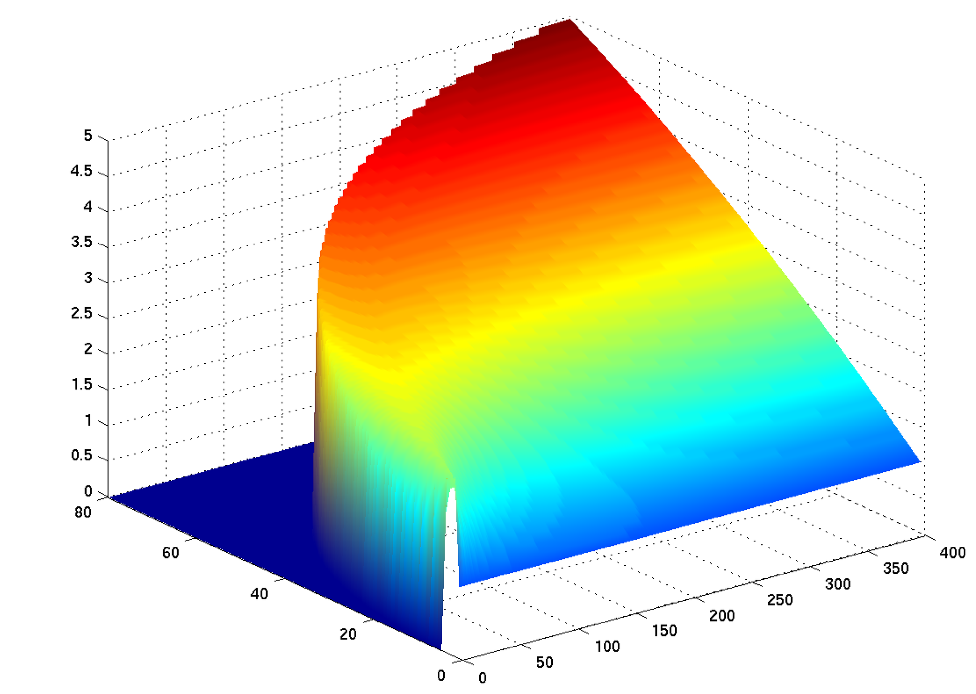
Simulation and approximating bivariate normal density.

The Effects of Habitat Dynamics

- We compare this model to the equivalent constant-landscape model (a special case of the stochastic logistic model).
- We also consider the consequences of using the standard model instead of our new model.
- FP = Fixed Point and PC = Persistence Condition.

Model	*FP*	*PC*
New Model	$\left(\frac{r}{r+s}, \frac{r}{r+s} - \frac{e+s}{c}\right)$	$\frac{r}{r+s} > \frac{e+s}{c}$
Stochastic Logistic Model	$1 - \frac{e}{c}$	$c > e$
Stochastic Logistic Model with $e+s$	$1 - \frac{e+s}{c}$	$c > e+s$
SLM with $e+s$ & reduced habitat	$\frac{r}{r+s}\left[1 - \frac{e+s}{c}\right]$	$c > e+s$

- Disturbance reduces the fraction of suitable habitat and also increases the extinction rate of the population.
- Existing models overestimate the average proportion of suitable habitat and provide incorrect persistence conditions. This is worrying when considering the increase in variance due to habitat dynamics.



Ratio of variance in occupied patches for our model to that of the stochastic logistic model with $c = 0.6$ and $e = 0.1$.

CONCLUSION

- We have developed a simple model for metapopulations with habitat dynamics.
- We have derived a diffusion approximation for the fluctuations of the process about the quasi-stationary point.
- We have derived simple formulae for the effects of habitat dynamics.

References

[1] Hanski, I.A. and Gaggiotti, O.E. (Eds.) (2004) *Ecology Genetics and Evolution of Metapopulations.* Academic Press, London.
[2] Kurtz, T. (1970) Solutions of ordinary differential equations as limits of pure jump Markov processes. *J. Appl. Probab.* 7, 49–58.
[3] Kurtz, T. (1971) Limit theorems for sequences of jump Markov processes approximating ordinary differential processes. *J. Appl. Probab.* 8, 344–356.

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